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A revision of the genus *Ecpyrrhorrhoe* Hübner, 1825 from China based on morphology and molecular data, with descriptions of five new species (Lepidoptera, Crambidae, Pyraustinae)

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Abstract

The genus *Ecpyrrhorrhoe* Hübner, 1825 is revised. Most type materials were examined, and a preliminary phylogeny is presented based on a combined dataset of COI, 16S rRNA, 28S rRNA and EF-1α gene regions. The tree topology and morphological characters suggest that *Paliga* Moore, 1886 is a new synonym of *Ecpyrrhorrhoe*, and *Yezobotys* Munroe & Mutuura, 1969 is restored as a valid genus. According to the morphological evidence and tree topology, 17 species are recorded, including five new species described from China: *E. allochroa* Zhang & Xiang, **sp. nov.**, *E. rosisquama* Xiang & Zhang, **sp. nov.**, *E. exigistria* Zhang & Xiang, **sp. nov.**, *E. brevis* Zhang & Xiang, **sp. nov.** and *E. longispinalis* Zhang & Xiang, **sp. nov.** Seven new combinations are created, *E. damastesalis* (Walker, 1859), **comb. nov.**, *E. minnehaha* (Pryer, 1877), **comb. nov.**, *E. obliquata* (Moore, 1888), **comb. nov.**, *E. rufipicta* (Butler, 1880), **comb. nov.**, *E. fimbriata* (Moore, 1886), **comb. nov.**, *E. machoeralis* (Walker, 1859), **comb. nov.**, and *E. rubellalis* (Snellen, 1890), **comb. nov.**, as well as eight new synonyms, namely *Leucocraspeda auratalis* Warren, 1895, **syn. nov.**, *Pionea schenklingi* Strand, 1918, **syn. nov.**, *Paliga rubicundalis* Warren, 1896, **syn. nov.**, *E. angustivalvaris* Gao, Zhang & Wang, 2013, **syn. nov.**, *Pyrausta pygmaealis* South, 1901, **syn. nov.**,

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E. multispinalis Gao, Zhang &Wang, 2013, **syn. nov.**, *E. aduncis* Gao, Zhang & Wang, 2013, **syn. nov.**, and *E. ruidispinalis* Zhang, Li & Wang, 2004, **syn. nov.** All adults and their genital structures are illustrated and an identification key based on adult external morphology and genitalia is provided.

Keywords

Molecular phylogeny, morphology, new combinations, new synonyms, *Yezobotys*

Introduction

The genus *Ecpyrrhorrhoe* Hübner, 1825, type species *Pyralis rubiginalis* Hübner, 1796, was regarded as monotypic from its original description until Maes (1994) synonymized *Harpadispar* Agenjo, 1952 with this genus. Later, records by Zhang et al. (2004), Zhang and Li (2008), Solis et al. (2010), Gao et al. (2013), Maes (2014), and Nuss et al. (2003–2022) show that this genus is more diverse and widely distributed than previously thought. Six new species are described, and four species are transferred to *Ecpyrrhorrhoe* in these studies. Additionally, Solis et al. (2010) treated *Yezobotys* Munroe & Mutuura, 1969 as a synonym of *Ecpyrrhorrhoe*. Thus, the species number of *Ecpyrrhorrhoe* was increased to 12.

There are striking apomorphic characters available to diagnose species of *Ecpyrrhorrhoe*. These are a narrowly lanceolate uncus, long dorsolateral arms of the juxta, the presence of spines on the anellus, a slender longitudinal sclerite located in the posterior part of the ductus bursae, and a second (posterior) signum with spines in the female genitalia. *Paliga* Moore, 1886 shares some of these characters with species of *Ecpyrrhorrhoe*, but *Yezobotys* does not share these characters. Therefore, the relationship of *Yezobotys* and *Paliga* with *Ecpyrrhorrhoe* needs to be resolved.

Upon examination of pyraustine collections from China, and type specimens and other material from the Natural History Museum, London, United Kingdom, and the Senckenberg Entomological Institute, Brandenburg, Germany, some known species, and undescribed species were found to agree with the circumscription of *Ecpyrrhorrhoe* based on genitalia characters. In order to evaluate the generic placements of these species and the taxonomic composition of *Ecpyrrhorrhoe*, the phylogenetic relationships of *Ecpyrrhorrhoe* were studied with molecular data.

Materials and methods

Molecular phylogenetic analysis

In total 24 species were included in the molecular phylogenetic analysis (Table 1), including the type species of *Yezobotys* and *Paliga*, five new species and six putative new combinations. *Euclasta stoetzneri* (Caradja, 1927) was chosen as the outgroup because it has been inferred as sister-group of the Pyraustini and Portentomorphini in Pyraustinae (Mally et al. 2019). Two species of *Pyrausta* Schrank, 1802, two species of *Pagyda*

Table 1. Species sampled for the molecular phylogenetic analyses; all species sequenced in this study except *Euclasta stoetzneri*, which was sequenced by Zhang et al. (2020).

Genus	Species	Voucher	Locality	GenBank accession number			
				COI	16S	EF-1α	28S
Euclasta	*stoetzneri*	SYSULEP0334	Shaanxi	MT738696	MT734412	MT724335	MT734404
Yezobotys	*dissimilis*	SYSULEP0029	Hubei	OM674485	OM672201	OM650166	OM672234
Yezobotys	*dissimilis*	SYSULEP0089	Hubei	OM674486	OM672202	N/A	N/A
Anamalaia	*lutusalis*	SYSULEP0088	Yunnan	OM674487	OM672205	OM650169	OM672237
Anamalaia	*fasciata*	SYSULEP0233	Yunnan	OM674488	OM672206	OM650170	OM672238
Pagyda	*salvalis*	SYSULEP0086	Yunnan	OM674489	OM672203	OM650167	OM672235
Pagyda	*recticlavata*	SYSULEP0091	Jiangxi	OM674490	OM672204	OM650168	OM672236
Pyrausta	*panopealis*	SYSULEP0072	Jiangxi	OM674491	OM672199	OM650164	OM672232
Pyrausta	*despicata*	SYSULEP0348	Xinjiang	OM674492	OM672200	OM650165	OM672233
Ecpyrrhorrhoe	*biaculeiformis*	SYSULEP0015	Hunan	OM674493	OM672174	OM650146	OM672213
Ecpyrrhorrhoe	*digitaliformis*	SYSULEP0016	Hubei	OM674494	OM672175	OM650147	OM672214
Ecpyrrhorrhoe	*celatalis*	SYSULEP0017	Hainan	OM674495	OM672176	OM650148	OM672215
Ecpyrrhorrhoe	*rubiginalis*	SYSULEP0019	Shanxi	OM674496	OM672177	N/A	N/A
Ecpyrrhorrhoe	*rosisquama*	SYSULEP0020	Yunnan	OM674497	OM672178	OM650149	OM672216
Ecpyrrhorrhoe	*rubellalis*	SYSULEP0023	Hainan	OM674498	OM672179	N/A	OM672217
Ecpyrrhorrhoe	*biaculeiformis*	SYSULEP0024	Hubei	OM674499	OM672180	N/A	N/A
Ecpyrrhorrhoe	*obliquata*	SYSULEP0034	Hainan	OM674500	OM672181	OM650150	OM672218
Ecpyrrhorrhoe	*damastesalis*	SYSULEP0035	Yunnan	OM674501	OM672182	N/A	N/A
Ecpyrrhorrhoe	*brevis*	SYSULEP0036	Guangdong	OM674502	OM672183	OM650151	OM672219
Ecpyrrhorrhoe	*puralis*	SYSULEP0037	Hunan	OM674503	OM672184	OM650152	OM672220
Ecpyrrhorrhoe	*rubiginalis*	SYSULEP0048	Shanxi	OM674504	OM672185	OM650153	N/A
Ecpyrrhorrhoe	*longispinalis*	SYSULEP0058	Hunan	OM674505	OM672186	OM650154	OM672221
Ecpyrrhorrhoe	*minnehaha*	SYSULEP0059	Jiangxi	OM674506	OM672187	OM650155	OM672222
Ecpyrrhorrhoe	*allochroa*	SYSULEP0060	Hainan	OM674507	OM672188	N/A	OM672223
Ecpyrrhorrhoe	*minnehaha*	SYSULEP0061	Jiangxi	OM674508	OM672189	N/A	N/A
Ecpyrrhorrhoe	*rufipicta*	SYSULEP0062	Hainan	OM674509	OM672190	N/A	OM672224
Ecpyrrhorrhoe	*exigistria*	SYSULEP0063	Yunnan	OM674510	OM672191	OM650156	OM672225
Ecpyrrhorrhoe	*exigistria*	SYSULEP0100	Jiangxi	OM674511	OM672192	OM650157	N/A
Ecpyrrhorrhoe	*fimbriata*	SYSULEP0111	Yunnan	OM674512	N/A	N/A	N/A
Ecpyrrhorrhoe	*rufipicta*	SYSULEP0107	Hainan	OM674513	OM672193	OM650158	OM672226
Ecpyrrhorrhoe	*rubiginalis*	SYSULEP0109	Jiangxi	OM674514	OM672194	OM650159	OM672227
Ecpyrrhorrhoe	*rubellalis*	SYSULEP0110	Guangxi	OM674515	N/A	OM650160	N/A
Ecpyrrhorrhoe	*damastesalis*	SYSULEP0163	Yunnan	OM674516	OM672195	OM650161	OM672228
Ecpyrrhorrhoe	*exigistria*	SYSULEP0211	Guangxi	OM674517	OM672196	OM650162	OM672229
Ecpyrrhorrhoe	*minnehaha*	SYSULEP0217	Guangdong	OM674518	OM672197	OM650163	OM672230
Ecpyrrhorrhoe	*obliquata*	SYSULEP0297	Guangdong	OM674519	OM672198	N/A	OM672231

Walker, 1859, and two species of *Anamalaia* Munroe & Mutuura, 1969 were included as related taxa because of the similar external and genital characters, and a previous taxonomic treatment of *Ecpyrrhorrhoe* as a subgenus of *Pyrausta* (Hannemann 1964).

Total DNA was extracted from two legs and sometimes additionally from the abdomen of the dry specimens using the TIANGEN DNA extraction kit following the manufacturer's instructions. The nucleotide sequences of two mitochondrial genes, cytochrome c oxidase subunit I (COI) and 16S ribosomal RNA (16S rRNA), and two nuclear genes, 28S ribosomal RNA (28S rRNA) and Elongation factor-1 alpha (EF-1α) were selected for study. Primers used in this study and all PCRs performed follow Zhang et al. (2020). PCR products were confirmed with 1.5% agarose gel electrophoresis in

TAE buffer, then were direct-sequenced at Majorbio Bio-pharm Technology Co., Ltd (Guangzhou), utilizing the same primers used for PCR amplification.

The sequences were aligned using Clustal W (Thompson et al. 1994) in MEGA 6 (Tamura et al. 2013) with default settings. The aligned matrix was corrected by eye. Gaps were treated as missing data. Phylogenetic analyses were inferred using Bayesian inference (BI) method in MrBayes 3.2.6 (Ronquist et al. 2012) and maximum likelihood (ML) in RAxML 8.2.10 (Stamatakis 2014). BI analysis was run with independent parameters all under the GTR + G + I model for four gene partitions, as suggested by jModelTest 0.1.1 (Posada 2008). Two independent runs, each with four Markov Chain Monte Carlo (MCMC) simulations, were performed for 20 million generations sampled every 1000th generation. The first 25% trees were discarded as burn-in, and posterior probabilities (PP) were determined from remaining trees. The ML analysis was executed under the GTR + G + I model for all gene partitions and with 1000 iterations for the bootstrap test. The bootstrap value (BS) ≥ 90 is considered absolute support, 75 ≤ BS < 90 is considered strong support, and 50 ≤ BS < 75 is considered weak support. PP ≥ 95 is considered strong support and 80 ≤ PP < 95 is considered weak support. The pairwise Kimura 2-Parameter (K2P) distances between species were calculated from the COI gene using MEGA 6 (Tamura et al. 2013).

Morphological analysis

The specimens studied, including the types of the newly described species, are deposited in the Museum of Biology, Sun Yat-sen University, Guangzhou, China (**SYSBM**), except for those held at the following institutions: Insect Collection of the College of Life Sciences, Nankai University, China (**NKU**), Natural History Museum, London, United Kingdom (**NHMUK**) and Senckenberg Deutsches Entomologisches Institut, Brandenburg, Germany (**SDEI**). Slides of dissected genitalia were prepared according to the protocols of Robinson (1976) and Li and Zheng (1996). Terminology of genitalia follows Maes (1995), except for "phallus" and "colliculum" for which we follow Kristensen (2003). Images of the specimens were taken using a Canon EOS 80D camera provided with a Canon 100 mm macro lens. The genitalia photographs were taken using a Zeiss Axio Scope.A1 in combination with a Zeiss AxioCam camera and the Axio Vision SE64 program on a Windows PC. Source images were then aligned and stacked with Helicon Focus to obtain a composite image. All the pictures were edited using Adobe Photoshop SC5.

Results

Phylogenetic relationships

The concatenated dataset of four genes consisted of 2503 nucleotide positions (657 for COI, 471 for 16S rRNA, 610 for 28S rRNA, and 765 for EF-1α). Pairwise distances of the barcoding region (COI) are given in Suppl. material 1. The genetic distances between *Ecpyrrhorrhoe* and other genera range from 8.5% (*Yezobotys*) to 15.0% (*Euclasta*). Interspecific genetic distances within *Ecpyrrhorrhoe* range from 6.6% (*E. celetalis* to *E. brevis*) to 14.3% (*E. damastesalis* to *E. rosisquama*), while intraspecific genetic distances in *Ecpyrrhorrhoe* range from 0% (*E. biaculeiformis*, *E. rufipicta*, *E. minnehaha*, and *Yezobotys dissimilis*) to 1.2% (*E. exigistria*).

Both BI and ML analyses of the concatenated dataset inferred fully congruent relationships with only subtle differences in posterior probability and bootstrap values (Fig. 1). The tree topology indicates that *Yezobotys* Munroe & Mutuura, 1969 should be restored as a valid genus because the type species, *Y. dissimilis* (Yamanaka, 1958), appears as sister to *Anamalaia* (PP = 1, BS = 100). The monophyly of *Ecpyrrhorrhoe* is supported (PP = 0.99, BS = 63). The genus *Pagyda* Walker, 1859 is the sister group of *Ecpyrrhorrhoe* (PP = 0.99, BS = 67). Among *Ecpyrrhorrhoe* species included in the analysis, the majority of the basal nodes are strongly supported in BI but relatively poorly supported in ML.

According to the tree topology and morphological characters, the genus *Ecpyrrhorrhoe* can be divided into three species groups (The A clade, B clade, and C clade). The A clade is the sister group to B clade + C clade (PP = 0.99, BS = 63). The A clade is composed of *E. allochroa* and *E. damastesalis*. The B clade consists

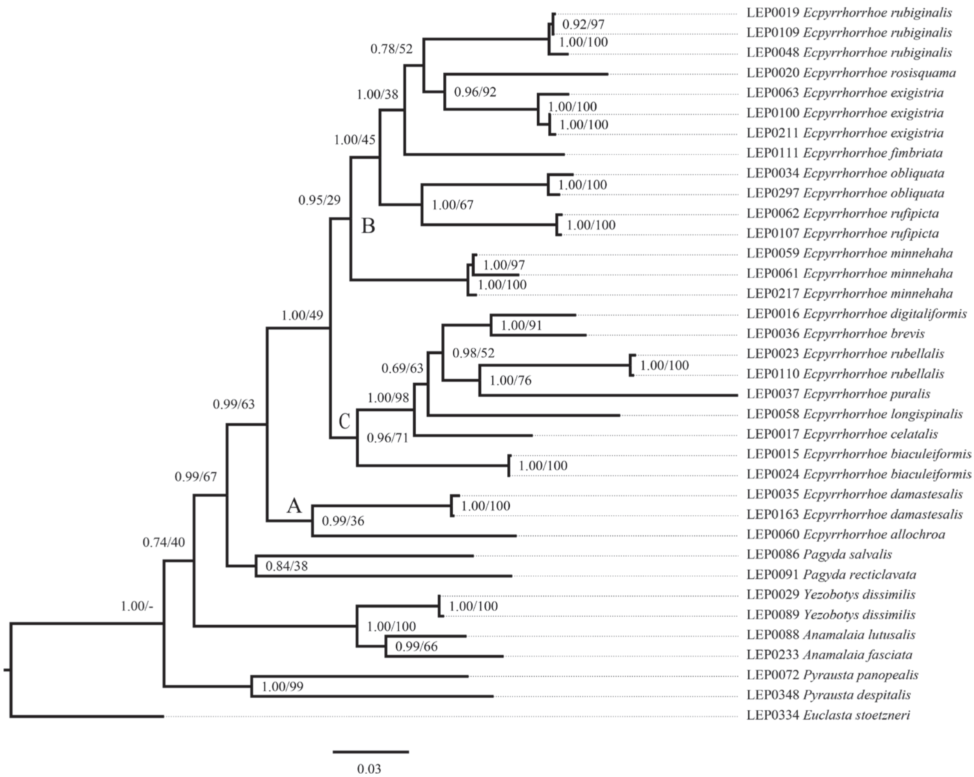


Figure 1. Phylogenetic hypothesis inferred from the BI analysis. Numbers on branches indicate Bayesian posterior probabilities and ML bootstrap values, respectively.

of *E. minnehaha*, *E. rufipicta*, *E. obliquata*, *E. fimbriata*, *E. rubiginalis*, *E. exigistria*, and *E. rosisquama*, in which *E. minnehaha* is the basal taxon, and *E. rufipicta* + *E. obliquata* is the sister group to *E. fimbriata* + (*E. rubiginalis* + (*E. exigistria* + *E. rosisquama*)) (PP = 1.00, BS = 45). The C clade is composed of seven species, namely *E. biaculeiformis*, *E. celatalis*, *E. longispinalis*, *E. puralis*, *E. rubellalis*, *E. brevis* and *E. digitaliformis*, in which *E. biaculeiformis* is the basal taxon, and *E. celatalis* is the sister group with the clade *E. longispinalis* + ((*E. puralis* + *E. rubellalis*) + (*E. brevis* + *E. digitaliformis*)) (PP = 1.00, BS = 98). The sister groups *E. exigistria* and *E. rosisquama* (PP = 0.96, BS = 92), *E. obliquata* and *E. rufipicta* (PP = 1.00, BS = 67), *E. digitaliformis* and *E. brevis* (PP = 1.00, BS = 91), and *E. rubellalis* and *E. puralis* (PP = 1.00, BS = 76) are supported in both BI and ML.

The results of the molecular phylogenetic analyses support the placement of five undescribed species (named as *E. allochroa* sp. nov., *E. rosisquama* sp. nov., *E. exigistria* sp. nov., *E. brevis* sp. nov., and *E. longispinalis* sp. nov.) in *Ecpyrrhorrhoe*, the transfer of *E. rubellalis* (Snellen, 1890), comb. nov. from *Pyrausta* Schrank, 1802 to *Ecpyrrhorrhoe*, the transfer of *E. obliquata* (Moore, 1888), comb. nov. and *E. fimbriata* (Moore, 1886), comb. nov. from *Anania* Hübner, 1823 to *Ecpyrrhorrhoe*, and the transfer of *E. damastesalis* (Walker, 1859), comb. nov., *E. rufipicta* (Butler, 1880), comb. nov., and *E. minnehaha* (Pryer, 1877), comb. nov. from *Paliga* Moore, 1886 to *Ecpyrrhorrhoe*. The taxonomic details are given below.

Taxonomy

***Ecpyrrhorrhoe* Hübner, 1825**

Ecpyrrhorrhoe Hübner, 1825. Type species: *Pyralis rubiginalis* Hübner, 1796, by subsequent designation by Hannemann, 1964.
Ecpyrrhorrhoea Hübner, 1825. Misspelling.
Ecpyrrhorrhoa Agassiz, 1846. Misspelling.
Paliga Moore, 1886. Type species: *Scopula damastesalis* Walker, 1859, by monotypy. Syn. nov.
Eutectona Wang & Sung, 1980. Type species: *Scopula machoeralis* Walker, 1859, by original designation.
Harpadispar Agenjo, 1952. Type species: *Botys diffusalis* Guenée, 1854, by original designation.
Pyraustegia Marion, 1963. Type species: *Botys diffusalis* Guenée, 1854, by original designation.

Diagnosis. The wings of species of *Ecpyrrhorrhoe* are usually yellow, sometimes decorated with pink or brown scales. In appearance, they are similar to some species of *Pyrausta* Schrank, 1802 and *Pseudopagyda* Slamaka, 2013, but can be distinguished by the usually obvious dark brown subterminal band on the underside of wings. They are characterized by the lanceolate, densely setose uncus; the mostly thumb-shaped sella extending to the ventral margin of the valva; the long arms of the bifid juxta, usually; usually the presence of several spines or sclerites on the anellus in the male genitalia. In the female genitalia, the strongly sclerotized antrum, the slender sclerite located in the posterior part of the ductus bursae, and the second (posterior) signum bearing spines are characteristic.

Description. Frons oblique, smoothly scaled. Vertex with moderately raised scales projecting between antennae. Labial palpus porrect, second segment pointing obliquely upward, third segment pointing slightly downward; exceeding frons by approximately as much as length of head. Maxillary palpus small. Forewing termen gently arched. Hindwing frenulum single in male, with two acanthae in female. Wings usually yellow or yellowish brown, sometimes pink or covered with brown scales; forewing with antemedial and postmedial lines, orbicular and reniform stigma; underside of wings usually with obvious blackish brown subterminal band. Wing venation as in Fig. 2.

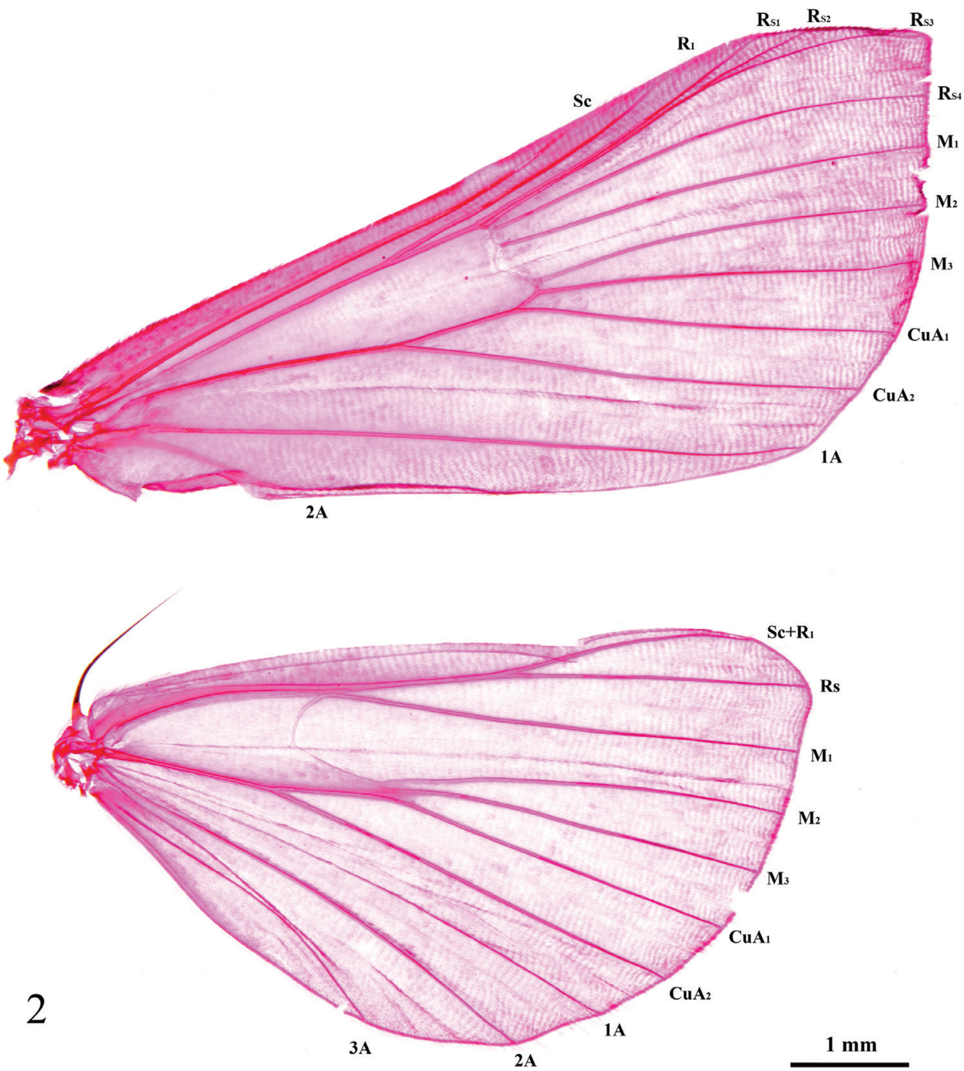


Figure 2. Wing venation of *Ecpyrrhorrhoe rubiginalis*.

Male genitalia. Uncus with lanceolate head and a nearly triangular, broad, naked base; densely covered with short simple, thick, setae, and every cluster of setae is made up of two independent setae. Transtilla inferior thin and stick-shaped. Valva elongated tongue-shaped; costa straight to concave; sella thumb-shaped or semicircular, extending to ventral margin of valva, usually with dense setae or spines; sacculus broad, usually with a wide dorsal protrusion. Dorsolateral arms of juxta usually long and tapering; anellus with several spines. Saccus nearly triangular. Phallus tubular.

Female genitalia. Ovipositor lobes densely setose. Anterior apophysis usually ~ 1.5–2.5× the length of posterior apophysis. Antrum usually cup-shaped, sometimes densely spinulose; the ductus seminalis inserting to anterior end of colliculum, sometimes wide and sclerotized at base; ductus bursae long and slender, posterior part with a slender sclerite; corpus bursae globular, appendix bursae arising from anterior part of corpus bursae; signum (anterior-most signum) rhombic, second signum (posterior signum) strongly sclerotized and bearing spines.

Distribution. Asia, Europe, South Africa, Australia, North America.

Key to studied species of *Ecpyrrhorrhoe*

1	Hindwing without postmedial line	**2**
–	Hindwing with postmedial line	**3**
2	Forewing without rosy scales (Fig. 3); excurved sella with longer setae ventrally; anellus with a long and curved, densely spinulose sclerite (Fig. 22)	***E. allochroa***
–	Forewing usually bearing rosy markings and scales on veins (Figs 4, 5); straight sella bearing short spines ventrally; anellus with three groups of spines (Fig. 23)	***E. damastesalis***
3	Forewing with covering of rosy-red scales or some specimens with rosy-red forewing	**4**
–	Forewing pale yellow, yellow, or yellowish brown	**5**
4	Forewing covering rosy-red scales; straight sella extending ventrad, bearing short spines on distal margin (Fig. 13); distal end of phallus not swirly; anellus with two groups of short and pointed spines (Fig. 29); inner wall of antrum without minute spines (Fig. 44)	***E. rosisquama***
–	Some specimens with rosy-red forewing (Figs 6, 7); excurved sella with dense covering of thick setae; distal end of phallus somewhat swirly; anellus with a cluster of short spines (Fig. 24); inner wall of antrum densely covered with minute spines (Fig. 39)	***E. minnehaha***
5	Forewing with an oblique and dark brown streak	**6**
–	Forewing without streak	**7**
6	Sella semicircular, bearing many short spines ventrally; weakly sclerotized arms of juxta without teeth (Fig. 25); antrum cup-shaped (Fig. 40)	***E. obliquata***
–	Sella short, thumb-shaped, with dense setae ventrally; strongly sclerotized arms of juxta with teeth (Fig. 30); antrum mostly tubular (Fig. 45)	***E. exigistria***
7	Sella spine-shaped or hook-shaped	**8**
–	Sella thumb-shaped, finger-shaped, or nearly triangular	**9**

8 Wings yellowish brown (Fig. 18); costa of valva somewhat straight; sella spine-shaped; phallus apically with a densely dentated, triangular cornutus; anellus with a thick spine bearing a broad and long, spinulose base (Fig. 34); antrum wrinkled medially (Fig. 49) .... ***E. rubellalis***
– Wings yellow (Fig. 19); costa of valva concave; sella hook-shaped; phallus apically with a long and strong spine; anellus bearing a small and sclerotized ball, with two small spines on opposite sides (Fig. 35); antrum decorated with many small spines forming a circle (Fig. 50) .... ***E. longispinalis***
9 Forewing length relatively small; subterminal band of wings distinct and dark brown or brown **10**
– Forewing length relatively large; subterminal band of wings indistinct and yellowish brown 13
10 Fringe alternating with pale and dark brown from the base to the end (Fig. 10).. ***E. fimbriata***
– Fringe concolorous **11**
11 Inner wall of antrum densely covered with minute spines (Fig. 41)...***E. rufipicta***
– Inner wall of antrum without minute spines **12**
12 Antrum with anterior 1/3 narrower than posterior 2/3 (Fig. 42)...***E. rubiginalis***
– Antrum with anterior half narrower than posterior half (Fig. 43) ....***E. machoeralis***
13 Sella almost without setae, bearing four spines; anellus with two spines between (Fig. 37).. ***E. biaculeiformis***
– Sella setose, without spine; anellus with a long, thick and large spine or a series of spines **14**
14 Costa of valva curved **15**
– Costa of valva nearly straight **16**
15 Arms of juxta bearing a small sclerotized tooth; anellus with a series of minute spines (Fig. 31) .... ***E. digitaliformis***
– Arms of juxta without tooth; anellus with a series of long spines standing on a long base (Fig. 32).. ***E. brevis***
16 Arms of juxta with a big tooth-like process; anellus with a long, thick and large spine (Fig. 36) .... ***E. celatalis***
– Arms of juxta without process; anellus with spines appearing comb-shaped (Fig. 33).. ***E. puralis***

Ecpyrrhorrhoe allochroa **Zhang & Xiang, sp. nov.**
http://zoobank.org/E9D003C7-8434-40EB-9961-03670363CD3D
Figs 3, 22

Diagnosis. In appearance *Ecpyrrhorrhoe allochroa* resembles *E. damastesalis* in the narrow forewing and yellowish hindwing without markings. However, it can be differentiated from *E. damastesalis* by its smaller size (forewing length: 8.0–10.0 mm), forewing scattered with yellowish brown scales and bearing brown markings (Fig. 3), in the male genitalia (Fig. 22) by the slender valva, the excurved sella with longer setae ventrally, the long and slender phallus, and long and curved, densely spinulose sclerite on anellus.

Description (Fig. 3). **Head.** Frons yellow, sometimes white medially, with white lateral bands. Vertex pale yellow. Labial palpus dark yellow or yellowish brown, contrastingly white at base ventrally. Maxillary palpus yellowish brown, pale terminally. **Thorax.** Dorsal side dark yellow or yellowish brown, ventral side white. Legs white to pale yellow. **Wings.** Forewing length: 8.0–10.0 mm. Forewing pale yellow, densely scattered with yellowish brown scales, lines and stigmata brown; antemedial line from ~ 1/4 of costa to 1/2 of posterior margin; orbicular stigma oblate, sometimes weak; reniform stigma comma-shaped, slightly concave or bending inwards at middle; postmedial line from 3/4 of costa, dentated beyond basal half of CuA_1, bending inward to 1/3 of CuA_2, then dentated to 2/3 of posterior margin; fringe dark brown. Hindwing yellowish white, with area pale yellow; fringe pale brown and whitish at tornus. **Abdomen.** Pale dark yellow or yellowish brown dorsally, white ventrally.

Male genitalia (Fig. 22). Uncus with basal 2/5 nearly triangular and naked. Valva slightly curved, of even width, apex obtusely rounded; sella thumb-shaped and excurved, setose, bearing several spines on ventral margin; sacculus with dorsal 3/5 inflated into a nearly triangular protrusion. Juxta shield-shaped, with base wide, distal 1/4 bifid into thick and short arms with membranous extension; anellus with a long and curved, densely spinulose sclerite (attached to distal end of phallus in Fig. 22). Saccus rounded triangular. Phallus long and slender, distal part slightly curved upward and sclerotized, with a cluster of interlaced spicules on vesica; distal end with a bent, spine-like cornutus.

Female genitalia. Unknown.

Material examined. Type material. ***Holotype*** **♂, CHINA: Yunnan:** Mengla, Xishuangbanna, 28.X.2010, Hu Bingbing, Zhang Jin, Cai Yanpeng leg., genitalia slide No. CXH12133 (SYSBM). ***Paratypes*****: CHINA: Guizhou:** 1♂, Fade Bridge, Shunchang, 29.IV–3.V.2019, Liu Qingming leg., genitalia slide No. SYSU1511; **Hainan:** 1♂, Hongxin Village, Yuanmen, Baisha, 19.07°N, 109.52°E, alt. 460 m, 30.VI.2014, Cong Peixin, Liu Linjie, Hu Sha leg., genitalia slide No. ZDD12045, molecular voucher No. LEP0060 (NKU).

Distribution. China (Guizhou, Hainan, Yunnan).

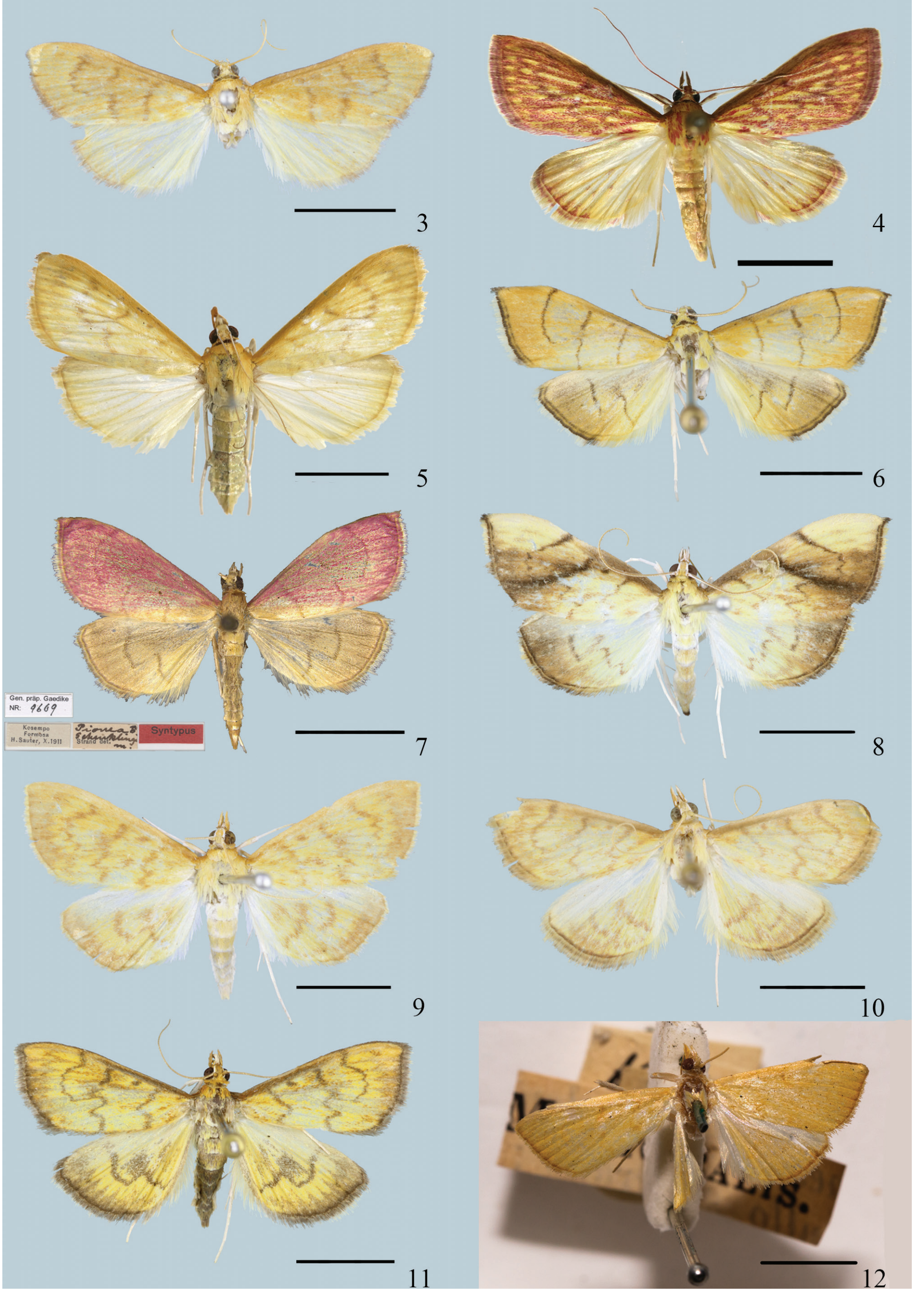
Etymology. The specific name is derived from the Latin *allochrous* (= heterochromatic), referring to the color difference between the forewing and hindwing.

Ecpyrrhorrhoe damastesalis (Walker, 1859), comb. nov.

Figs 4, 5, 23, 38

Scopula damastesalis Walker, 1859: 1013.

Diagnosis. In the male genitalia (Fig. 23), *E. damastesalis* can be characterized by the relatively thick and tapered uncus, the slender and straight sella bearing more strongly sclerotized short spines almost vertically placed on ventral and distal margins,



Figures 3–12. Adults of *Ecpyrrhorrhoe* spp. **3** *E. allochroa*, sp. nov., holotype, male (Yunnan) **4** *E. damastesalis*, male (Guangdong) **5** *E. damastesalis*, male (Yunnan) **6** *E. minnehaha*, male (Guangdong) **7** *E. minnehaha*, male (Taiwan) **8** *E. obliquata*, male (Hainan) **9** *E. rufipicta*, female (Hainan) **10** *E. fimbriata*, male (Guangxi) **11** *E. rubiginalis*, female (Xinjiang) **12** *E. machoeralis,* type, female (Sri Lanka). Scale bars: 5.0 mm.

and the three groups of spines present on anellus. The female genitalia (Fig. 38) are unique, readily separable by the triangular antrum, the wrinkled corpus bursae, the significantly large and generally subtriangular rhomboid signum with anterior and posterior parts asymmetrical and bearing a slightly curved carina, as well as the longer spines on markedly large second (posterior) signum.

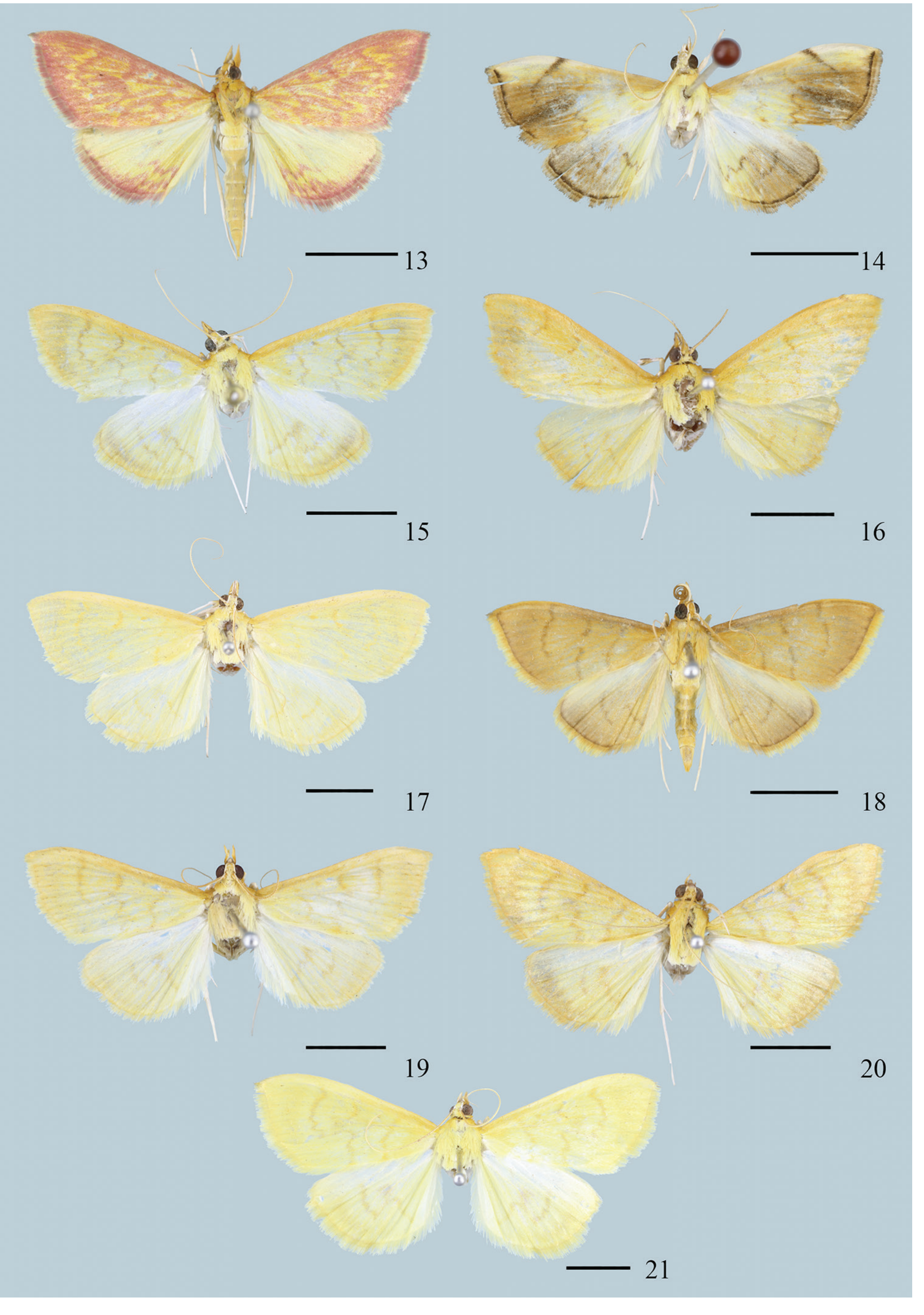
Redescription (Figs 4, 5). **Head.** Frons yellow, or yellowish brown scattered with rosy scales, with white lateral bands. Vertex pale yellow, usually scattered with rosy scales. Labial palpus yellowish brown or brown, usually scattered with rosy scales, contrastingly white at base ventrally. Maxillary palpus yellowish brown or brown, usually scattered with rosy scales, pale yellow terminally. **Thorax.** Dorsal side yellow, and ventral side white; tegula yellow or mixed with rosy scales sometimes. **Wings.** Forewing length: 10.0–14.0 mm. Forewing narrow and elongated; pale yellow, usually covered with rosy scales on veins, markings yellowish brown or rosy; antemedial line obliquely from 1/4 of costa to beyond posterior margin of cell, then deeply dentated to basal 1/3 of dorsum; orbicular stigma oval and distinct; reniform stigma comma-shaped, short and thick, sometimes concave; postmedial line bent inwards from 3/4 of costa, then arched and crenulated to basal half of CuA_1, finally sharply dentated to 2/3 of posterior margin; subterminal line crenulated, sometimes faint; vein ends sometimes bearing triangular spots; fringe pale yellow, mostly mixed with rosy scales sometimes. Hindwing yellowish white, termen yellowish brown or rosy; fringe pale yellow, sometimes with some pink toward apex. **Abdomen.** Pale yellow dorsally, white ventrally.

Male genitalia (Fig. 23). Uncus relatively thick and tapered, with basal 1/3 nearly triangular and naked. Valva slightly broad, with costa nearly straight or concave and ventral margin curved, basal part weakly narrowed, remainder of even width, apex obtusely rounded; sella thumb-shaped and straight, extending inward, bearing short spines vertically settled on ventral and distal margins; sacculus with dorsal 3/5 inflated into a nearly triangular protrusion. Juxta shield-shaped, medially weakly sclerotized, bifid; anellus with three groups of spines (attached to distal juxta in Fig. 23). Saccus narrowly triangular. Phallus long and slender, basal part slightly curved, with a bunch of interlaced spicules on vesica.

Female genitalia (Fig. 38). Anterior apophysis ~ 2× length of posterior apophysis. Antrum subtriangular, strongly sclerotized; colliculum short; ductus bursae ~ 1.5–2× as long as diameter of corpus bursae, posterior sclerite absent. Corpus bursae globular, strongly wrinkled; rhomboid signum large, nearly triangular, with anterior and posterior parts asymmetrical, bearing slightly curved carina; second (posterior) signum larger than in other species, bearing dense and long spines.

Material examined. Type material. ***Type*:** 1♀, Ceylon (NHMUK).

Other material examined. Thailand: 1♂, Chiengma, on eyes of horse, 24.VI.1963, W.W.G. Buttiker, Pyralidae Brit. Mus. Slide No. 12700 (NHMUK). **India:** 1♂, Bombay, 21.2.[18]92, Pyralidae Brit. Mus. Slide No. 010315440 (NHMUK). **China. Fujian:** 1♂1♀, Mt. Tianzhushan, Xiamen, 21, 24.VII.2014, Yang Xiaofei leg., genitalia slide No. ZDD12030 (♀) (NKU); **Guangdong:** 5♂3♀, Longyuan Ecological Garden, Zhepu Village, Hengli, Huizhou, 23.26°N, 114.60°E, 6.X.2021, Zhang Dandan leg.; **Hainan:** 2♂, Shuiman Village, Wuzhishan, 18.88°N, 109.66°E,



Figures 13–21. Adults of *Ecpyrrhorrhoe* spp. **13** *E. rosisquama*, sp. nov., holotype, male (Yunnan) **14** *E. exigistria*, sp. nov., holotype, male (Yunnan) **15** *E. digitaliformis*, male (Guizhou) **16** *E. brevis*, sp. nov., paratype, male (Guangdong) **17** *E. puralis*, male (Hainan) **18** *E. rubellalis*, male (Hainan) **19** *E. longispinalis*, sp. nov., holotype, male (Hunan) **20** *E. celatalis*, male (Yunnan) **21** *E. biaculeiformis*, female (Anhui). Scale bars: 5.0 mm.

alt. 667 m, 14.V.2013, 6.IX.2013, Chen Xiaohua, Li Jinwei leg., genitalia slide No. CXH12189; 1♂, Bawangling Natural Reserve, 19.08°N, 109.12°E, alt. 169 m, 10.V.2013, Li Jinwei leg., genitalia slide No. CXH12187; 2♂3♀, Jianfengling, 1–3. VI.2010, Kang Li leg.; 1♀, Jianling Natural Reserve, alt. 143 m, 18.52°N, 110.16°E, 8.IX.2013, Xie Weicai leg.; 1♂, Jianfeng, Ledong, 18.70°N, 108.80°E, alt. 58 m, 28.IV.2019, Xiang Lanbin leg.; 1♀, Yinggeling Natural Reserve, 19.05°N, 109.50°E, alt. 954 m, 4.IX.2013, Chen Xiaohua leg., genitalia slide No. SYSU0247, molecular voucher No. LEP0021; 1♂, Qijiafang, Limushan Natural Reserve, alt. 681 m, 15.IV.2016, Wei Xueli leg.; 1♂, Yaxing Village, Nankai, Baisha, 19.02°N, 109.40°E, alt. 321 m, 20.VI.2015, Cong Peixin, Guan Wei, Hu Sha leg. (NKU); 2♂1♀, Songtao Reservoir, Lanyang, alt. 194 m, 16–17.IV.2016, Wei Xueli leg.; **Yunnan:** 2♂5♀, Nabang Village, Yingjiang, 24.75°N, 97.56°E, alt. 239 m, 27.V.2016, Duan Yongjiang leg., genitalia slide No. SYSU0926 (♂, molecular voucher No. LEP0163); 1♂2♀, Longmen Village, Mengla, 23.VII.2011, Li Jinwei leg., genitalia slide No. SYSU0237 (♂, molecular voucher No. LEP0035); 1♂3♀, Tuanshan Village, Liming, Ninger, alt. 1162 m, 29.IV.2020, Xiang Lanbin leg.

Distribution. China (Fujian, Guangdong, Guangxi, Hainan, Yunnan), Sri Lanka, India, Thailand, Malaysia, Indonesia, Papua New Guinea, Australia.

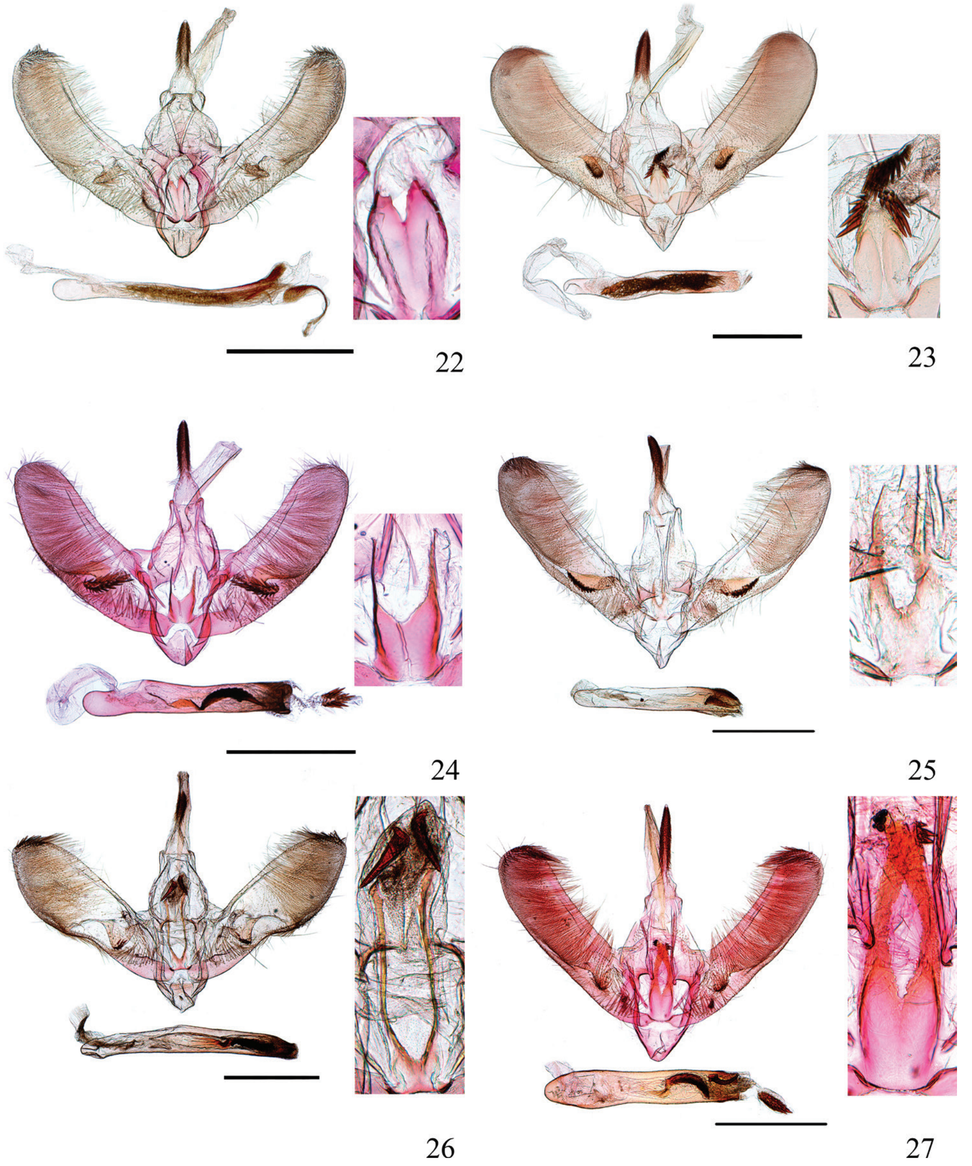
Remarks. The larvae of *Ecpyrrhorrhoe damastesalis* are leaf skeletonizers of teak (*Tectona grandis*). Severe infestations, causing 90%–100% defoliation, has been recorded from Malaysia and Guangdong, China (Intachat 1998; Lin et al. 2018). The misidentification of *E. damastesalis* as *Ecpyrrhorrhoe machoeralis* (Walker, 1859), comb. nov. is common and has been verified in Java and Thailand (Intachat 1998) and Hainan, China (Wu et al. 1977; Wang 1980). We speculate that there are more misidentifications in the literature of this species as *E. machoeralis*.

Ecpyrrhorrhoe minnehaha **(Pryer, 1877), comb. nov.**

Figs 6, 7, 24, 39

Pyrausta minnehaha Pryer, 1877: 234.
Leucocraspeda auratalis Warren, 1895: 472. Syn. nov.
Pionea auratalis ab. *obscura* Caradja, 1935: 41.
Pionea schenklingi Strand, 1918: 79. Syn. nov.

Diagnosis. This species can be differentiated from other species of the genus by its smaller forewing length (8.0–10.0 mm) and the yellow or rosy-red forewing usually bearing strongly contrasting spots and relatively smooth and slender lines (Figs 6, 7). In the male genitalia (Fig. 24), *E. minnehaha* is somewhat similar to *E. fimbriata*, but can be distinguished by the much more rounded ventral margin of valva, excurved sella densely bearing thick setae, pointed arms of juxta without tooth, and presence of a group of spines on the anellus. The female genitalia (Fig. 39) can be distinguished from congeners by the short cup-shaped antrum densely covered with minute spines.



Figures 22–27. Male genitalia of *Ecpyrrhorrhoe* spp., with enlarged detail of juxta (right) **22** *E. allochroa*, sp. nov., holotype, Yunnan (genitalia slide No. CXH12133) **23** *E. damastesalis*, Yunnan (genitalia slide No. SYSU0237) **24** *E. minnehaha,* Jiangxi (genitalia slide No. SYSU0271) **25** *E. obliquata*, Hainan (genitalia slide No. SYSU0228) **26** *E. rufipicta*, Hainan (genitalia slide No. ZDD12031) **27** *E. fimbriata*, Yunnan (genitalia slide No. SYSU0281). Scale bars: 1.0 mm.

Redescription (Figs 6, 7). **Head.** Frons yellow or yellowish brown with white lateral bands. Vertex pale yellow. Labial palpus yellow or yellowish brown, contrastingly white at base ventrally. Maxillary palpus yellow or yellowish brown, pale yellow terminally.

Thorax. Dorsal side yellow or yellowish brown, ventral side white. **Wings.** Forewing length: 8.0–10.0 mm. Forewing yellowish brown, or rosy-red with posterior area straw yellow, markings blackish brown; antemedial line slightly arched from 1/4 of costa to 1/3 of posterior margin; orbicular stigma very small, dot-shaped, sometimes indistinct in rosy-red individuals; reniform stigma comma-shaped, nearly straight or weakly concave; postmedial line from 3/4 of costa to middle of $CuA_{1,}$ bending to 1/3 of CuA_2, then weakly curved to 2/3 of posterior margin; without distinct fuzzy patch posterolateral of cell indistinct; terminal line brown to dark brown; fringe with basal half brown to dark brown, distal half silver-white. Hindwing yellowish brown, with basal and subterminal area scattered with blackish brown scales, posterior area pale yellow; postmedial line from 2/3 of costa to 1/2 of CuA_1, bending inward to 1/3 of CuA_2, then weakly convex to 2/3 of posterior margin; the fuzzy patch posterolateral of cell blackish brown; terminal line and fringe as in forewing. **Abdomen.** Pale yellow dorsally, white ventrally.

Male genitalia (Fig. 24). Uncus with basal 1/3 nearly triangular and naked. Valva with costa slightly concave and ventral margin curved, with apex rounded; sella excurved, thumb-shaped, densely bearing thick setae; sacculus with distal 3/5 inflated into a broad and nearly triangular protrusion. Juxta with base wide, distal half bifid into slender, straight, and widely separated arms; anellus with a cluster of short spines (attached to distal end of phallus in Fig. 24). Saccus rounded triangular. Phallus long and moderately thick; cornuti presented as a bunch of spines, with a large spine distally and connected with a lanceolate sclerite at base.

Female genitalia (Fig. 39). Anterior apophysis ~ 2× length of posterior apophysis. Antrum cup-shaped, short and broad, strongly sclerotized, inner wall densely covered with minute spines; colliculum long, with two longitudinal ridges; ductus seminalis inserting to anterior end of colliculum and with a wide sclerite located opposite to colliculum; ductus bursae ~ 2× as long as length of corpus bursae, basal 2/3 bearing a slim sclerite. Corpus bursae oval; rhomboid signum narrow, with maximal length equal to half length of corpus bursae; second (posterior) signum small and somewhat curved, bearing short spines.

Material examined. Type material. *Pyrausta minnehaha*: ***Holotype*** ♂, **[China]:** Chekiang, 80.123 (NHMUK). *Leucocraspeda auratalis*: ***Holotype*** ♀, Japan (NHMUK). *Pionea schenklingi*: ***Lectotype*** ♂, **[China]:** Kosempo, Formosa, X.1911, H. Sauter Coll., Gen. präp. Gaedike NR: 9669 (SDEI); ***Syntypes*:** 1♀, **[China]:** Suisharyo, Formosa, X.[19]11, H. Sauter Coll., Gen. präp. Gaedike NR: 9670 (SDEI); 1♂, **[China]:** Suisharyo, Formosa, II.[19]12, H. Sauter Coll. (SDEI).

Other material examined. Material with yellowish brown forewing: China: Fujian: 1♀, Mt. Mangdangshan, Maodi Village, 26.70°N, 118.08°E, alt. 812 m, 17.VIII.2016, Chen Kai, Duan Yongjiang leg.; **Guangdong:** 3♂, Niupoling, Yangchun, 18.VIII.2009, He Fengxia leg., genitalia slide LJW12053; 1♂, Mt. Danxiashan, Shaoguan, 25.04°N, 113.64°E, alt. 96 m, 7.VI.2012, Li Jinwei leg.; 1♂, Chebaling Nature Reserve, Shixing, 24.72°N, 114.26°E, alt. 496 m, 28.V.2017, Zhang Dandan leg., genitalia slide No. SYSU1013, molecular voucher No. LEP0217; 1♂, Dunzi Forest Farm, Huizhou, 10.IX.2015, Li Zhiqiang et al. leg.; **Guangxi:** 5♂, Gaozhai, Xing'an, 28.VIII.2011, Zhang Dandan, Li Jinwei leg., genitalia slide No. SYSU0225; 1♂, Gaozhai, Mt. Maoershan, Guilin, alt. 1100 m, 27.VII.2015, Liu Kaili, Zhao Jingxia leg.; **Guizhou:** 2♂, Baishao, Kuankuoshui Natural Reserve, alt. 800 m, 11.VIII.2010, Du Xicui leg.; **Yunnan:** 1♀, Yuanjiang, Yuxi, 23.97°N, 102.05°E, alt. 390 m, 16–17. VII.2019, Xiang Lanbin leg.; **Hubei:** 1♂, Wujiashan, Yingshan, 31.05°N, 115.47°E, alt. 880 m, 29.VI.2014, Chen Xiaohua, Pan Chang leg.; 1♂, Taohuachong, Mt. Dabieshan, alt. 590 m, 30.VI.2014, Xu Lijun leg. genitalia slide No. SYSU1043; **Hunan:** 1♂, Baimaoping, Chengbu, Shaoyang, 26.25°N, 110.37°E, alt. 550 m, 7–9. IX.2020, Jin Mengjie, Xiang Lanbin leg.; 2♂, Yangmeiao, Mt. Jiuwandashan, 25.19°N, 108.65°E, alt. 1183 m, 22.VII.2015, Chen Kai leg.; **Jiangxi:** 9♂, Shixi Village, Fengxin, 28.44°N, 114.54°E, alt. 506 m, 22.IX.2012, Li Jinwei, Yang Lijun leg., genitalia slide No. SYSU0227, molecular voucher No. LEP0033; 2♂, Guanyinyan, Jing'an, 29.03°N, 115.25°E, alt. 195 m, 20.VII.2014, Chenkai leg. genitalia slide No. SYSU0270, molecular voucher No. LEP0059; 1♂, Xiangzhou, Mt. Jinggangshan, 26.IV.2011, Yu Yali leg., genitalia slide No. SYSU0271, molecular voucher No. LEP0061; **Shanxi:** 9♂6♀, Miaoping, Manghe, 35.25°N, 112.46°E, alt. 557 m, 19–20.VIII.2018, Chen Kai, Xiang Lanbin leg.; **Shaanxi:** 1♀, Haopingsi, Yingtou, 34.05°N, 107.42°E, alt. 1251 m, 18.VII.2012, Li Jinwei leg., genitalia slide No. SYSU0272.

Material with rosy-red forewing: Japan: 1♂, Nagasaki, May.1886, Leech, Pyralidae Brit. Mus. Slide No. 010315142 (NHMUK); **China: Hainan:** 1♀, Yinggeling, alt. 620 m, 18.IV.2010, Zhang Jing, Hu Bingbing leg. (abdomen missing).

Distribution. China (Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Shaanxi, Shanghai, Shanxi, Taiwan, Yunnan, Zhejiang), Korea, Japan.

Remarks. The type material of *Pyrausta minnehaha* Pryer, 1877 has rosy-red forewings bearing strongly contrasting spots and relatively smooth and slender lines, and the type series of *Pionea schenklingi* Strand, 1918 has the same appearance. *Leucocraspeda auratalis* Warren, 1895 has a yellowish brown forewing, but bears the same markings, hindwings and fringe as *Pyrausta minnehaha* and *Pionea schenklingi*. The genitalic characters indicate that these all belong to the same species. Although there is striking variation in this species, it is most easily identified by its appearance and its small body size. On the basis of currently available material, specimens with yellowish brown forewings are the commonest form in its range.

Ecpyrrhorrhoe obliquata (Moore, 1888), comb. nov.

Figs 8, 25, 40

Ebulea obliquata Moore, 1888: 224.
Leucocraspeda nissoralis Swinhoe, 1894: 145.

Diagnosis. In appearance, *Ecpyrrhorrhoe obliquata* is similar to *E. exigistria* in the brown subterminal area of the wings, as well as in the oblique, dark brown streak on forewing which distinguish them from all other species of the genus. Genitalia characters readily distinguish *E. obliquata* from other members of the genus in the semi-circular sella with basal half of ventral margin bearing curved spines. It can be best distinguished from *E. exigistria* by the larger forewing length (forewing length: 10.0–12.0 mm), the more distinct and longer streak of the forewing, in the male genitalia (Fig. 25) by the shape of sella, and the weakly sclerotized arms of the bifid juxta, which is without teeth, and in the female genitalia (Fig. 40) by the shape of antrum.

Redescription (Fig. 8). **Head.** Frons and vertex yellow, frons with lateral white bands. Labial palpus yellowish brown, contrastingly white at base ventrally. Maxillary palpus yellowish brown, white terminally. **Thorax.** Dorsal side yellow and ventral side white; tegula yellow with brown base. **Wings.** Forewing length: 10.0–12.0 mm. Forewing pale yellow, basal half of costal band and posterior half of subterminal area brown; stigmata and lines dark brown; antemedial line strongly oblique from 1/5 of costa to 1/2 of 1A, then dentated to 2/5 of posterior margin; orbicular stigma dot-shaped, sometimes indistinct; reniform stigma comma-shaped, thick and straight; an oblique, dark brown streak from posterior end of reniform stigma weakly curved and extended to tornus; postmedial line obliquely outwards from 3/5 of costa to 1/2 of M_1, then dentated inwards to 2/3 of posterior margin; terminal line dark brown and intermittent; fringe with basal half yellow and blackish brown, distal half with anterior half yellow and posterior half dark brown. Hindwing pale yellow, subterminal area from dark brown to brown, gradually paler to tornus; postmedial line dark brown, slightly dentate from 2/3 of M_1 to 1/2 of CuA_1, then bending inwards to base of CuA_1, finally undulated to 2/3 of posterior margin; terminal line and fringe as in forewing. **Abdomen.** Pale yellow dorsally, each segment with posterior margin whitish, black on distal end; white ventrally.

Male genitalia (Fig. 25). Uncus with basal 1/3 nearly triangular and naked. Valva with costa nearly straight or concave and ventral margin curved, basal part weakly narrowed, remainder of even width, apex obtusely rounded; sella nearly semi-circular, bearing short and curved spines on distal half of ventral margins; sacculus with middle part inflated into a thumb-shaped protrusion. Juxta with base wide, distal 3/4 bifid into pointed arms. Saccus narrowly triangular. Phallus long and straight, with a bundle of short spines assembling into cone-shape at distal end.

Female genitalia (Fig. 40). Anterior apophysis ~ 2× length of posterior apophysis. Antrum cup-shaped, with anterior 1/3 strongly sclerotized and covered with spinules on inner wall, posterior 1/3 abruptly broad and partly wrinkled; colliculum long; ductus seminalis connecting to anterior end of colliculum and with a short sclerite located opposite to colliculum; ductus bursae ~ 2.5–3× as long as diameter of corpus bursae, basal 1/3 bearing a slim sclerite. Corpus bursae globular; rhomboid signum with maximal length approximately 1/2 as long as diameter of corpus bursae; the second (posterior) signum nearly thumb-shaped bearing a wide base, sparsely covered with long spines.

Material examined. Type material. *Leucocraspeda nissoralis*: ***Lectotype*** (designated here) ♂, Kahsia Hs [Hills]. 94–66, Pyralidae Brit. Mus. Slide No. 10897 (NHMUK); ***Paralectotype*** **(designated here):** 1♂, [India]: Cherre Punji (NHMUK).

Other material examined. China: Zhejiang: 1♂, Mt. Jiulongshan, 5.VIII.2011, Fu Xiaobing leg.; **Jiangxi:** 2♂, Mt. Jiulianshan, Longnan, 24.58°N, 114.43°E, alt.

620 m, 26.IX.2016, 24.IX.2017, Chen Kai, Duan Yongjiang leg.; **Hunan:** 1♂, Xijialing, Mt. Shunhuangshan, Xinning, Shaoyang, 26.43°N, 111.01°E, alt. 1000 m, 6.IX.2020, Jin Mengjie, Xiang Lanbin leg.; 6♂2♀, Mt. Shunhuangshan, Xinning, Shaoyang, 26.40°N, 111°E, alt. 810 m, 4–6.IX.2020, Jin Mengjie, Xiang Lanbin leg.; 1♂, Dupangling National Natural Reserve, Dao County, Yongzhou, 25.48°N, 111.37°E, alt. 430 m, 29–30.VIII.2020, Jin Mengjie, Xiang Lanbin leg.; 1♀, Dupangling National Natural Reserve, Dao County, Yongzhou, 25.49°N, 111.39°E, alt. 350 m, 28–31.VIII.2020, Jin Mengjie, Xiang Lanbin leg.; 1♂, Qiaotoupu, Chengbu, Shaoyang, 26.25°N, 110.38°E, alt. 640 m, 8.IX.2020, Jin Mengjie, Xiang Lanbin leg.; **Guangdong:** 2♂1♀, Heishiding, Fengkai, 15.VI.2009, 9.X.2010, 2.VIII.2011, 9.VII.2017, 23.47°N, 111.90°E, alt. 214 m, Zhang Dandan et al. leg., genitalia slide No. LJW121067 (♂), SYSU0239 (♂), SYSU1236 (♀, molecular voucher no. LEP0297); 1♀, Yanshuitian, Fengkai, 6.IX.2011, Yang Lijun, Liao Junlei leg., genitalia slide No. SYSU0269; 2♂, Mt. Danxiashan, Shaoguan, 25.04°N, 113.64°E, alt. 96 m, 6–7.VI.2012, Li Jinwei leg., genitalia slide No. LJW12075, CXH12186; 1♀, Mt. Nankunshan, Huizhou, 16.VII.2003, Zhang Dandan, Li Zhiqiang leg., genitalia slide No. ZDD03057; 3♂2♀, Hongri Village, Mt. Nankunshan, Huizhou, 6–9.XI.2020, Jin Mengjie leg.; **Hainan:** 2♂, Bawangling Natural Reserve, 8.V.2011, Yang Lijun leg., genitalia slide No. LJW12101; 2♂, Yinggeling Natural Reserve, 19.05°N, 109.50°E, alt. 954 m, 4.IX.2013, Chen Xiaohua leg., genitalia slide No. CXH12212, SYSU0228 (molecular voucher No. LEP0034); 2♂, Hongkan, Yinggeling Natural Reserve, 19.08°N, 109.50°E, alt. 508 m, 15–16.VI.2015, Cong Peixin, Guan Wei, Hu Sha leg. (NKU); 1♂, Limushan Forest Park, 19.17°N, 109.73°E, alt. 607 m, 25.VII.2014, Cong Peixin, Liu Linjie, Husha leg. (NKU); 1♂, Wuzhishan Forest Park, 18.88°N, 109.67°E, alt. 766 m, 9.I.2016, Teng Kaijian, Bai Xia, Chen Mengting leg. (NKU); **Guangxi:** 1♂, Nonggang, Longzhou, 22.47°N, 106.96°E, alt. 271 m, 19.IV.2012, Li Jinwei leg., genitalia slide No. CXH12185; 1♂, Hekou, Dayaoshan Natural Reserve, Jinxiu, 24.14°N, 110.09°E, alt. 823 m, 20.VII.2015, Qi Mujie, Zhao Shengnan leg. (NKU); 2♂, Mt. Jiuwanshan, Hechi, alt. 1600 m, 23.VII.2015, Wang Jiping leg.; 1♂, Technology Building, Huaping Natural Reserve, Guilin, 25.63°N, 109.91°E, alt. 760 m, 10–12.IX.2020, Jin Mengjie, Xiang Lanbin leg.; **Yunnan:** 1♂, Taiyanghe Natural Reserve, alt. 1450 m, 23.VIII.2014, Zhang Zhenguo leg. (NKU); 1♂, Liaowangtai, Taiyanghe Forest Park, Pu'er, 22.60°N, 101.11°E, alt. 1626 m, 8.VII.2013, LiuShurong, Wang Yuqi, Teng Kaijian leg. (NKU); **Sichuan:** 1♂, Nuoshuihe Natural Reserve, Tongjiang, alt. 700 m, 5.VII.2013, He Guiqing, Xu Lijun leg.; **Chongqing:** 1♂, Daheba, Mt. Jinfoshan, alt. 800–850 m, 15.VII.2010, Du Xicui, Song Lifang leg.; 1♂, Tudiyan, Mt. Simianshan, alt. 1200 m, 9.VIII.2011, He Guiqing, Song Lifang leg.; **Tibet:** 1♂, Air-raid shelter, Beibeng, Medog, 29.24°N, 95.17°E, alt. 750 m, 31.VII.2018, Qi Mujie leg. (NKU); 1♂, Gelin, Beibeng, Medog, 29.25°N, 95.19°E, alt. 1063 m, 29.VII.2018, Qi Mujie leg. (NKU); 1♂, Yadong, Medog, 29.33°N, 95.34°E, alt. 833 m, 2.VIII.2018, Qi Mujie leg. (NKU).

Distribution. China (Zhejiang, Jiangxi, Hunan, Guangdong, Hainan, Guangxi, Yunnan, Sichuan, Chongqing, Tibet), Burma, India, Sri Lanka.

Ecpyrrhorrhoe rufipicta (Butler, 1880), comb. nov.

Figs 9, 26, 41

Asopia rufipicta Butler, 1880: 682.
Paliga rubicundalis Warren, 1896: 96. Syn. nov.

Diagnosis. Within the genus, *E. rufipicta* resembles *E. fimbriata* (Moore, 1886) in having nearly the same forewing length, yellow wings bearing brown markings and an almost indistinct, brown subterminal band (Fig. 9). However, it can be differentiated from *E. fimbriata* by more dentated and relatively thick postmedial line on both wings, in the male genitalia (Fig. 26) by the nearly oval valva, the thumb-shaped dorsal sella, the triangular ventral sella bearing several spines, the longer and strongly sclerotized arms of the juxta, and two long and pointed spines located on anellus.

Redescription (Fig. 9). **Head.** Frons yellow, with lateral white bands. Vertex pale yellow. Labial palpus yellow, contrastingly white at base ventrally. Maxillary palpus yellow, white terminally. **Thorax.** Dorsal side yellow, and ventral side white; tegula yellow, with base brown. **Wings.** Forewing length: 9.0–12.0 mm. Wings yellow, with brown markings. Forewing with costal base brown; antemedial line dentated from 1/4 of costa slightly arched to 1/3 of posterior margin; orbicular stigma oblate; reniform stigma comma-shaped and thick; postmedial line dentated from 3/4 of costa to 2/5 of CuA_2, then deeply dentated to 2/3 of posterior margin; subterminal band indistinct, with inner margin crenulated; fringe pale yellow. Hindwing with postmedial line brown, slightly dentated from 2/3 of M_1 arched to 1/2 of CuA_1, bending inward to basal 1/3 of CuA_1, then dentated to near tornus; subterminal line and fringe as in forewing. **Abdomen.** Pale yellow dorsally, gradually brown to distal part, white ventrally.

Male genitalia (Fig. 26). Uncus with basal 1/2 nearly triangular and naked. Valva with costa slightly convex and ventral margin curved, with basal part narrowed, remainder nearly oval, apex rounded; sella nearly triangular, bearing short spines on distal and inner margins, with a curved, finger-shaped dorsal projection; sacculus with middle part inflated into a triangular and setose protrusion. Juxta with base wide, distal 4/5 forming slender, long, and sclerotized arms dentate apically; anellus with two long and pointed spines (connected with distal arms of juxta in Fig. 26). Saccus rounded triangular. Phallus long and straight, cornuti presented as a narrow sclerite with dense and short spines.

Female genitalia (Fig. 41). Anterior apophysis ~ 2.5× length of posterior apophysis. Antrum cylindrical, tuberculate laterally on anterior end, strongly sclerotized and covered with spinules on inner wall; colliculum long and broad, narrower medially; ductus seminalis connecting to anterior end of colliculum and with a wide sclerite located opposite to colliculum; ductus bursae ~ 2.5–3× as long as diameter of corpus bursae, basal 2/5 bearing a slim sclerite. Corpus bursae globular; rhomboid signum with maximal length > 1/2 of diameter of corpus bursae; second (posterior) signum composed of a pair of round sclerites bearing dense and long spines.

Material examined. Type material. *Asopia rufipicta*: **Type:** 1♀, **[China:]** Formosa, Pyralidae Brit. Mus. Slide No. 8682 (NHMUK). *Paliga rubicundalis*: **Type:** 1♂, **[India]:** Khasis [Khasia] Nat. Coll., Pyralidae Brit. Mus. Slide No. 8685 (NHMUK).

Other material examined. [India]: 1♂, Khasis [Khasia] Nat. Coll., NHMUK slide No. 010315123 (NHMUK); 1♂, Assam, NHMUK slide No. 010315163 (NHMUK); **Philippines:** 1♂, Mt. Makiling, Luzon, Baker, 1917–79, Pyralidae Brit. Mus. Slide No. 19893 (NHMUK); **China: Guangxi:** 1♂, Miaozhai, Mt. Jinzhongshan, alt. 1450 m, 31.VII.2014, Wei Xueli, Ran Chao leg., genitalia slide No. SYSU1509; **Hainan:** 1♂, Baodao Village, Jiaxi Natural Reserve, 18.09°N, 109.05°E, alt. 149 m, 11.IX.2013, Xie Weicai leg., genitalia slide No. SYSU0645, molecular voucher No. LEP0038; 1♀, Jianling Natural Reserve, 18.87°N, 110.27°E, alt. 143 m, 8.IX.2013, Chen Xiaohua leg., genitalia slide No. SYSU0278, molecular voucher No. LEP0107; 1♂, Hongxin Village, Yuanmen, Baisha, 19.07°N, 109.52°E, alt. 460 m, 29.VI.2014, Cong Peixin, Liu Linjie, Hu Sha leg., genitalia slide No. ZDD12031, molecular voucher no. LEP0062 (NKU); 1♀, Hongkan, Yinggeling Natural Reserve, 19.08°N, 109.50°E, alt. 508 m, 15.VI.2015, Cong Peixin, Guan Wei, Hu Sha leg., genitalia slide No. SYSU0341 (NKU).

Distribution. China (Guangxi, Hainan, Taiwan), India, Philippines.

Remarks. Based on the substantial morphological similarity in the male genitalia between the types of *Asopia rufipicta* Butler, 1880 and *Paliga rubicundalis* Warren, 1896, *Paliga rubicundalis* is considered as a junior synonym of *E. rufipicta* (Butler).

Ecpyrrhorrhoe fimbriata (Moore, 1886), comb. nov.

Figs 10, 27

Ebulea fimbriata Moore, 1886: 346.
Ecpyrrhorrhoe angustivalvaris Gao, Zhang & Wang, 2013: 314. Syn. nov.

Diagnosis. Forewing length: 9.0–11.0 mm. *Ecpyrrhorrhoe fimbriata* is similar to *E. rubiginalis* both in appearance and in the male genitalia, but it can be differentiated from it by the relatively smooth and slender postmedial line on both wings (Fig. 10), in the male genitalia (Fig. 27), by the even width of the valva, dorsal projection of sella absent and the setose, thumb-shaped sella, the weakly sclerotized arms of the juxta with several short spines at apex, and the cluster of spines on the anellus (attached to distal end of phallus in Fig. 27).

Material examined. Type material. *Ebulea fimbriata*: ***Holotype*** ♂, Ceylon, Pyralidae Brit. Mus. Slide No. 8684 (NHMUK); ***Paratype*:** 1♀, same data as holotype (NHMUK). *Ecpyrrhorrhoe angustivalvaris*: ***Holotype*** ♂, **China: Guizhou:** Dahe Dam, 28.33° N, 108.29°E, alt. 430 m, 6.VI.2007, Du Xicui leg., genitalia slide No. GQ11081 (NKU).

Other material examined. China: Guangxi: 1♂, Nonggang, Longzhou, 22.47°N, 106.96°E, alt. 271 m, 19.VI.2012, Li Jinwei leg., genitalia slide No. LJW12065, molecular voucher No. LEP0039; 1♂, Shaoping Forestry Station, Pingxiang, alt. 280 m, 31.III.2012, Yang Xiaofei leg., genitalia slide No. CXH12139, molecular voucher No. LEP0099; 1♂, Huaping National Natural Reserve, Guilin, 25.63°N, 109.91°E, alt. 520 m, 11–12.IX.2020, Jin Mengjie, Xiang Lanbin leg., genitalia slide No. SYSU1507; **Guizhou:** 1♂, Fade Bridge, Shunchang, Shuicheng, 26.24°N, 104.85°E, alt. 857 m, 29.IV–3.V.2019, Liu Qingming leg., genitalia slide No. SYSU1506; **Yunnan:** 5♂, Baihualing, Baoshan, 11–13.VIII.2007, Zhang Dandan leg., genitalia slide No. CXH112169 (molecular voucher No. LEP0098), SYSU0115, SYSU0281 (molecular voucher No. LEP0111).

Distribution. China (Guangxi, Guizhou, Yunnan), Sri Lanka.

Remarks. After examination of the male genitalia of the holotypes of *Ebulea fimbriata* Moore, 1886 and *Ecpyrrhorrhoe angustivalvaris* Gao, Zhang & Wang, 2013, we conclude that they are the same species, sharing the same sella, juxta and phallus, even though the valva of the holotype of *E. angustivalvaris* is slightly narrower.

Ecpyrrhorrhoe rubiginalis (Hübner, 1796)

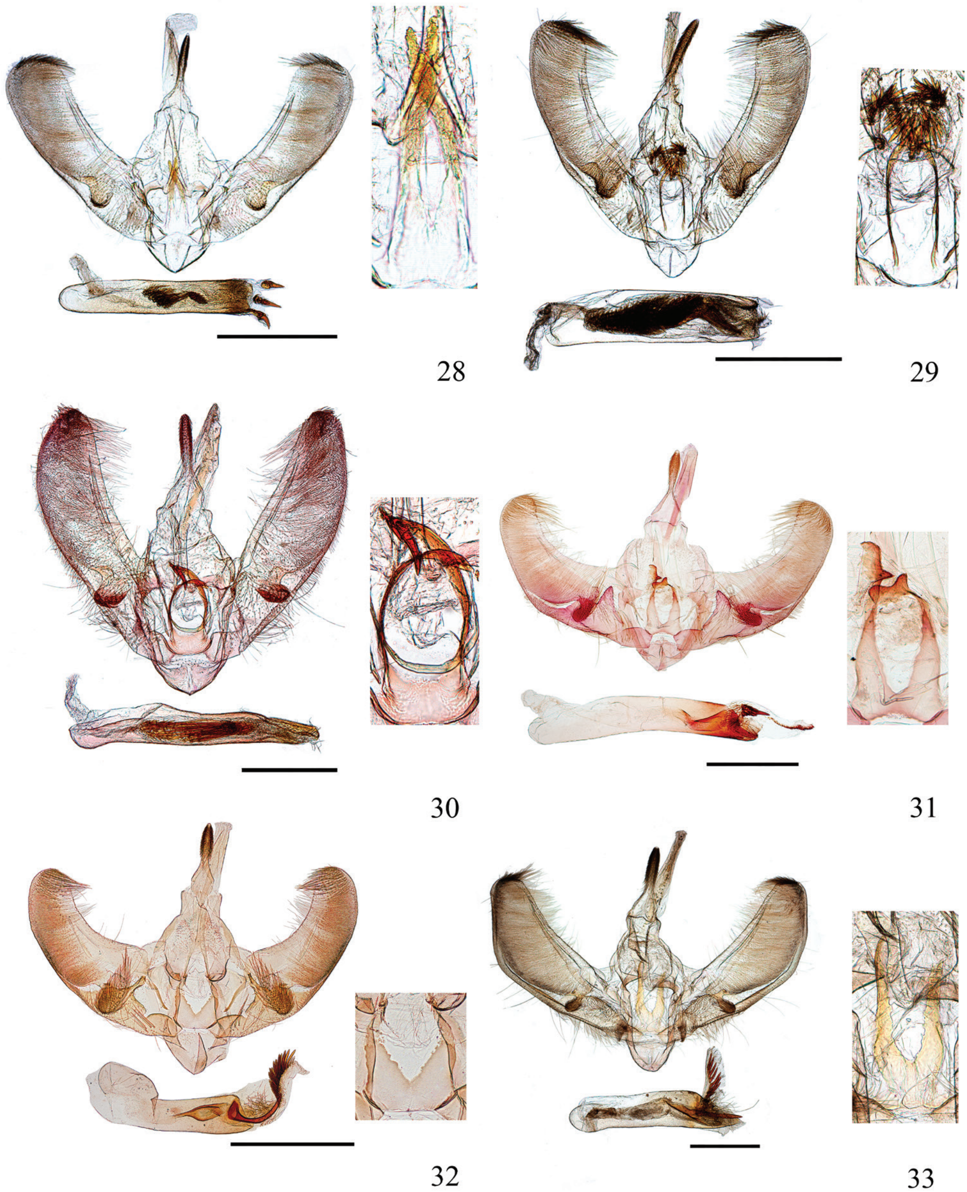
Figs 11, 28, 42

Pyralis rubiginalis Hübner, 1796: 22.
Pyrausta pygmaealis South, 1901: 505. Syn. nov.
Pionea rubiginalis delimbalis Schawerda, 1913: 170.
Pionea rubiginalis f. *denigratalis* Hartig & Amsel, 1952[1951]: 62.
Perinephela rubiginalis microlimbalis Amsel, 1959: 25.
Ecpyrrhorrhoe multispinalis Gao, Zhang & Wang, 2013: 312. Syn. nov.

Diagnosis. Forewing length: 9.0–12.0 mm. In appearance, *Ecpyrrhorrhoe rubiginalis* is similar to *E. fimbriata*, but the coloration of the wings and markings of *E. rubiginalis* is darker, and the patch in the hindwing is larger (Fig. 11). In the male genitalia (Fig. 28), the phallus of *E. rubiginalis* has a cluster of interlaced spicules and an oval sclerite bearing spines on the vesica, with three separate spines on the anellus (attached to distal end of phallus in Fig. 28).

Material examined. Type material. *Pyrausta pygmaealis*: ***Lectotype*** (designated here) ♀, **[China: Hubei]:** Ichang, Mrs Pratt Coll., June 1888, Pyralidae Brit. Mus. Slide No. 8681 (NHMUK). *Ecpyrrhorrhoe multispinalis*: ***Holotype*** ♂, **China: Tianjin:** Qilihai, 39.17°N, 117.34°E, 9.IX.2001, You Ping leg., genitalia slide No. GQ11075 (NKU).

Other material examined. China: Fujian: 1♂, Chishui Station, Mt. Daiyunshan, 25.64°N, 118.14°E, alt. 1015 m, 22.V.2012, Li Jinwei leg., genitalia slide No. CXH12159; **Hainan:** 1♂, Yaxing Village, Nankai, Baisha, 19.02°N, 109.40°E, alt. 321 m, 20.VI.2015, Cong Peixin, Guan Wei, Hu Sha leg. (NKU); **Hebei:** 1♂ (abdomen missing), Pianchen Forestry Station, 36.44°N, 113.39°E, alt. 1109 m, 31.VII.2013, Liu Xiaolin leg.; **Heilongjiang**: 5♂1♀, Jiagedaqi, 13–14.VII.2012, Zhang Dandan, Yang Lijun leg., genitalia slide No. SYSU0238 (♂), CXH12176 (♂), CXH12177 (♂), CXH12179 (♂), CXH12264 (♀); 1♂, Dailing, Yichun, 20.VII.2012, Zhang Dandan, Yang Lijun leg.,



Figures 28–33. Male genitalia of *Ecpyrrhorrhoe* spp., with enlarged detail of juxta (right) **28** *E. rubiginalis*, Shanxi (genitalia slide No. SYSU0245) **29** *E. rosisquama* sp. nov., holotype, Yunnan (genitalia slide No. SYSU0246) **30** *E. exigistria* sp. nov., holotype, Yunnan (genitalia slide No. ZDD12044) **31** *E. digitaliformis*, Zhejiang (genitalia slide No. CXH12193) **32** *E. brevis* sp. nov., holotype, Guangdong (genitalia slide No. CXH12182) **33** *E. puralis*, Guangxi (genitalia slide No. SYSU0254). Scale bars: 1.0 mm.

genitalia slide No. CXH12181; 1♂, Liangshui, Yichun, 19.VII.2012, Chen Xiaohua, Yang Lijun leg.; **Hubei:** 1♂, Huangbaoping Village, Hongping, Shennongjia, 31.61°N, 110.30°E, 24–25.VI.2019, 1530 m, Xiang Lanbin leg.; **Hunan:** 1♀, Yueyan Forestry Station, Dupangling National Natural Reserve, Dao County, Yongzhou, 25.49°N, 111.39°E, alt. 400 m, 28–31.VIII.2020, Jin Mengjie, Xiang Lanbin leg., genitalia slide No. SYSU1508, molecular voucher No. LEP0439; **Inner Mongolia:** 1♂, Linjiang Village, Erguna, 51.41°N, 119.97°E, alt. 475 m, 8.VIII.2019, Xiang Lanbin leg.; **Jiangxi:** 1♂, Xiaoxidong, Mt. Jinggangshan, 1.VII.2011, Yang Lijun leg.; 1♀, Mt. Jinggangshan, 2.X.2010, Chen Haidong, Xie Weicai leg., genitalia slide No. SYSU0215; 2♂, Mt. Guanggushan, Wuzhifeng, Shangyou, 25.92°N, 114.05°E, alt. 846 m, 22.VI.2015, Chen Kai leg., genitalia slide No. SYSU0207, SYSU0263; 1♂, Mt. Guanggushan, Shangyou, 25.92°N, 114.05°E, alt. 183 m, 20.IX.2016, Chen Kai, Duan Yongjiang leg.; 1♂, Qianmo Village, Nanfengmian Natural Reserve, Suichuan, 26.28°N, 114.06°E, alt. 816 m, 19.VI.2015, Chen Kai leg.; 1♂, Qianmo Village, Nanfengmian Natural Reserve, Suichuan, 26.29°N, 114.06°E, alt. 820 m, 19.IX.2017, Chen Kai leg.; 1♂1♀, Mt. Wugongshan, Luxi, 27.48°N, 114.15°E, alt. 500 m, 23.IX.2016, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU0280 (♀), molecular voucher No. LEP0109; **Jilin:** 2♂, Wanbao Village, Antu, 23.VII.2012, Yang Lijun, Chen Xiaohua leg., genitalia slide No. CXH12180; 1♂, Huashan, Linjiang, 25.VII.2012, Yang Lijun, Chen Xiaohua leg., genitalia slide No. CXH12119; 1♂, Duanmusong, Linjiang, 26.VII.2012, Yang Lijun, Chen Xiaohua leg., genitalia slide No. CXH12016; 1♂, Hongshi Village, Hujia, Jiutai, 8.VIII.2018, Zhang Dandan leg.; **Shanxi:** 2♂, Dahe Forestry Station, Yicheng, 35.46°N, 111.93°E, alt. 1212 m, 13–15.VIII.2018, Xiang Lanbin leg.; 1♂, Dahe Village, Yicheng, 35.27°N, 111.56°E, alt. 1204 m, 28.VII.2013, Liu Xiaolin leg., genitalia slide No. SYSU0245, molecular voucher No. LEP0019; 1♂, Shangchuan Village, Qinshui, 35.28°N, 112.01°E, alt. 1619 m, 25.VII.2013, Liuxiaolin leg.; 3♂, Xiachuan Village, Qinshui, 35.44°N, 112.02°E, alt. 1514 m, 16–18.VIII.2018, Chen Kai, Xiang Lanbin leg.; 2♂1♀, Miaoping, Manghe, 35.25°N, 112.46°E, alt. 557 m, 19–20.VIII.2018, Chen Kai, Xiang Lanbin leg.; **Xinjiang:** 1♂, Nalati, Xinyuan, 43.31°N, 84.03°E, alt. 1389 m, 24.VII.2013, Li Jinwei leg., genitalia slide No. CXH12055; 1♂1♀, Baishahu, Habahe, Altay, 48.37°N, 85.74°E, alt. 553 m, 10.VII.2017, Chen Kai, Duan Yongjiang leg.; 5♂3♀, Yeguolin, Xinyuan, 43.38°N, 83.56°E, alt. 1282 m, 1.VII.2017, Chen Kai, Duan Yongjiang leg.

Distribution. China (Beijing, Fujian, Hainan, Hebei, Heilongjiang, Henan, Hubei, Hunan, Inner Mongolia, Jiangxi, Jilin, Shaanxi, Shanxi, Tianjin, Xinjiang), Russia, Japan, Iran, Europe.

Ecpyrrhorrhoe machoeralis (Walker, 1859), comb. nov.

Figs 12, 43

Scopula machoeralis Walker, 1859: 1013.
Eutectona machaeralis [sic]: Wang & Sung, 1980: 305.

Diagnosis. Forewing length: 8.0–10.0 mm. *Ecpyrrhorrhoe machoeralis* can be differentiated from congeners by the antrum with anterior half narrower than posterior half.

Female genitalia (Fig. 43). Anterior apophysis ~ 1.5× length of posterior apophysis. Antrum long and tubular, with anterior half broad and slightly wrinkled, posterior half slightly narrow and as wide as colliculum; colliculum moderately long, somewhat difficult to differentiate from antrum; ductus seminalis connecting to anterior end of colliculum and with a weak sclerite located opposite to colliculum; ductus bursae ~ 2–2.5× as long as diameter of corpus bursae, basal 2/5 bearing a slim sclerite. Corpus bursae globular; rhombic signum with maximal length < ~ 1/2 length of diameter of corpus bursae; second (posterior) signum curved, with both ends bearing sparse and long spines.

Material examined. Type material. ***Type*****:** 1♀, Ceylon, genitalia slide No. 8680 (NHMUK).

Distribution. Sri Lanka.

Remarks. Based on the examined material, this species only occurs in Sri Lanka, from where the type was described (Walker 1859). However, because of the misidentifications as *Ecpyrrhorrhoe machoeralis* of *E. damastesalis*, records of the former are widely present in the literature (Wu et al. 1977, Intachat 1998, Lin et al. 2018, Wang 1980). The reported biology of *E. machoeralis* needs to be confirmed.

The damaged female type material of *E. machoeralis* and lacks the original wing pattern because of its lack of scales, and the genital dissection is of low quality, which makes the identification and diagnosis of *E. machoeralis* difficult.

Ecpyrrhorrhoe rosisquama Xiang & Zhang, sp. nov.

http://zoobank.org/1D83FACD-6109-46DB-8735-27A387D7974B
Figs 13, 29, 44

Diagnosis. This species differs from all other species of the genus by the yellow forewing bearing rosy markings and mottled covering of rosy scales, the rosy markings on tornal area of the hindwing (Fig. 13), in the male genitalia (Fig. 29) by the longer and more strongly sclerotized arms on the juxta, with two groups of short and pointed spines on the anellus, in the female genitalia (Fig. 44) by the smaller and less developed antrum, and the smaller corpus bursae.

Description (Fig. 13). **Head.** Frons and vertex yellow, frons with lateral white bands. Labial palpus yellow or orange, contrastingly white at base ventrally. Maxillary palpus yellow, pale terminally. Frons, vertex, labial and maxillary palpi sometimes mixed with rosy scales. **Thorax.** Dorsal side and tegula yellow, mixed with rosy scales; ventral side white. **Wings.** Forewing length: 10.0–12.0 mm. Forewing with termen weakly oblique; ground color yellow, with mottled covering of rosy scales forming indistinct markings except the totally rosy costa; antemedial line blurred, from 1/5 of costa oblique to 1/3 of 1A, then dentate to 2/5 of posterior margin; orbicular stigma nearly square; reniform stigma comma-shaped, thick and concave; postmedial line blurred, arched from 3/4 of costa to base of CuA_2, connected with oval-shaped patch posterolateral of cell, and finally dentated to 2/3 of posterior margin; subterminal band with anterior part broad, inner margin serrated; fringe with basal half dark rosy and distal half pale yellow. Hindwing pale yellow; postmedial and subterminal lines rosy and serrated, but only with posterior part distinct; terminal line sometimes rosy; fringe as in forewing, with apex and tornus pale yellow. Underside: costal and terminal areas grey; reniform stigma and patch posterolateral of cell grey and distinct; postmedial line grey and faint. **Abdomen.** Yellowish to yellowish brown dorsally, the first two segments whitish, posterior margin of each segment paler. Dirty white ventrally.

Male genitalia (Fig. 29). Uncus with basal 1/4 nearly triangular and naked. Valva slightly curved, of almost even width, apex obtusely rounded; sella thick and setose, thumb-shaped, bearing short spines on distal margin, extending ventrad; sacculus with distal 3/4 inflated into a broad and round protrusion. Juxta with base wide, distal 4/5 bifid into slender, long, and sclerotized arms; anellus with two groups of short and pointed spines (connected with distal arms of juxta in Fig. 29). Saccus rounded triangular. Phallus rather stout and straight, with interlaced spicules on vesical and cornuti present as a sclerite with dense and long spines.

Female genitalia (Fig. 44). Anterior apophysis ~ 2× the length of posterior apophysis. Antrum cup-shaped, weakly sclerotized, slightly wrinkled medially; colliculum moderately long and broad; ductus seminalis inserting to anterior end of colliculum and with a wide sclerite and a nearly semi-circular, strong sclerotized sclerite located opposite colliculum; ductus bursae ~ 3–4× diameter of corpus bursae, basal half bearing a slim sclerite. Corpus bursae globular; rhombic signum with maximal length < 1/2 of diameter of corpus bursae; second (posterior) signum composed of a pair of narrow and pointed sclerites without spines.

Material examined. Type material. ***Holotype*** ♂, **China: Yunnan:** Baihualing Natural Reserve, Baoshan, 24.30°N, 98.80°E, alt. 1535 m, 20.IV.2015, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU0246, molecular voucher No. LEP0020 (SYSBM). ***Paratypes*****: Guangxi:** 1♀, Songshuping, Mt. Jinzhongshan, alt. 940 m, 28.VII.2014, Wei Xueli, Ran Chao leg.; **Yunnan:** 5♂7♀, Baihualing Natural Reserve, Baoshan, alt. 1520 m, 11, 13.VIII.2007, Zhang Dandan leg., genitalia slide No. SYSU0209 (♂), SYSU0229 (♂), SYSU0262 (♀); 1♀, Baihualing Natural Reserve, Baoshan, 25.30°N, 98.80°E, alt. 1473 m, 7.VIII.2014, Teng Kaijian, Liu Shurong, Rong Hua leg. (NKU); 1♀, Hanlongzhai, Baihualing Natural Reserve, Baoshan, 25.31°N, 98.80°E, alt. 1616 m, 11.V.2021, Jin Mengjie, Guo Muyu, Fu Haiyun leg.; 1♂, Taizhong Village, Jingdong, 24.51°N, 100.94°E, alt. 1395 m, 14.IV.2015, Chen Kai, Duan Yongjiang leg.; 2♀, Tuanshan Village, Liming, Ninger, alt. 1162 m, 29.IV.2020, Xiang Lanbin leg.

Distribution. China (Guangxi, Yunnan).

Etymology. The specific name is derived from the Latin *rose-* (= rosy) and *squama* (= scales), referring to rosy scales on wings.

Ecpyrrhorrhoe exigistria **Zhang & Xiang, sp. nov.**

http://zoobank.org/F4EE0BEE-14BF-4D43-A4EA-54AE5F66F4CA
Figs 14, 30, 45

Diagnosis. This species is similar to *E. obliquata* but can be best distinguished from it by the smaller size (forewing length: 7.0–9.0 mm), the pale brown reniform stigma and the indistinct and short streak of the forewing (Fig. 14), in the male genitalia (Fig. 30) by the excurved, finger-shaped and setose sella, the strongly sclerotized arms of the juxta, and anellus with a long spine and one or two short spines and in the female genitalia (Fig. 45) by the mostly tubular antrum.

Description (Fig. 14). **Head.** Frons and vertex yellow, frons with lateral white bands. Labial palpus yellowish brown, contrastingly white at base ventrally. Maxillary palpus yellowish brown, white terminally. **Thorax.** Dorsally yellow, ventrally white; tegula yellow with brown base. **Wings.** Forewing length: 7.0–9.0 mm. Forewing pale yellow, posterior half of subterminal area brown; antemedial line dark brown, almost straight from 1/5 of costa to 2/5 posterior margin, slightly dentate; reniform stigma comma-shaped, brown; an oblique, dark brown streak from posterior end of reniform stigma, fuzzy, extended to tornus; postmedial line black brown, obliquely outwards from 3/5 of costa to 1/2 of M1, then dentated inwards to 2/3 of posterior margin; terminal line black brown; fringe with basal half brown, distal half dark brown. Hindwing pale yellow, subterminal area from dark brown to yellow, gradually paler to tornus; postmedial line black-brown, slightly dentate from 2/3 of M_1 to 1/2 of CuA_1, then bending inwards to base of CuA_1, finally undulated to 2/3 of posterior margin; terminal line and fringe as in forewing. **Abdomen.** Pale yellow dorsally, black distally, white ventrally.

Male genitalia (Fig. 30). Uncus with basal 2/5 nearly triangular and naked. Valva narrowly oval, costa straight or slightly concave and ventral margin curved, with apex rounded; sella excurved, thumb-shaped, thick, and setose, bearing thick setae on distal half; sacculus with distal 3/5 inflated into a broad and nearly triangular protrusion. Juxta with base wide, distal 3/4 bifid into slender, curved, sclerotized, and widely separated arms; anellus with a long spine and one or two short spines (attached to distal part of juxta in Fig. 30). Saccus rounded triangular. Phallus long and tapering, distal end spinulose and weakly sclerotized, with interlaced spicules cluster on vesica.

Female genitalia (Fig. 45). Anterior apophysis ~ 1.5× length of posterior apophysis. Antrum long tubular and sclerotized, with anterior 1/3 broad, weakly sclerotized and wrinkled medially; colliculum long; ductus seminalis connecting to anterior end of colliculum and with a weak sclerite located opposite to colliculum; ductus bursae ~ 2–2.5× as long as diameter of corpus bursae, basal 1/3 bearing a slim sclerite. Corpus bursae globular; rhomboid signum with maximal length > 1/2 of diameter of corpus bursae; second (posterior) signum curved, oval, bearing sparse and long spines.

Material examined. Type material. ***Holotype*** ♂, **China: Yunnan:** Wild Elephant Valley, Xishuangbanna, 22.17°N, 100.87°E, alt. 762 m, 12.VII.2015, Teng Kaijian, Bai Xia leg., genitalia slide No. ZDD12044, molecular voucher No. LEP0063 (SYSBM). ***Paratypes*.** **China: Guangxi:** 1♂, Lianhuashan, Mt. Dayaoshan, alt. 1250 m, 22.VII.2015, Liu Kaili, Zhao Jingxia leg., genitalia slide No. SYSU1009, molecular voucher No. LEP0211; 1♂, Mt. Shengtangshan, Jinxiu, 25.VIII.2011, Cheng Muchun leg., genitalia slide No. LJW12080; **Hainan:** 1♂, Jianfenling Natural Reserve, 18.75°N, 108.85°E, alt. 969 m, 12.V.2013, Li Jingwei leg., genitalia slide No. SYSU1247; 2♂, Diaoluoshan, Lingshui, 18.72°N, 109.87°E, alt. 942 m, 29–30.IV.2019, Xiang Lanbin leg., genitalia slide No. SYSU1514; **Jiangxi:** 1♀, Mt. Jiulianshan, Longnan, 24.58°N, 114.43°E, alt. 620 m, 26.IX.2016, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU0276, molecular voucher no. LEP0100; 1♂, Xiagongtang, Mt. Jiulianshan, Ganzhou, 24.54°N, 114.46°E, alt. 600 m, 16.VIII.2020, Jin Mengjie leg., genitalia slide No. SYSU1513; **Tibet:** 1♂, Dexing Village, Medog, 29.32°N, 95.30°E, alt. 833 m, 18.VIII.2017, Qi Mujie, Yang Xiaofei leg. (NKU); **Yunnan:** 2♂, Wild Elephant Valley, Xishuangbanna, 22.17°N, 100.87°E, alt. 762 m, 18, 20.VII.2014, Teng Kaijian, Guan Wei, Wang Xiuchun, Liu Shurong leg. (NKU).

Distribution. China (Guangxi, Hainan, Jiangxi, Tibet, Yunnan).

Etymology. The specific name is derived from the Latin *exigu-* (= short) and *stria* (= streak), referring to the short streak on forewings.

Ecpyrrhorrhoe digitaliformis Zhang, Li & Wang, 2004

Figs 15, 31, 46

Ecpyrrhorrhoe digitaliformis Zhang, Li & Wang, 2004: 318.

Diagnosis. Forewing length: 9.0–14.0 mm. In appearance, *Ecpyrrhorrhoe digitaliformis* is indistinguishable from *E. celatalis* (Walker, 1859), but it can be distinguished from it in the male genitalia (Fig. 31) by the tapering and curved valva, the thumb-shaped, excurved and setose sella inflated distally, by the stout, sclerotized, finger-shaped dorsal protrusion of the sacculus, by the anellus with a string of minute spines and a cone-shaped group of large spines (attached to distal phallus in Fig. 31), the modified distal ends of the arms of the juxta, and the shape of cornuti; in the female genitalia (Fig. 46), by the antrum with a vertical wrinkled area in the middle.

This species is closely related to *E. brevis* based on molecular data, and similar in appearance and male genitalia, but can be differentiated by the slender and excurved sella, the thick protrusion of sacculus, and the slender arms of juxta bearing a tooth-shaped process, as well as the characters mentioned above.

Material examined. ***Holotype*** ♂, **China: Henan:** Xinyang, 32.06°N, 114.07°E, alt. 700 m, 13.VII.2013, Zhang Dandan leg., genitalia slide No. ZDD02107 (NKU). ***Paratypes*: China: Henan:** 1♀, same data as holotype, genitalia slide No. ZDD02115 (NKU); **Zhejiang:** 1♂1♀, Mt. Tianmushan, 30.26°N, 119.34°E, 16.VIII.1999, Li Houhun leg. (NKU).

Other material examined. China: Chongqing: 2♂, Wuli, Qianjiang, alt. 870 m, 24.VII.2012, Zhang Jun, Xu Lijun leg., genitalia slide No. SYSU1528; 1♂1♀, Mt. Jinyinshan, Qianjiang, alt. 1100 m, 25.VII.2012, Zhang Jun, Xu Lijun leg., genitalia slide No. SYSU1551 (♂); 3♂2♀, Xiaonanhai, Qianjiang, alt. 370 m, 21.VII.2012, Zhang Jun, Xu Lijun leg., genitalia slide No. SYSU1550 (♂); **Guangdong:** 1♂, Niupoling, Yangchun, 18.VIII.2009, He Fengxia leg., genitalia slide No. HFX08237; 2♀, Dawuling, Xinyi, alt. 900 m, 7–14.VIII.2003, Zhang Dandan, Jian Yuening, Lin Meiying leg., genitalia slide No. ZDD003023, ZDD03072; **Guangxi:** 5♂2♀, Mt. Shengtangshan, Jinxiu, 25–26.VIII.2011, Yang Lijun, Cheng Muchun, Zhang Dandan leg., genitalia slide No. CXH12164(♂), CXH12175(♂), CXH12183(♂), CXH12214(♀), SYSU0274(♀, molecular voucher No. LEP0402); 1♂, Hekou, Dayaoshan Natural Reserve, Jinxiu, 24.14°N, 110.09°E, alt. 823 m, 20.VII.2015, Qin Mujie, Zhao Shengnan leg. (NKU);

1♀, Gaozhai Village, Xing'an, 28.VIII.2011, Li Jinwei leg., genitalia slide No. SYSU1522; 1♂, Anjiangping Natural Reserve, 25.56°N, 109.93°E, alt. 1751 m, 10.VII.2013, Chen Xiaohua leg., genitalia slide No. SYSU1527; **Guizhou:** 3♂, Maolan Natural Reserve, Libo, 25.25°N, 107.90°E, alt. 814 m, 25.VII.2015, Chen Kai leg., genitalia slide No. SYSU0217, SYSU0221, SYSU0051; 1♂, Taojiang, Leishan, 27.VIII.2012, Li Jinwei leg., genitalia slide No. CXH12160; **Hainan:** 2♂1♀, Yinggeling, 19.05°N, 109.50°E, alt. 954 m, 4.IX.2013, Chen Xiaohua, Xie Weicai leg., genitalia slide No. SYSU0224 (♂); **Hubei:** 2♂, Taohuachong, Mt. Dabieshan, 30.59°N, 116.19°E, alt. 661 m, 24.VI.2014, Chen Xiaohua, Pan Chang leg., genitalia slide No. SYSU0208, SYSU0241; 1♂, Qingtaiguan, Luotian, 31.11°N, 115.41°E, alt. 524 m, 2.VII.2014, Liu Zhenhua, Pan Chang leg., genitalia slide No. SYSU0214; **Hunan:** 1♀, Baiyun Reservoir, Baimaoping, Chengbu, Shaoyang, 26.27°N, 110.36°E, alt. 560 m, 7.IX.2020, Jin Mengjie, Xiang Lanbin leg., genitalia slide No. SYSU1565; 1♂, Zhupo Village, Huitong, 23.VIII.2012, Li Jinwei, Chen Xiaohua leg., genitalia slide No. CXH12198; 1♂, Yueyan Village, Dao County, 21.VIII.2012, Li Jinwei, Chen Xiaohua leg., genitalia slide No. CXH12197; **Jiangxi:** 1♂, Xiaoxidong, Mt. Jinggangshan, 1.VII.2011, Yang Lijun leg., genitalia slide No. SYSU0235; 1♀, Xiaoxidong, Mt. Jinggangshan, 2.VIII.2011, Li Jinwei leg.; 2♂4♀, Mt. Jiulianshan, Longnan, 24.58°N, 114.43°E, alt. 620 m, 26.IX.2016, 24.IX.2017, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU1547; 1♂, Mt. Wugongshan, Luxi, 27.48°N, 114.15°E, alt. 500 m, 23.IX.2016, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU1549; **Shaanxi:** 1♂, Yueba, Foping, 33.55°N, 107.82°E, alt. 1052 m, 1–3.VIII.2018, Liu Qingming, Xiang Lanbin leg., genitalia slide No. SYSU1543; 1♂, Longcaoping, Foping, 33.65°N, 107.97°E, alt. 1218 m, 4.VIII.2018, Liu Qingming, Xiang Lanbin leg., genitalia slide No. SYSU1544; **Yunnan:** 1♂1♀, Taiyanghe Reserve, alt. 1450 m, 15.VIII, 2.IX.2014, Zhang Zhenguo leg., genitalia slide No. ZDD12027(♂), ZDD12118(♀) (NKU); **Zhejiang:** 1♂, Mt. Tianmushan, Lin'an, 30.31°N, 119.44°E, alt. 295 m, 11.V.2012, Li Jinwei leg., genitalia slide No. CXH12193; 1♂2♀, Mt. Tianmushan, alt. 400 m, 25.VII.2011, Du Xicui leg., genitalia slide No. SYSU1529(♂).

Distribution. China (Chongqing, Guangdong, Guangxi, Guizhou, Hainan, Henan, Hubei, Hunan, Jiangxi, Shaanxi, Yunnan, Zhejiang).

Ecpyrrhorrhoe brevis Zhang & Xiang, sp. nov.

http://zoobank.org/595A86BB-2342-4A3D-89DD-701F073EEA44
Figs 16, 32, 47

Diagnosis. *Ecpyrrhorrhoe brevis* can be distinguished from *E. digitaliformis* and *E. celatalis* in the male genitalia (Fig. 32) by the much more slender protrusion of the sacculus, the much thicker and straight sella, the broader arms of the juxta without a tooth-shaped process, a long, strongly sclerotized and hook-like cornutus present on the vesica, and a series of long spines standing on a long and curved base on the anellus; in the female genitalia (Fig. 47) by anterior end of the antrum bearing a lateral protrusion.

Description (Fig. 16). **Head.** Frons yellow, with white lateral bands. Vertex pale yellow, sometimes whitish medially. Labial palpus dark yellow, contrastingly white at base ventrally. Maxillary palpus dark yellow, pale terminally. **Thorax.** Dorsal side dark yellow or yellowish brown, ventral side white. Legs white to pale yellow. **Wings.** Forewing length: 11.0–13.0 mm. Forewing with termen moderately oblique and apex somewhat pointed; bright yellow, markings yellowish brown; antemedial line arched from 1/4 of costa to 2/5 of posterior margin; orbicular stigma dot-shaped, sometimes indistinct; reniform stigma comma-shaped, slightly concave; postmedial line from 3/4 of costa, obliquely inward then arched to middle of CuA_1, slightly dentate, then bending to 1/3 of CuA_2, and finally undulated to 2/3 of posterior margin; fringe bright yellow. Hindwing bright yellow; postmedial line yellowish brown, slightly dentate and arched from 2/3 of M_1 to 1/2 of CuA_1 and bending inward along CuA_1, then undulated to 2/3 of posterior margin; fringe as in forewing. **Abdomen.** Bright yellow dorsally, black on distal end; white ventrally.

Male genitalia (Fig. 32). Uncus with basal half nearly triangular and naked. Valva curved and slowly tapering to rounded apex; sella thickly sclerotized, thumb-shaped, and densely setose; sacculus with distal 3/5 inflated into a broad protrusion bearing a slender finger-shaped process medially. Juxta with base wide, distal 4/5 bifid into stout and tapering, slightly curved and closely separated arms; anellus with a series of long spines standing on a long and curved base (attached to distal end of phallus in Fig. 32). Saccus broadly triangular. Phallus long and moderately stout, cornuti presented as a lancet-shaped sclerite connected with a hook-shaped, strong spine on apical end.

Female genitalia (Fig. 47). Anterior apophysis ~ 2× length of posterior apophysis. Antrum shortly cup-shaped, anterior end of antrum bearing a lateral thumb-shaped protrusion; colliculum very short and broad; ductus seminalis connecting to anterior end of colliculum; ductus bursae length ~ 4–5× as long as diameter of corpus bursae, basal 1/3 bearing a slim sclerite. Corpus bursae globular; rhomboid signum with maximal length > diameter of corpus bursae; second (posterior) signum with both ends round, margin bearing sparse and long spines.

Material examined. Type material. ***Holotype*** ♂, **China: Guangdong:** Heishiding, Fengkai, 5.X.2011, Tong Bo, Li Yun leg., genitalia slide No. CXH12182(♂) (SYSBM). ***Paratypes*****: China: Guangdong:** 2♂1♀, same data as holotype, genitalia slide No. SYSU0234(♂), SYSU0236(♂), CXH12213(♀, molecular voucher No. LEP0398); 1♂, Heishiding, Fengkai, 15.VI.2009, Han Xiaolei leg., genitalia slide No. SYSU1532; 1♀, Heishiding, Fengkai, 25.V.2013, Chen Xiaohua leg., genitalia slide No. SYSU1533; 1♂, Yanshuitian, Fengkai, 6.X.2011, Tong Bo leg., genitalia slide No. SYSU0253; 1♂, Mt. Danxiashan, Shaoguan, 25.04°N, 113.64°E, alt. 96 m, 6.VI.2012, Li Jinwei leg., genitalia slide No. SYSU0212, molecular voucher No. LEP0036. **Guangxi:** 1♂, Yangmeiao, Mt. Jiuwandashan, 25.19°N, 108.65°E, alt. 1183 m, 22.VII.2015, Chen Kai leg., genitalia slide No. SYSU0268.

Distribution. China (Guangdong, Guangxi).

Etymology. The specific name is derived from the Latin *brevis* (= short), referring to the short arms of juxta in the male genitalia.

***Ecpyrrhorrhoe puralis* (South, 1901)**
Figs 17, 33, 48

Pionea puralis South, 1901: 493.

Diagnosis. Forewing length: 11.0–14.0 mm. *Ecpyrrhorrhoe puralis* is almost indistinguishable from *E. longispinalis* and *E. biaculeiformis* in appearance, but can be distinguished in the male genitalia (Fig. 33) by the small and excurved sella, much larger juxta with distal 2/3 bifid, anellus with comb-shaped spines (attached to distal phallus end of in Fig. 33), and in the female genitalia (Fig. 48) by the antrum with two rounded sclerotized processes, and basal 2/3 of ductus bursae bearing a slim sclerite.

Material examined. ***Type***: 1♂, **[China: Hubei:]** Ichang, Mrs Pratt Coll., June 1888, Pyralidae Brit. Mus. Slide No. 8676 (NHMUK).

Other material examined. China: Guangdong: 2♂4♀, Heishiding, Fengkai, 5.IX, 1.V, 5.X.2011, Tong Bo, Zhang Dandan, Li Yun, Yang Lijun, Cheng Muchun, Liao Junlei leg., genitalia slide No. CXH12170(♂), CXH12216(♀); **Guangxi:** 1♂1♀, Mt. Jinzhongshan, 24.67°N, 104.88°E, alt. 957 m, 18.VII.2013, Chen Xiaohua leg., genitalia slide No. SYSU0205(♀); 4♂2♀, Yangmeiao, Mt. Jiuwandashan, 25.19°N, 108.65°E, alt. 1183 m. 22.VII.2015, Chen Kai leg., genitalia slide No. SYSU0254(♂, molecular voucher No. LEP0161), SYSU0257(♀), SYSU0258(♂, molecular voucher No. LEP0399); **Hebei:** 1♂1♀, Piancheng Forestry Station, She County, 36.44°N, 113.39°E, alt. 1109 m, 31.VII.2013, Xie Weicai, Liu Xiaolin leg., genitalia slide No. SYSU1539(♂); **Hubei:** 1♀, Wujiashan, Yingshan, 31.05°N, 115.47°E, alt. 880 m, 29.VI.2014, Chen Xiaohua, Pan Chang leg., genitalia slide No. SYSU1540; 2♂, Qingtaiguan, Luotian, 31.11°N, 115.41°E, alt. 524 m, 2.VII.2014, Liu Zhenhua, Pan Chang leg., genitalia slide No. SYSU1518(♂); **Hunan:** 1♀, Jiashui, Taoyuandong, 26.59°N, 113.99°E, alt. 420 m, 19.V.2014, Chen Xiaohua leg., genitalia slide No. SYSU0252, molecular voucher No. LEP0037; **Jiangxi:** 1♂, Daqiutian, Mt. Jiulianshan, alt. 500 m, 31.VIII.2007, Zhang Dandan leg., genitalia slide No. HFX08056; 2♂5♀, Mt. Jiulianshan, Longnan, 24.58°N, 114.43°E, alt. 620 m, 26.IX.2016, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU1546 (♂); 1♀, Mt. Jinggangshan, 2.X.2010, Chen Haidong, Xie Weicai leg., genitalia slide No. SYSU0216; **Shanxi:** 2♂, Dahe Forestry Station, Yicheng, 35.46°N, 111.93°E, alt. 1212m, 13–15. VIII.2018, Xiang Lanbin leg., genitalia slide No. SYSU1542; 2♂, Miaoping, Manghe, Yangcheng, 35.25°N, 112.46°E, alt. 557 m, 19–20.VIII.2018, Xiang Lanbin leg., genitalia slide No. SYSU1545.

Remarks. *Ecpyrrhorrhoe puralis* is mainly reported from central and southern China and Japan. Solis et al. (2010) considered it was introduced in eastern North America and spread following the invasive host *Paulownia tomentosa* (Thunb.) Steud.

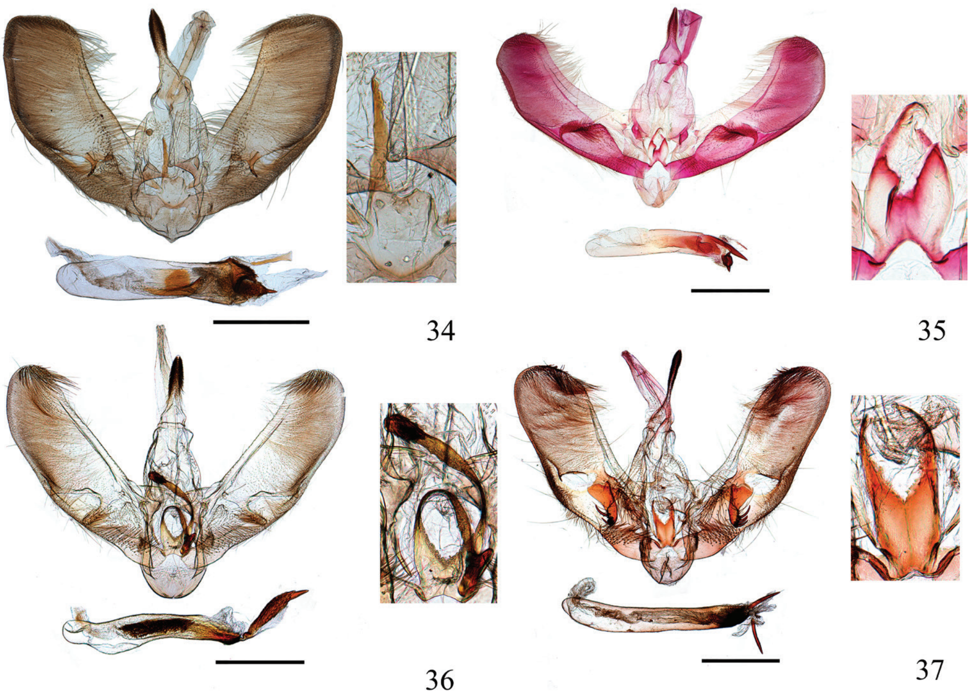
Distribution. China (Guangdong, Guangxi, Hebei, Henan, Hubei, Hunan, Jiangxi, Shandong, Shanxi), Japan, India, North America.

Ecpyrrhorrhoe rubellalis **(Snellen, 1890), comb. nov.**
Figs 18, 34, 49

Botys rubellalis Snellen, 1890: 577.
Ecpyrrhorrhoe aduncis Gao, Zhang & Wang, 2013: 312. Syn. nov.

Diagnosis. Forewing length: 11.0–14.0 mm. In appearance, *Ecpyrrhorrhoe rubellalis* resembles *E. minnehaha*, but can still be recognized by its larger forewing length, yellowish brown ground color of wings with yellow fringe, and more oblique antemedial line of forewing (Fig. 18); in the male genitalia (Fig. 34) by the broader valva with truncate tip, and the nearly spine-shaped, thin and short sella, by the phallus apically with a densely dentated, triangular projection and a thick spine bearing a broad and long, spinulose base on the anellus; in the female genitalia (Fig. 49) by the antrum without spinules and large second (posterior) signum.

Material examined. Type material. *Botys rubellalis*: ***Lectotype*** (newly designated in this study) ♂, Sikkim, ?000 feet, 1886, O. Möller [leg.], NHMUK slide No. 010315144 (NHMUK). *Ecpyrrhorrhoe aduncis*: ***Holotype*** ♂, **China: Taiwan:** Sikanshui, Taipei, 25.01° N, 121.27°E, alt. 550–600 m, 4.VIII.2006, Li Houhun leg., genitalia slide No. GQ11127 (NKU).



Figures 34–37. Male genitalia of *Ecpyrrhorrhoe* spp., with enlarged detail of juxta (right) **34** *E. rubellalis*, Hainan (genitalia slide No. SYSU0230) **35** *E. longispinalis* sp. nov., holotype, Hunan (genitalia slide No. CXH12194) **36** *E. celatalis*, Hainan (genitalia slide No. SYSU0242) **37** *E. biaculeiformis*, Fujian (genitalia slide No. SYSU0261). Scale bars: 1.0 mm.

Other material examined. **China: Guangxi:** 1♀, Hekou Station, Mt. Dayaoshan, 24.14°N, 110.09°E, alt. 823 m, 18.VII.2015, Zhao Shengnan, Qi Mujie leg. (NKU); 2♂, Lianhuashan, Mt. Dayaoshan, 24.15°N, 110.11°E, alt. 1000 m, 22.VII.2015, Zhao Shengnan, Qi Mujie leg., genitalia slide No. ZDD12046, molecular voucher No. LEP0110 (NKU); 1♂, Bainan, Napo, 23.03°N, 105.48°E, alt. 300 m, 23.VII.2013, Chen Xiaohua leg., genitalia slide No. SYSU1561; **Hainan:** 2♂1♀, Mt. Yinggeling, 19.05°N, 109.50°E, alt. 954 m, 4.IX.2013, Chen Xiaohua leg., genitalia slide No. SYSU0008 (♂), SYSU0230 (♂), SYSU0243 (♀, molecular voucher No. LEP0023); 1♂, Yingzui, Mt. Yinggeling, 23.V.2010, Du Xicui, Liao Li leg., genitalia slide No. SYSU1562; 1♂2♀, Shuiman Village, Mt. Wuzhishan, 18.88°N, 109.67°E, alt. 667 m, 6.IX.2013, Li Jinwei, Chen Xiaohua, Xie Weicai leg.; 1♂, Mt. Wuzhishan, 18.53°N, 109.39°E, alt. 742 m, 22.V.2015, Cong Peixin, Guan Wei, Hu Sha. leg. (NKU); 1♂1♀, Mt. Wuzhishan, alt. 795 m, 19, 20.V.2014, Xu Lijun, Xu Dan leg.; 1♂, Mt. Diaoluoshan, alt. 500 m, 24.V.2014, Xu Lijun, Xu Dan leg.; 1♀, Mt. Diaoluoshan, 18.43°N, 109.52°E, alt. 922 m, 26.V.2015, Cong Peixin, Guan Wei, Hu Sha. leg. (NKU); 1♀, Nankai Village, Baisha, 19.07°N, 109.42°E, alt. 294 m, 19.V.2013, Li Jinwei leg.; 1♀, Mt. Limushan, 19.18°N, 109.73°E, alt. 755 m, 2.XI.2013, Chen Kai, Chen Xiaohua leg.

Distribution. China (Guangxi, Hainan, Taiwan), India.

Remarks. Snellen (1890) described *E. rubellalis* from two specimens collected by Möller in Sikkim. One of them is here designated as the lectotype.

Ecpyrrhorrhoe longispinalis Zhang & Xiang, sp. nov.

http://zoobank.org/746AB7EC-3DED-43A3-8EDE-DBB26AB448A1

Figs 19, 35, 50

Diagnosis. *Ecpyrrhorrhoe longispinalis* can be distinguished from *E. digitaliformis* and *E. puralis* in the male genitalia (Fig. 35) by the valva gradually broadening to the subapex, a hook-shaped sella, a small, sclerotized, ball-shaped sclerite bearing two small spines on opposite sides on the anellus; in the female genitalia (Fig. 50) by the antrum without sclerotized processes or triangular, wrinkled sclerites.

Description (Fig. 19). **Head.** Frons pale yellow, with white lateral bands. Vertex pale yellow. Labial palpus dark yellow, contrastingly white at base ventrally. Maxillary palpus dark yellow, pale terminally. **Thorax.** Dorsal side dark yellow or yellowish brown, ventral side white. Legs white to pale yellow. **Wings.** Forewing length: 9.0–13.0 mm. Forewing bright yellow, termen moderately arched; antemedial line fulvous, outwardly curved from 1/4 of costa to 1/3 of posterior margin; orbicular stigma dot-shaped, small, sometimes indistinct; reniform stigma comma-shaped, concave; postmedial line from anterior 3/4 distinctively curved to middle of CuA_1, then bending to 1/3 of CuA_2, and finally undulated to 2/3 of posterior margin; terminal line and fringe bright yellow. Hindwing yellow, costal area white, postmedial line fulvous, slightly dentate curved, outward from 2/3 of M_1 to 1/2 of CuA_1, arc-shaped, then bending inward along CuA_1, reaching discocellular, then undulated to 2/3 of posterior margin; terminal line and fringe as in forewing. **Abdomen.** Pale yellow dorsally, black on distal part, white ventrally.

Male genitalia (Fig. 35). Uncus relatively thick, with basal half nearly triangular and naked. Valva curved and slowly broadening to rounded apex, with maximal width at sub-apex; sella hook-shaped with basal half densely setose; sacculus with distal 3/5 inflated into a triangular, rounded protrusion. Juxta with basal margin concave, distal half bifid into stout and pointed arms; anellus bearing a small and sclerotized ball, with two small spines on opposite sides (attached to distal end of phallus in Fig. 35). Saccus rounded triangular. Phallus long and slightly curved, cornuti presented as a long sclerite and a long and strong spine on apical end.

Female genitalia (Fig. 50). Anterior apophysis ~ 2× length of posterior apophysis. Lamella postvaginalis presented as a nearly trapezoidal sclerite. Antrum cup-shaped, strongly sclerotized, decorated with lots of small spines, those spines forming a circle, with a thumb-shaped, sclerotized process on the side of circle; colliculum narrow and moderately long; ductus seminalis connecting to anterior end of colliculum and with a short sclerite located opposite to colliculum; ductus bursae slender, length ~ 2× as long as diameter of corpus bursae, basal 1/3 bearing a slim sclerite. Corpus bursae globular; rhomboid signum with maximal length almost 1/3 as long as diameter of corpus bursae; second (posterior) signum nearly V-shaped bearing sparse and long spines.

Material examined. ***Holotype*** ♂, **China: Hunan:** Zhupo Village, Huitong, 23.VIII.2012, Li Jinwei, Chen Xiaohua leg., genitalia slide No. CXH12194 (SYSBM). ***Paratypes*:** **China: Hubei:** 1♀, Taohuachong, Mt. Dabieshan, 30.59°N, 116.19°E, alt. 661 m, 24.VI.2014, Chen Xiaohua, Pan Chang leg., genitalia slide No. SYSU1541; **Hunan:** 1♂1♀, same data as holotype, genitalia slide No. SYSU0301 (♂, molecular voucher No. LEP0401), CXH12200 (♀, molecular voucher No. LEP0058).

Distribution. China (Hubei, Hunan).

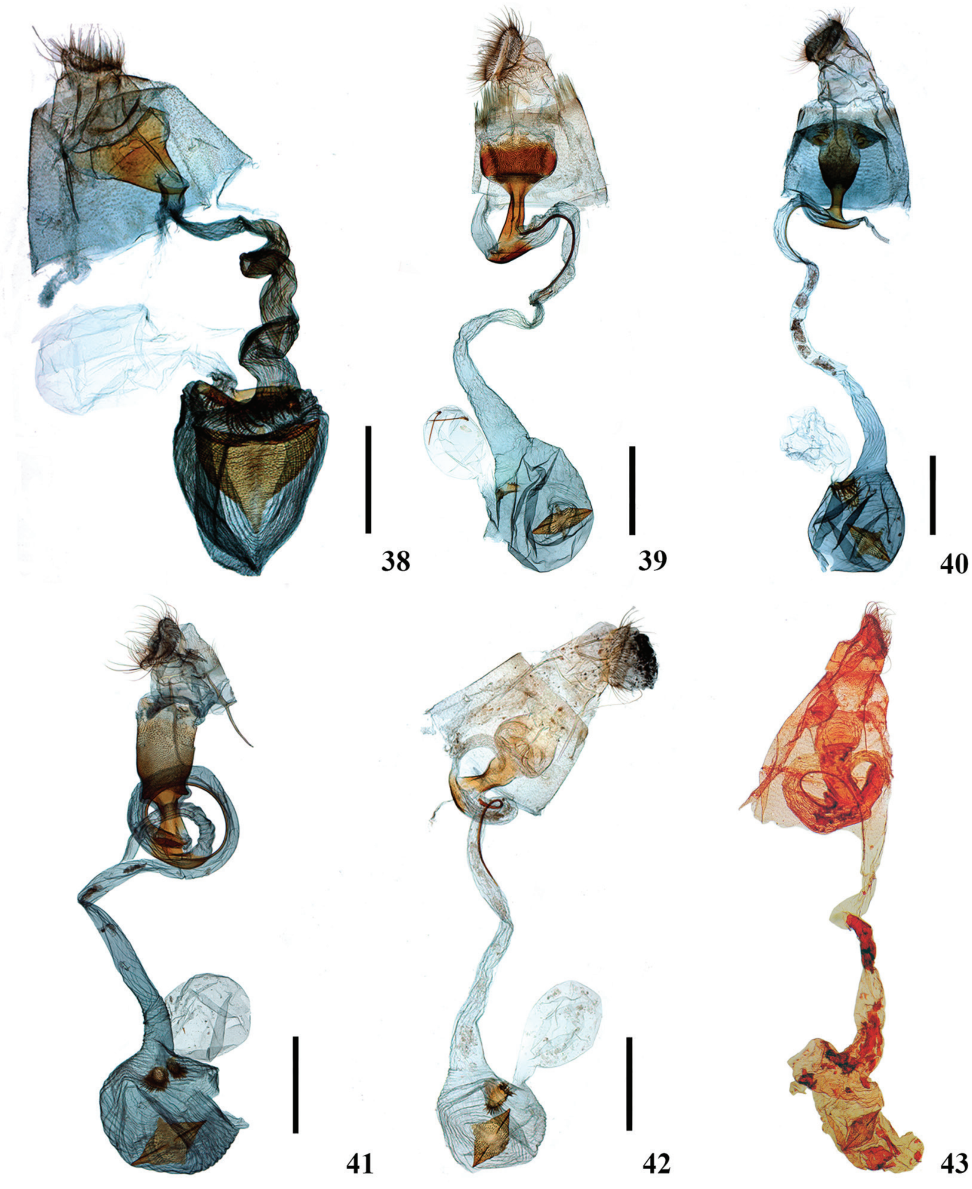
Etymology. The specific name is derived from the combination of Latin *long-* and *spinalis* (= with spine), referring to the vesica with a long and thick spine.

Ecpyrrhorrhoe celatalis **(Walker, 1859)**

Figs 20, 36, 51

Botys celatalis Walker, 1859: 657.
Botys rhoecusalis Walker, 1859: 1000.
Pyrausta retostalis E. Hering, 1901: 54–56.
Ecpyrrhorrhoe ruidispinalis Zhang, Li & Wang, 2004: 322. Syn. nov.

Diagnosis. Forewing length: 10.0–13.0 mm. *Ecpyrrhorrhoe celatalis* can be differentiated from *E. digitaliformis* and *E. brevis* in the male genitalia (Fig. 36) by the straight costa of the valva, the extremely long arms of the juxta with an apical, large, and sclerotized tooth, and the anellus with a long, thick and large spine, and decorated

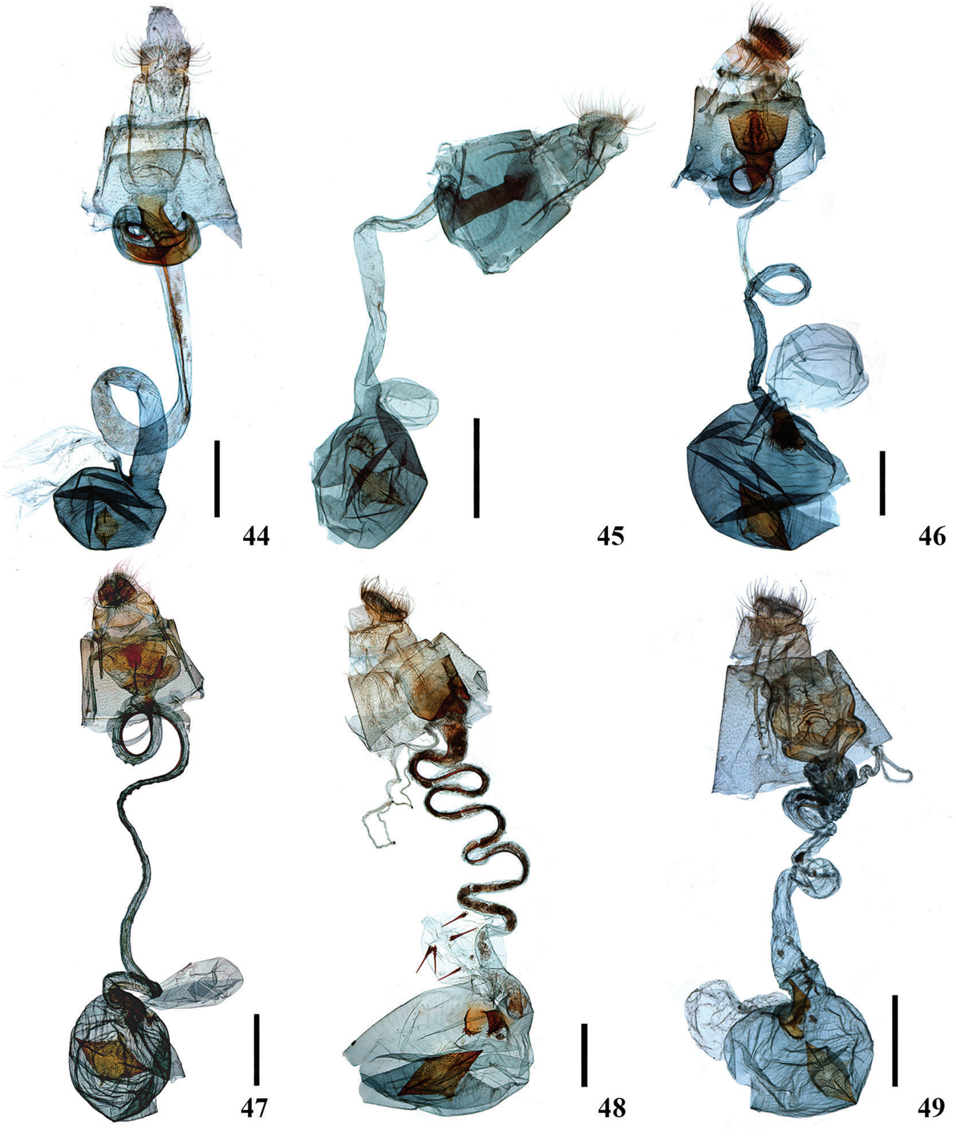


Figures 38–43. Female genitalia of *Ecpyrrhorrhoe* spp. **38** *E. damastesalis*, Hainan (genitalia slide No. SYSU0247) **39** *E. minnehaha*, Shaanxi (genitalia slide No. SYSU0272) **40** *E. obliquata*, Guangdong (genitalia slide No. SYSU0269) **41** *E. rufipicta*, Hainan (genitalia slide No. SYSU0341) **42** *E. rubiginalis*, Jiangxi (genitalia slide No. SYSU0215) **43** *E. machoeralis*, type, Ceylon (genitalia slide No. 8680 (NHMUK)). Scale bars: 1.0 mm.

with many tiny spines on its basal 3/4 (attached to distal end of phallus in Fig. 36), in the female genitalia (Fig. 51) by the posterior part of the antrum looking like a pair of triangular sclerites.

Material examined. *Botys celatalis*: ***Type***: 1♀, Ceylon, Pyralidae Brit. Mus. Slide No. 8686 (NHMUK). *Ecpyrrhorrhoe ruidispinalis*: ***Holotype*** ♂, **China: Guangxi:** Shangsi, 22.09°N, 107.58°E, alt. 770 m, 3.IV.2002, Hao Shulian, Xue Huaijun leg., genitalia slide No. ZDD02357 (NKU).

Other material examined. India: 1♂, Khasi Hills, 5.3[III].1972, S. N. A. Jacobs, Pyralidae Brit. Mus. Slide No. 010891075 (NHMUK). **China: Chongqing:** 1♀, Mt. Jinfoshan, alt. 1100 m, 4.VIII.2012, Yang Xiaofei, Liu Tengteng leg., genitalia slide No. SYSU1530 (NKU); **Fujian:** 1♂, Letu Village, Nanjing, 24.90°N, 117.22°E, alt. 270 m, 10.VII.2014, Zhang Dandan leg., genitalia slide No. SYSU0232; 1♀, Mt. Tianzhushan, 24.VII.2014, Yang Xiaofei leg., genitalia slide No. ZDD12028 (NKU); **Guangdong:** 3♂2♀, Mt. Danxiashan, Shaoguan, 25.04°N, 113.64°E, alt. 96 m, 6–7.VI.2012, Li Jinwei leg., genitalia slide No. SYSU0249(♂), SYSU0250(♀), CXH12173(♂), ZDD10072(♀); 5♀, Guangzhou, 1948, genitalia slide No. ZDD03025; 1♂, Dawuling, Xinyi, alt. 900 m, 9.VIII.2003, Zhang Dandan, Li Zhiqiang leg., genitalia slide No. ZDD03018; 1♀, Neilingding Island, Shenzhen, 5.VII.1998, Wen Ruizhen leg., genitalia slide No. ZDD03024; 1♂, Mt. Nankunshan, Huizhou, 16.VII.2003, Zhang Dandan, Li Zhiqiang leg., genitalia slide No. ZDD03022; 1♀, Bijialing, Mt. Potoushan, Zhanjiang, 4.VI.2016, Li Zhiqiang leg., genitalia slide No. SYSY0264, molecular voucher No. LEP0400; 1♂, Heishiding, Fengkai, 5.IX.2011, Yang Lijun, Cheng Muchun, Liao Junlei leg., genitalia slide No. SYSU0231(♂); 1♀, Yanshuitian, Fengkai, 3.VI.2011, Chen Haidong, Tong Bo leg., genitalia slide No. SYSU0220; 1♂, Lianping, 12.VIII.2009, Zeng Yanyi leg., genitalia slide No. SYSU1534; **Guangxi:** 6♂, Huaping National Natural Reserve, Guilin, 25.63°N, 109.91°E, alt. 520 m, 11–12.IX.2020, Jin Mengjie, Xiang Lanbin leg.; 3♂1♀, Technology Building, Huaping Natural Reserve, Guilin, 25.63°N, 109.91°E, alt. 760 m, 10–12.IX.2020, Jin Mengjie, Xiang Lanbin leg.; 5♂3♀, the lookout, Huaping Natural Reserve, Guilin, 25.61°N, 109.90°E, alt. 950 m, 10.IX.2020, Jin Mengjie, Xiang Lanbin leg.; 3♂1♀, Nonggang, Longzhou, 22.47°N, 106.96°E, alt. 271 m, 20–21.VIII.2011, 19.VI.2012, Li Jinwei, Cheng Muchun leg., genitalia slide No. SYSU0052(♂), SYSU0223(♀), CXH12191(♂); 1♀, Jinxiazhai, Mulun Natural Reserve, 22.47°N, 106.96°E, alt. 288 m, 19.VII.2015, Xu Dan Leg., genitalia slide No. SUSU0307; 1♀, Yangmeiao, Mt. Jiuwandashan, 25.19°N, 108.65°E, alt. 1183 m. 22.VII.2015, Chen Kai leg., genitalia slide No. SYSU0306, molecular voucher No. LEP0403; 1♀, Mt. Jinzhongshan, 24.67°N, 104.88°E, alt. 957 m, 18.VII.2013, Chen Xiaohua leg., genitalia slide No. SYSU1526; 1♂, Gaozhai, Mt. Maoershan, Guilin, alt. 1100 m, 27.VII.2015, Liu Kaili, Zhao Jingxia leg., genitalia slide No. SYSU1531; **Hainan:** 2♂1♀, Yinggeling Natural Reserve, 19.05°N, 109.50°E, alt. 954 m, 4.IX.2013, Xie Weicai, Chen Xiaohua leg., genitalia slide No. CXH12188(♂), SYSU0242(♂, molecular voucher No. LEP0017), SYSU1536(♀); 1♂, Bangxi Natural Reserve, 19.37°N, 109.10°E, alt. 97 m, 2.IX.2013, Xie Weicai leg., genitalia slide No. SYSU0300; 1♀, Mt. Diaoluoshan, 18.67°N, 109.93°E, alt. 94 m, 16.V.2013, Li Jinwei Leg., genitalia slide No. SUSU0305; **Hunan:** 33♂9♀, Hydro-electric power station, Yueyan Forestry farm, Dupangling National Reserve, Yongzhou, 25.48°N, 111.36°E, alt. 430 m,



Figures 44–49. Female genitalia of *Ecpyrrhorrhoe* spp. **44** *E. rosisquama* sp. nov., paratype, Yunnan (genitalia slide No. SYSU0262) **45** *E. exigistria* sp. nov., paratype, Jiangxi (genitalia slide No. SYSU0276) **46** *E. digitaliformis* (genitalia slide No. SYSU0274) **47** *E. brevis* sp. nov., paratype, Guangdong (genitalia slide No. SYSU1533) **48** *E. puralis*, Jiangxi (genitalia slide No. SYSU0216) **49** *E. rubellalis*, Hainan (genitalia slide No. SYSU0243). Scale bars: 1.0 mm.

29–30.VIII.2020, Jin Mengjie, Xiang Lanbin leg., genitalia slide No. SYSU1566 (♂), SYSU1567 (♂), SYSU1569 (♂), SYSU1570 (♂), SYSU1571 (♀), SYSU1580 (♀), SYSU1581 (♂), SYSU1582 (♂), SYSU1583 (♀), SYSU1584 (♂), SYSU1585 (♀); 1♂1♀, Northeast of Yueyan Forestry farm, Dupangling National Reserve, Yongzhou, 25.49°N, 111.39°E, alt. 350 m, 28–31.VIII.2020, Jin Mengjie, Xiang Lanbin leg.; 1♀, Mt. Shunhuangshan, Xinning, Shaoyang, 26.40°N, 111.00°E, alt. 810 m, 4–6. IX.2020, Jin Mengjie, Xiang Lanbin leg.; **Jiangxi:** 1♀, Xiaoxidong, Mt. Jinggangshan, 2.VIII.2011, Li Jingwei leg., genitalia slide No. SYSU0273; 1♂, Daqiutian, Mt. Jiulianshan, Longnan, 31.VIII.2007, alt. 500 m, Jia Fenglong leg., genitalia slide No. HFX08084; **Tibet:** 1♂1♀, Medog, 29.20°N, 95.20°E, alt. 1103 m, 8.VII.2013, Li Jinwei leg., genitalia slide No. SYSU0219 (♀), SYSU1535(♂); **Yunnan:** 2♂7♀, Baihualing Natural Reserve, Baoshan, alt. 1520 m, 11, 13.VIII.2007, Zhang Dandan leg., genitalia slide No. CXH 12178(♀), SYSU0007(♂), SYSU0037(♀), SYSU0222(♂); 1♂, Baihualing Natural Reserve, Mt. Gaoligongshan, Baoshan, 24.30°N, 98.80°E, alt. 1535 m, 20. IV.2015, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU0211; 1♀, Hanlongzhai, Baihualing, Baoshan, 25.31°, 98.80°E, alt. 1616 m, 11.V.2021, Jin Mengjie, Guo Muyu, Fu Haiyun leg., genitalia slide No. SYSU1555.

Distribution. China (Chongqing, Fujian, Guangdong, Guangxi, Hainan, Hunan, Jiangxi, Tibet, Yunnan), India, Sri Lanka.

Ecpyrrhorrhoe biaculeiformis Zhang, Li & Wang, 2004

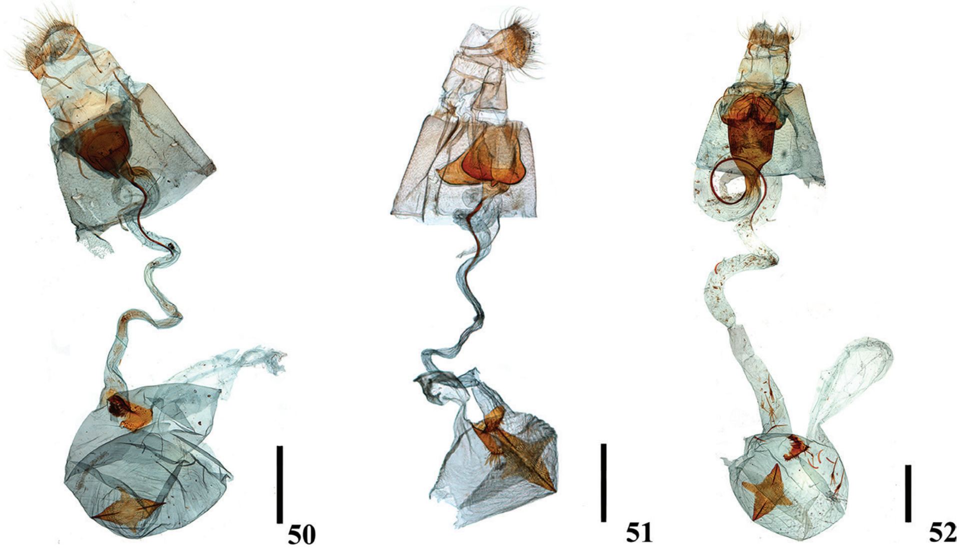
http://zoobank.org/669B6A2F-ED99-4B4B-A145-5DED918C2DFE
Figs 21, 37, 52

Ecpyrrhorrhoe biaculeiformis Zhang, Li & Wang, 2004: 317.

Diagnosis. Forewing length: 12.0–16.0 mm. *Ecpyrrhorrhoe biaculeiformis* is similar to *E. puralis* in habitus, but can be distinguished by the much larger size and much paler coloration (Fig. 21), in the male genitalia (Fig. 37) by the width of valva relatively even or slowly widening distally, a sella with the basal part bearing 4 spines on the apex and with a distal process, the narrow and short juxta with distal half bifid, the anellus with two separate spines (attached to distal end of phallus in Fig. 37); in the female genitalia (Fig. 52) by the antrum bearing a pair of nearly triangular and wrinkled sclerites at posterior margin, and the short sclerite of ductus bursae ~ 2/5 of its length.

Material examined. ***Holotype*** ♂, **China: Guizhou:** Mt. Fanjingshan, 27.55°N, 108.41°E, alt. 1300 m, 2.VIII.2001, Li Houhun, Wang Xinpu Leg., genitalia slide No. ZDD02119 (NKU).

Other material examined. China: Anhui: 2♂1♀, Tangkou, Mt. Huangshan, 30.05°N, 118.11°E, alt. 580 m, 19–20.IX.2012, Yang Lijun leg., genitalia slide No.SYSU1515(♂), CXH12205 (♀, molecular voucher No. LEP0397); **Fujian:** 1♂, Tongmu, Mt. Wuyishan, 27.75°N, 117.68°E, alt. 759 m, 19.V.2012, Li Jinwei leg., genitalia slide No. SYSU0261; **Guangdong:** 2♂1♀, Heishiding, Fengkai, 7.V, 9.X.2010, 1.V, 5.IX, 5.X.2011, Zhang Dandan, Tong Bo, Chen Haidong, Jin Zhenyu, Li Yun leg., genitalia slide No. CXH12171 (♂), CXH12184 (♂), CXH12204 (♀); 1♂, Lianping, 12.VIII.2009, Zeng Yanyi leg., genitalia slide No. CXH12202; 1♂1♀, Mt. Nankunshan, Huizhou, 16.VII.2003, Zhang Dandan, Li Zhiqiang leg., genitalia slide



Figures 50–52. Female genitalia of *Ecpyrrhorrhoe* spp. **50** *E. longispinalis* sp. nov., paratype, Hunan (genitalia slide No. CXH12200) **51** *E. celatalis*, Fujian (genitalia slide No. ZDD12028) **52** *E. biaculeiformis* (genitalia slide No. CXH12217). Scale bars: 1.0 mm.

No. ZDD03019 (♀), ZDD03020 (♂); **Guangxi:** 5♂2♀, Gaozhai Village, Xing'an, 28.VIII.2011, Zhang Dandan, Li Jinwei leg., genitalia slide No. SYSU0204(♂), CXH12168(♂); 1♂, Anjiangping Natural Reserve, 25.56°N, 109.93°E, alt. 1751 m, 10.VII.2013, Chen Xiaohua leg.; 1♀, Yinshan Natural Reserve, Jinxiu, 24.15° N, 110.21°E, alt. 1464 m, 8.VII.2013, Chen Xiaohua leg.; **Guizhou:** 1♀, Maolan Reserve, 1.IX.2011, Li Jinwei leg., genitalia slide No. CXH12199; 1♂, Taojiang, Leishan, 27.VIII.2012, Li Jinwei, Chen Xiaohua leg.; 1♂, Weng'ang, Maolan Reserve, Libo, 25.25°N, 107.90°E, alt. 814 m, 25.VII.2015, Chen Kai leg., genitalia slide No. SYSU0255; **Hubei:** 2♀, Maoping Village, Wufeng, 30.08°N, 110.40°E, alt. 1175 m, 11.IX.2012, Li Jinwei leg.; 1♂, Qingtaiguan, Luotian, 31.11°N, 115.41°E, alt. 524 m, 2.VII.2014, Liu Zhenhua, Pan Chang leg.; 1♂, Tiantangzhai, Luotian, 31.06°N, 115.44°E, alt. 570 m, 17.IX.2012, Yang Lijun leg.; 1♂, Wujiashan, Yingshan, 31.05°N, 115.47°E, alt. 880 m, 29.VI.2014, Chen Xiaohua, Pan Chang leg., genitalia slide No. SYSU0244, molecular voucher No. LEP0024; **Hunan:** 5♂4♀, Zhangjiajie Forest Park, 29.18°N, 110.26°E, alt. 625 m, 13.IV.2012, Li Jinwei, Yang Lijun leg., genitalia slide No. SYSU0012(♂); 1♂1♀, Mt. Tianzishan, Zhangjiajie, 29.23°N, 110.29°E, alt. 1096 m, 14.IX.2012, Li Jinwei, Yang Lijun leg., genitalia slide No. CXH12158(♂); 3♀, Zhupo Village, Huitong, 23.VIII.2012, Li Jinwei, Chen Xiaohua leg., genitalia slide No. CXH12201, CXH12219, SYSY0302; 2♂, Jinyinpu, Bamianshan Natural Reserve, Guidong, 25.97°N, 113.71°E, alt. 973 m, 16.VI.2015, Chen Kai leg., genitalia slide No. SYSU0240, molecular voucher No. LEP0015; 5♂1♀, Mt. Huilongshan, Zixing, 26.08°N, 113.39°E, alt. 886 m, 17.IX.2017, Chen Kai leg., genitalia slide No.

SYSU1521(♂); 1♂, Shennonggu Forest Park, Yanling, 26.52°N, 114.01°E, alt. 379 m, 17.VI.2017, Chen Kai leg., genitalia slide No. SYSU1520; **Jiangxi:** 4♂2♀, Qianmo Village, Nanfengmian Nature Reserve, Suichuan, 26.28°N, 114.06°E, alt. 816 m, 19.VI.2015, Chen Kai leg.; 3♂, Qianmo Village, Nanfengmian Nature Reserve, Suichuan, 26.29°N, 114.06°E, alt. 820 m, 19.IX.2017, Chen Kai leg.; 2♂1♀, Mt. Guanggushan, Wuzhifeng, Shangyou, 25.92°N, 114.05°E, alt. 846 m, 22.VI.2015, Chen Kai leg., genitalia slide No. SYSU0203(♂); 4♂1♀, Mt. Guanggushan, Shangyou, 25.92°N, 114.05°E, alt. 183 m, 20.IX.2016, Chen Kai, Duan Yongjiang leg.; 1♂, Zaodu Village, Nanshan, 29.01°N, 115.16°E, alt. 315 m, 19.VII.2014, Chen Kai leg.; 1♂, Guanyinyan, Jing'an, 29.03°N, 115.25°E, alt. 195 m, 20.VII.2014, Chen Kai leg.; 9♂, Daqishan Forestry Station, Jing'an, 28.67°N, 115.07°E, alt. 350 m, 16.VII.2014, Chen Kai leg., genitalia slide No. SYSU0256; 6♂, Xiaoxidong, Mt. Jinggangshan, 1–2.VII.2011, Xie Weicai leg., genitalia slide No. CXH12203, CXH12207, CXH12210; 4♂4♀, Zhufeng, Mt. Jinggangshan, 28.IV, 30.VI, 3.VIII, 1.IX.2011, Li Jinwei, Mei Yan, Liu Ping, Cheng Muchun leg., genitalia slide No. CXH12208(♀), CXH12215(♀); 2♀, Luofu, Mt. Jinggangshan, 27.IV, 3, 30.VIII.2011, Li Jinwei, Cheng Muchun leg., genitalia slide No. CXH12217; 1♂, Luofu, Mt. Jinggangshan, 18.IX.2010, Zhang Dandan, Zhao Shuang, Tong Bo leg., genitalia slide No. CXH12206; 1♂3♀, Mt. Jiulianshan, Longnan, 24.58°N, 114.43°E, alt. 620 m, 26.IX.2016, 24.IX.2017, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU1525(♂), SYSU1548(♀); 2♂, Guanshan National Natural Reserve, Yifeng, 28.55°N, 114.58°E, alt. 394 m, 14.VI.2016, Chen Kai, Duan Yongjiang leg., genitalia slide No. SYSU1519(♂); 1♀, Shixi Village, Fengxin, 28.44°N, 114.54°E, alt. 506 m, 22.IX.2012, Li Jinwei leg; **Shaanxi:** 1♂, Huoditang Forestry Station, Ningshan, 33.43°N, 108.45°E, alt. 1497 m, 29–31.VII.2018, Liu Qingming, Xiang Lanbin leg., genitalia slide No. SYSU1516; 2♀, Yueba, Foping, 33.55°N, 107.82°E, alt. 1052 m, 1–3.VIII.2018, Liu Qingming, Xiang Lanbin leg., genitalia slide No. SYSU1517; **Sichuan:** 8♂4♀, Xixi Village, Huagaoxi, alt. 1181 m, 10–13.IX.2014, Xu Dan, Wei Xuli leg., genitalia slide No. SYSU0303(♂), SYSU1523(♂); 1♂, Reserve Station of Huagaoxi, alt. 621 m, 5.IX.2014, Xu Dan, Wei Xuli leg., genitalia slide No. SYSU1524(♂); 2♂, Guandou Village, Huagaoxi, alt. 763 m, 30.VIII, 2.IX.2014, Xu Lijun, Xu Dan, Wei Xuli leg.; 1♂, Dahonghai, Mt. Simianshan, alt. 1120 m, 17.VII.2010, Du Xicui, Song Lifang leg.; **Zhejiang:** 1♂, Mt. Tianmushan, Lin'an, 30.31°N, 119.44°E, alt. 295 m, 11.V.2012, Li Jinwei leg., genitalia slide No. SYSU0097.

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Shaanxi, Sichuan, Zhejiang).

Discussion

Based on the results of the phylogenetic analysis and the presence of specialized sclerotized structures on the anellus, *Paliga* is here treated as a new synonym of *Ecpyrrhorrhoe*. Based on the examination of type material, seven species of *Paliga*, *P. auratalis* (Warren, 1895), *P. damastesalis* (Walker, 1859), *P. machoeralis* (Walker, 1859), *P. minnehaha* (Pryer, 1877), *P. rubicundalis* Warren, 1896, *P. rufipicta* (Butler, 1880) and *P. schenklingi* Strand, 1918 are confirmed to belong in *Ecpyrrhorrhoe*. In the case of *P. anpingialis* Strand, 1918, the female genitalia of the holotype (♀, Anping, Formosa, IV.1912, H. Sauter Coll., Gen. präp. Gaedike NR: 9668 (SDEI)) does not have the diagnostic characters of *Ecpyrrhorrhoe* (absence of lamella antevaginalis, longitudinal stripe on ductus bursae, and second (posterior) signum) and is not congeneric with *Ecpyrrhorrhoe*, but its correct placement is unclear due to the lack of male material. The abdomens of the types of *P. leucanalis* Swinhoe, 1890 and *P. suavalis* (Walker, 1866) are lost. The genitalia slide of the type of *P. fuscicostalis* Swinhoe, 1894 is incorrect and may have been confused with that of Pyralidae Brit. Mus. Slide No. 8683, which is labelled with “incorrect abdomen? See 8683 for correct abdomen”. The types of *P. quadrigalis* (Hering, 1901) and *P. ignealis* (Hampson, 1899) were not examined. Therefore, these six species are transferred to *Ecpyrrhorrhoe* temporarily, with their generic placement unconfirmed. Further study is needed to confirm their generic placement.

Also, based on our phylogenetic results and study of genitalic characters, another three species, *Anania fimbriata* (Moore, 1886), *Anania obliquata* (Moore, 1888) and *Pyrausta rubellalis* (Snellen, 1890) are placed in *Ecpyrrhorrhoe*.

The genus *Yezobotys* Munroe & Mutuura, 1969 differs significantly in structure from *Ecpyrrhorrhoe*, and is more closely related to *Anamalaia* Munroe & Mutuura, 1969, based on examination the paratype material of *Yezobotys ainualis* Munroe & Mutuura, 1969 (Pyralidae Brit. Mus. Slide No. 19693 (NHMUK)). The generic characters of *Yezobotys*, the short and triangular uncus, the sacculus with finger-shaped process in male genitalia, and the strongly sclerotized lamella antevaginalis and postvaginalis in female genitalia, are extremely similar to those of *Anamalaia* Munroe & Mutuura. Thus, *Yezobotys* is restored as a valid genus.

According to the tree topology (Fig. 1), the results of the phylogenetic analyses robustly support the monophyly of *Ecpyrrhorrhoe* in BI, but there is low support in ML (PP = 0.99, BS = 63) possibly caused by the missing data in the concatenated dataset. The genus *Pagyda* is the sister group of *Ecpyrrhorrhoe* (PP = 0.99, BS = 67), and *Ecpyrrhorrhoe* can be divided into three species groups (A clade, B clade and C clade), the B clade and C clade forming a sister group (PP = 1, BS = 49). The A clade (PP = 0.99, BS = 36), consisting of *E. allochroa* + *E. damastesalis*, can be distinguished from species in B clade and C clade by the following morphological characters: hindwing yellowish white without any lines or spot, instead of the brown postmedial line present on B clade and C clade; bifid arms of juxta short in male genitalia, ductus bursae without a slender, sclerotized, longitudinal sclerite in female genitalia. The B clade (PP = 0.95, BS = 29), consisting of seven species, can be differentiated by the transverse sclerite on the bottom of ductus seminalis in female genitalia. *E. machoeralis*, without molecular data and phylogenetic analysis, is assigned to B clade on the basis of morphological characters. The C clade (PP = 0.96, BS = 71), consisting of seven species, can be distinguished from species in A clade by a sclerotized and longitudinal stripe on ductus bursae in female genitalia, and distinguished from species in B clade by the absence of transverse sclerite on the base of ductus seminalis.

In this study, bootstrap values of the majority of the basal nodes are relatively low. Future research might utilize a broader sampling per species, fresher material more suitable for DNA studies, and additional genetic data to shed further light onto the phylogenetic relationships of this species complex.

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Supplementary material 1

Table S1

Authors: Lanbin Xiang, Kai Chen, Xiaohua Chen, Yongjiang Duan, Dandan Zhang

Data type: Table

Explanation note: Pairwise distance of the COI barcoding region based on Kimura-2-parameter model.

Link: https://doi.org/10.3897/zookeys.1090.78442.suppl1

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Description of immature stages of *Gymnetron* species (Coleoptera, Curculionidae, Curculioninae), with particular emphasis on the diagnostic morphological characters at the generic and specific levels

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Abstract

The immature stages of the following five Palaearctic *Gymnetron* species are described for the first time: *G. tibiellum* Desbrochers des Loges, 1900, *G. veronicae* (Germar, 1821), *G. rotundicolle* Gyllenhal, 1838, *G. melanarium* (Germar, 1821), and *G. villosulum* Gyllenhal, 1838. These species belong to four different groups previously established according to a phylogenetic analysis: the first two belong to the *G. veronicae* group and the other three to groups respectively bearing their name (*G. rotundicolle*, *G. melanarium*, and *G. villosulum* groups). All these species exhibit several diagnostic characters distinguishing them from each other. Some characters that can be used to separate *Gymnetron* from other genera in the tribe are also suggested. Three highly significant characters for the larvae and three for the pupae were identified. For the larvae they are: (1) labial palpi with single palpomeres, (2) all spiracles unicameral, and (3) epipharynx with a single pair of *mes* or none at all. For the pupae they are: (1) the pronotum with prominent pronotal protuberances, (2) abdominal segment VIII with a conical abdominal protuberance dorsally, and (3) very short or even reduced urogomphi. The species studied here are compared with those *Gymnetron* species already known and with other genera in the tribe Mecinini. Keys to the larvae and pupae described here are provided. All the characters used for identification are illustrated by photographs or drawings.

Keywords
Biology, mature larva, Mecinini, morphology, pupa, taxonomy, weevils

Introduction

The genus *Gymnetron* Schoenherr, 1825 belongs to the tribe Mecinini (Curculionidae, Curculioninae) and includes some 35 Palaearctic species (Caldara 2008a; Alonso-Zarazaga et al. 2017) and 70 Afrotropical species (Caldara 2003). The adults of this tribe were recently subjected to morphological revision and phylogenetic analysis (Caldara 2003, 2008a). Based on this analysis, nine Palaearctic species groups and 13 Afrotropical species groups were recognized. Within this tribe the genus *Gymnetron* seems more closely related to *Rhinusa* Stephens, 1829 than to other genera (Caldara 2001). Preliminary molecular studies appear to confirm this placement (Hernández-Vera et al. 2013; I. Toševski unpublished data).

The Palaearctic *Gymnetron* species live on *Veronica* (Caldara 2008a), currently included in Plantaginaceae (Olmstead et al. 2001; Albach et al. 2004), whereas those in the Afrotropical region (Caldara 2003; Caldara et al. 2010), where Plantaginaceae are poorly represented, appear to live on various genera of Scrophulariaceae distributed mainly in the southern hemisphere, i.e., *Diascia*, *Hemimeris* and *Nemesia* (Hemimerideae), *Hebenstreitia*, *Selago*, *Sutera* and *Tetraselago* (Selagineae), *Buddleja* (Buddlejeae), as well as on Stilbaceae, i.e., *Anastrebe*, a plant genus previously placed within Scrophulariaceae (Olmstead et al. 2001; APG 2016). The larvae develop inside the ovaries, stems or roots of the host plants and can sometimes induce the formation of galls (Hoffmann 1958; Caldara 2001).

To date, larvae and pupae of only three species of *Gymnetron* (*G. auliense* Reitter, 1907, *G. miyoshii* Miyoshi, 1922, and *G. vittipenne* Marseul, 1876) have been adequately described (Jiang and Zhang 2015). Immatures of some other *Gymnetron* species – *G. anagallis* Marshall, 1933 (Gardner 1934; van Emden 1938); *G. beccabungae* (Linnaeus, 1760) and *G. villosulum* Gyllenhal, 1838 (van Emden 1938; Scherf 1964) – have been previously studied, but no detailed descriptions are available.

Therefore, the aims of the present study are to describe larvae and pupae of five *Gymnetron* species in detail for the first time, to find characters that are diagnostic at the generic and specific levels, and finally, to compare the characters of the immature stages of this genus with other genera of the same tribe that might be phylogenetically informative.

Materials and methods

The material for this study, i.e., L3 larvae and pupae from each of the species studied was collected from their host plants together with the adult, and subsequently preserved in 2 ml screw-cap micro tubes (Sarstedt, Germany) filled with 96% ethanol at 4–6 °C. The insect taxa were identified by Roberto Caldara, those of the plants by Ivo Toševski.

Part of the larval and pupal material was preserved in glycol or Pampel fixation liquid (see Skuhrovec and Bogusch 2016) and used for the morphological descriptions. These specimens are now deposited in the Group Function of Invertebrate and Plant Biodiversity in Agro-ecosystems of the Crop Research Institute (Prague, Czech Republic). Slide preparation basically followed May (1994). The larvae selected for study under the microscope were cleared in 10% potassium hydroxide (KOH), then rinsed in distilled water and dissected. After clearing, the head, mouthparts and body (thoracic and abdominal segments) were separated and mounted on permanent microscope slides in Faure-Berlese fluid (50 g gum arabic and 45 g chloral hydrate dissolved in 80 g of distilled water and 60 cm^3 of glycerol) (Hille Ris Lambers 1950).

All the specimens described were fixed in 95% ethanol and examined under an optical stereomicroscope (Olympus SZ 60 and Nikon Eclipse 80i) with calibrated oculars. The following measurements of larval instars were made: body length (BL), body width (BW) (at the third abdominal segment) and width of the head capsule (HW) (see Gosik et al. 2016). The pupal measurements included body length (BL), body width (BW) (at the level of the mid legs), head width (HW) (at the level of the eyes), length of rostrum (RL) and width of pronotum (PW). All the measurements are given in Table 1 (mature larva) and Table 2 (pupa).

Table 1. Measurements (in mm) of body parts (mature larva) in the *Gymnetron* species studied here; ^{n} = number of specimens.

Species	Body length	Body width	Head width
G. melanarium	2.33^{2}, 3.00^{1}, 2.66^{1}	0.76^{1}, 1.00^{3}	0.50^{2}, 0.53^{2}
G. rotundicolle	2.20^{13}, 2.25^{12}, 2.33^{5}, 2.26^{7}	0.75^{28}, 0.86^{9}	0.40^{14}, 0.47^{13}, 0.50^{14}
G. tibiellum	2.25^{1}, 2.37^{4}, 2.50^{4}	0.87^{6}, 0.95^{3}	0.42^{7}, 0.45^{2}
G. veronicae	2.16^{1}, 2.56^{1}, 2.83^{1}, 3.00^{1}	0.76^{1}, 1.00^{3}	0.50^{2}, 0.53^{2}
G. villosulum	2.25^{1}, 2.33^{2}, 2.46^{1}	0.83^{2}, 1.10^{2}	0.40^{1}, 0.51^{3}

Table 2. Measurements (in mm) of body parts (pupa) in the *Gymnetron* species studied here; ^{n} = number of specimens; BL = body length; BW = body width; THW = head width.

Species	Female			Male		
	BL	BW	THW	BL	BW	THW
G. melanarium	2.12^{2}, 2.32^{1}	1.25^{3}	0.75^{3}	2.25^{1}	1.32^{1}	0.82^{1}
G. rotundicolle	2.37^{1}, 2.62^{3}	1.32^{3}, 1.42^{1}	0.75^{3}, 0.85^{1}	2.20^{2}, 2.22^{1}	1.12^{2}, 1.32^{1}	0.70^{3}
G. tibiellum	1.87^{1}, 2.25^{1}, 2.50^{1}	0.62^{3}, 0.75^{1}	0.75^{1}, 1.12^{3}	1.92^{1}, 2.07^{3}	0.92^{1}, 1.1^{2}, 1.25^{1}	0.67^{1}, 1.00^{3}
G. veronicae	2.12^{2}, 2.32^{1}	1.25^{3}	0.70^{1}, 0.75^{2}	2.25^{1}	1.32^{1}	0.80^{1}
G. villosulum	2.24^{3}, 2.50^{5}, 2.73^{3}	1.30^{2}, 1.35^{4}, 1.50^{3}, 1.55^{2}	0.82^{4}, 0.87^{4}, 0.88^{3}	2.24^{1}, 2.40^{3}, 2.60^{2}	1.32^{2}, 1.35^{4}	0.82^{3}, 0.87^{3}

The drawings and outlines were made using a drawing tube (MNR–1) installed on a stereomicroscope (Amplival) and processed by computer software (Corel Photo-Paint X7, Corel Draw X7). The thoracic spiracle was located on the prothorax near the boundary of the prothorax and mesothorax, as shown in the drawing, but this spiracle is of mesothoracic origin (Marvaldi et al. 2002; Marvaldi 2003). The drawings show the thoracic and abdominal spiracles. The lengths of all setae are visible in the figures. The numbers of setae of the bilateral structures are given for one side.

The terms and abbreviations for the setae of the mature larvae and pupae are as in Scherf (1964), May (1977, 1994) and Marvaldi (1997, 1999), but see also Skuhrovec (2007). The antennae terminology follows Zacharuk (1985).

The sequence of the species follows that proposed by Caldara and Fogato (2013) and Caldara et al. (2013).

The botanical taxonomy follows APG IV (APG 2016).

Results

Morphology of immature stages

Genus *Gymnetron* Schoenherr, 1825

Description of mature larva (L3). ***Measurements*** (in mm). Body length: 2.16–3.00. The widest point in the body (meso- and metathorax) measures up to 1.20. Head width: 0.36–0.53.

General. Body elongate or relatively elongate, slender, weakly curved, rounded in cross section.

Colouration. Pale yellow or dark brown head. All thoracic and abdominal segments white, cuticle smooth or with many reddish or brown asperities.

Vestiture. Setae on body thin, distinctly different in length (minute to very short or long).

Head capsule. Head almost oval or suboval, endocarinal line present. Frontal sutures on head distinct, extended to antennae. One stemma, in the form of a pigmented spot with convex cornea, both located on each side anterolaterally, above frontal suture. Dorsum of epicranium with three or five setae; des_1 located in central part of epicranium; des_2 lateral, sometimes absent; des_3 located anteriorly on epicranium close to frontal suture; des_4 often medially, sometimes absent; des_5 located anterolaterally. Frons with three to four *fs*, fs_1 absent, fs_2 located medially, fs_3 sometimes absent, fs_4 and fs_5 subequal. Head with two *les*, one or two *ves*, and two to six *pes*.

Antennae located at end of frontal suture on each side, membranous and distinctly convex basal article bearing one conical sensorium, relatively long.

Clypeus trapezium-shaped, ~ 3–4× as wide as long with two relatively long *cls*, located posterolaterally.

Mouth parts. Labrum ~ 3–4× as wide as long, with three piliform *lms*, relatively long; anterior margin doubly sinuate. Epipharynx with two or three long digitate *als*; with two or three *ams*, and one or without *mes*; labral rods indistinct. Mandibles distinctly broad, bifid, teeth of unequal height; slightly truncate; both *mds* relatively long, piliform, located in distinct holes. Maxilla: stipes with one *stps*, two *pfs* and sensillum, with or without *mbs*; mala with four or five elongated digitate *dms*; three or four *vms*, of various length; all *vms* distinctly shorter than *dms*. Maxillary palpi with two palpomeres; basal palpomere with one *mxps* and one sensillum; distal palpomere with one sensillum and a group of conical, cuticular apical processes. Praelabium oval, with one *prms*; ligula with two *ligs*. Labial palpi with one palpomere; palpomere with one sensillum and short, cuticular apical processes. Postlabium with two or three *pms*, all located laterally; membranous area finely or distinctly asperate.

Thorax. Prothorax distinctly smaller than meso- and metathorax. Spiracle unicameral, situated between pro- and mesothorax (see Material and methods). Prothorax with seven to eleven *prns*; two *ps*; and two *eus*. Mesothorax with or without two *prs*; two or three *pds*; one long *as*; two or three *ss*; one *eps*; one *ps*; and one or two *eus*. Each pedal area of thoracic segments well separated, with three or five *pda*.

Abdomen. Abdominal segments I–III of almost equal length, next abdominal segments shortening gradually to the terminal parts of the body. Abdominal segment X reduced to four anal lobes of unequal size, the lateral lobes being distinctly the largest, and the dorsal and ventral ones very small. Anus located terminally; ambulatory ampullae bilobate to circular. Spiracles unicameral, seven abdominal spiracles located laterally. Abdominal segments I–VI with one or two *prs*; one or two *pds*; two *ss*; one *eps*; one or two *ps*; one *lsts* and one or two *eus*. Abdominal segments VII–VIII without, one or two *prs*; one or two *pds*; one or two *ss*; one *eps*; one or two *ps*; without or one *lsts*; and one or two *eus*. Abdominal segment IX with one or two *ds*; one or two *ps*; and one or two *sts*. Abdominal segment X with one or two setae (*ts*).

Description of pupa. ***Measurements*** (in mm). Body length: 1.87–2.73. Body width: 0.62–1.55. Thorax width: 0.67–1.12.

Body. Moderately stout, yellowish or brownish. Pronotal protuberances (p-pr) sclerotized, prominent, body covered with fine, knobby asperities; fused at base or well separated. Rostrum rather or moderately slender, ~ 4× as long as wide, extending to mesocoxae. Antennae rather short, clava smooth. Pronotum 1.5–2.2× as wide as long. Mesonotum slightly or sometimes distinctly smaller than metanotum. Abdominal segments I–V of equal length; segments VI–VIII tapering gradually to the terminal part of the body, segment IX distinctly reduced. Spiracles on abdominal segments I–V functional. Urogomphi reduced or short. Abdominal segment VIII with well visible conical abdominal protuberance dorsally (a-pr), extending the outline of the body.

Chaetotaxy. Sparse, setae of different lengths, transparent. Head with one or two *os*. Rostrum with or without one *rs*. Pronotum with one or two *as*, one or two *ds*, with two or without *sls*, one or three *ls* and three or four *pls*. Dorsal parts of meso- and metathorax with two or three setae. Apex of femora with one or two *fes*. Abdominal segments I–VIII with two or five setae dorsally. Each lateral part of abdominal segments I–VIII with one or two setae. Ventral parts of abdominal segments I–VIII with two or three setae. Abdominal segment IX with two setae ventrally.

Descriptions of immature stages of the species

Gymnetron tibiellum Desbrochers des Loges, 1900

Material examined. Serbia, Bela Palanka, 43°13.150'N, 22°18.886'E, 288 m, ex *Veronica anagallis-aquatica*, 29.06.2020, leg. Toševski (9 larvae and 9 pupae).

Description of mature larva (Figs 1A, B, 2A–F, 3A–C). ***Measurements*** (in mm). Body length: 2.25–2.50. The widest point in the body (meso- and metathorax) measures up to 0.95. Head width: 0.42–0.45.

General. Body elongate, slender, weakly curved, rounded in cross section (Fig. 1A).

Colouration. Head pale brown (Fig. 1B). All thoracic and abdominal segments white, cuticle smooth (Fig. 1A).

Vestiture. Setae on body thin, yellowish, distinctly different in length (minute to very short or long).

Head capsule (Figs 1B, 2A). Head suboval, endocarinal line present, extending for 2/3 of length of frons. Frontal sutures on head very broad and distinct. Stemma, in the form of a very small pigmented spot with convex cornea. Des_1 long, located in middle of central part of epicranium; des_2 medium; des_3 long, located anteriorly on epicranium close to border with frontal suture; des_4 short; des_5 long, located anterolaterally above stemma (Fig. 2A). Fs_1 absent; fs_2 short, located medially; fs_3 short; fs_4 short, located anteriorly; and fs_5 long, located anterolaterally, close to antenna (Fig. 2A). Les_1 and les_2 as long as des_5; one short *ves*. Epicranial area with six postepicranial setae.

Antennae membranous and distinctly convex basal membranous article bearing one relatively long conical sensorium and three sensilla of different types: two basiconical and one ampullaceum (Fig. 2B).

Clypeus (Fig. 2C) ~ 3× as wide as long with two medium *cls*, located posterolaterally, without sensillum; fused to labrum.

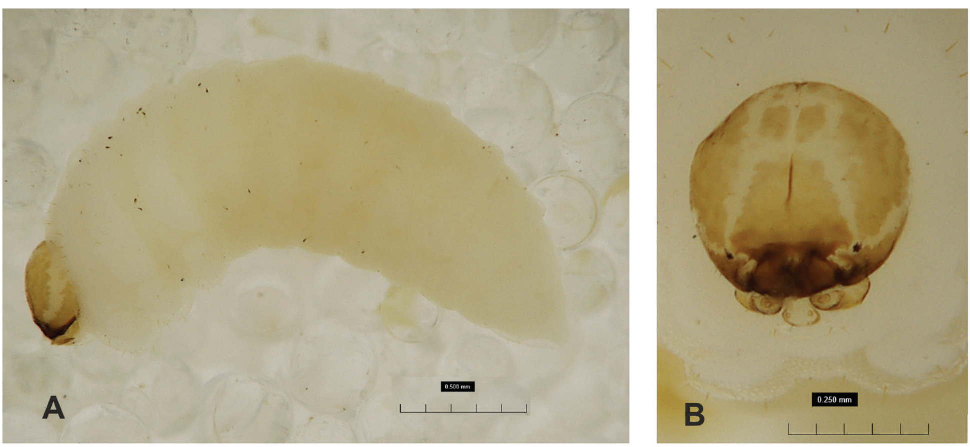

Figure 1. *Gymnetron tibiellum* Desbrochers des Loges mature larva **A** habitus **B** head, dorsal view. Scale bars: 0.5 mm (**A**); 0.25 mm (**B**).

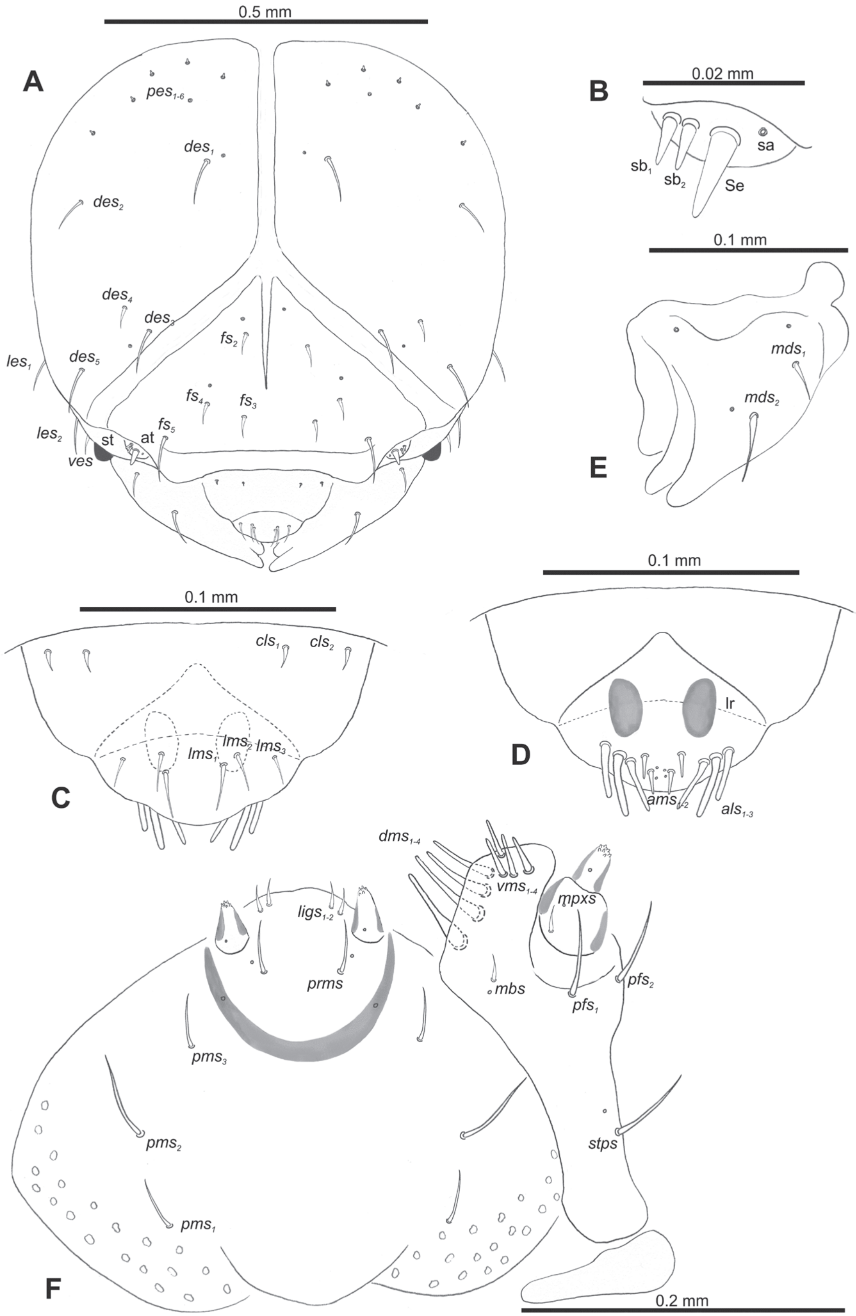

Figure 2. *Gymnetron tibiellum* Desbrochers des Loges mature larva, head and mouth parts **A** head **B** antenna **C** clypeus and labrum **D** epipharynx **E** left mandible **F** maxillolabial complex. Abbreviations: at – antenna, lr – labral rods, sa – sensillum ampullaceum, sb – sensillum basiconicum, Se – sensorium, st – stemma; setae: *als* – anteriolateral, *ams* – anteromedial, *cls* – clypeal, *des* – dorsal epicranial, *dms* – dorsal malar, *fs* – frontal epicranial, *les* – lateral epicranial, *ligs* – ligular, *lms* – labral, *mbs* – basioventral, *mds* – mandibular dorsal, *mpxs* – maxillary palps, *pes* – postepicranial, *pfs* – palpiferal, *pms* – postmental, *prms* – premental, *stps* – stipital, *ves* – ventral, *vms* – ventral malar.

Mouth parts. Labrum (Fig. 2C) ~ 2× as wide as long, with three piliform *lms*, relatively long, of almost equal length; lms_1 located anteromedially, lms_2 located partly close to clypeus, and lms_3 located anterolaterally. Epipharynx (Fig. 2D) with three very long digitate *als*, almost identical in length; with two piliform, medium *ams*; without *mes*; labral rods indistinct, irregular in shape. Mandibles (Fig. 2E) with two relatively long, piliform *mds*, located in distinct holes. Maxilla (Fig. 2F): stipes with one *stps*, two *pfs* and with one *mbs* and one sensillum, *stps* and both $pfs_{1–2}$ relatively long; mala with four elongate, digitate *dms*; four *vms*, almost equal in length. Maxillary palpi with two palpomeres; length ratio of basal and distal palpomeres: 1:0.6. Praelabium (Fig. 2F) oval, with one long *prms*; ligula with sinuate margin and two short *ligs*; premental sclerite broad, well visible. Postlabium (Fig. 2F) with three *pms*, medium pms_1 located medially, elongated pms_2 located laterally, and medium pms_3 located anterolaterally; membranous area sparsely and finely asperate.

Thorax. Prothorax (Fig. 3A) with 11 long and one short to minute *prns*, small pigmented dorsal sclerite present with five long and one short *prns*, this sclerite subdivided into two triangular plates medially; two long *ps*; and two short to very short *eus*. Mesothorax (Fig. 3A) without *prs*, two long and one short *pds*; one long *as*; two long and one very short to minute *ss*; one long *eps*; one long *ps*; and two short *eus*. Chaetotaxy of metathorax (Fig. 3A) almost identical to that of mesothorax. Each pedal area of thoracic segments well separated, with three long and two short *pda*.

Abdomen. Spiracles on abdominal segments I–VI close to anterior margin, functional, spiracles on abdominal segment VII not functional. Abdominal segments I–VII (Fig. 3B, C) with two minute *prs*; two long *pds*; one long and one very short to minute *ss*; one short *eps*; one short *ps*; one short *lsts*; and two very short and sometimes one additional minute *eus*. Abdominal segment VIII (Fig. 3C) with two minute *prs*; two long *pds*; one very short to minute *ss*; one short *eps*; one short *ps*; one short *lsts*; and two very short and sometimes one additional minute *eus*. Abdominal segment IX (Fig. 3C) with two short *ds*; two short *ps*; and two very short *sts*. Abdominal segment X (Fig. 3C) with two minute setae (*ts*).

Description of pupa (Figs 4A–C, 5A–C). ***Measurements*** (in mm). Body length: 1.87–2.50. Body width: 0.62–1.25. Thorax width: 0.67–1.12.

Body. Brownish, pronotal protuberances (p-pr) sclerotized, covered with conical asperities; apical parts of femora, head, rostrum and pronotum darker than rest of body. Rostrum moderately slender. Pronotal protuberances fused at base. Pronotum 1.5× as wide as long. Mesonotum slightly smaller than metanotum. Urogomphi in form of minute sclerotized protuberances, almost invisible. Abdominal segment VIII dorsally with rounded, prominent abdominal protuberance (a-pr) (Fig. 5A–C).

Chaetotaxy. Sparse, setae short to medium, transparent. Head with one medium *os*. Rostrum without setae (Fig. 5B). Pronotum with one *as*, one *ds*, two *sls*, one *ls* and three *pls* almost equal in length. Dorsal parts of meso- and metathorax with two setae of various length, placed medially. Apex of pro- and mesofemora with two medium-sized *fes*, metafemora with one seta (Fig. 5A–C). Abdominal segments I–VIII with three short setae of equal length dorsally: first placed medially, the next two more laterally. Each lateral part of abdominal segments I–VIII with single, medium-sized seta. Ventral parts of abdominal segments I–VIII with three medium-sized setae. Abdominal segment IX with two minute setae ventrally (Fig. 5A–C).

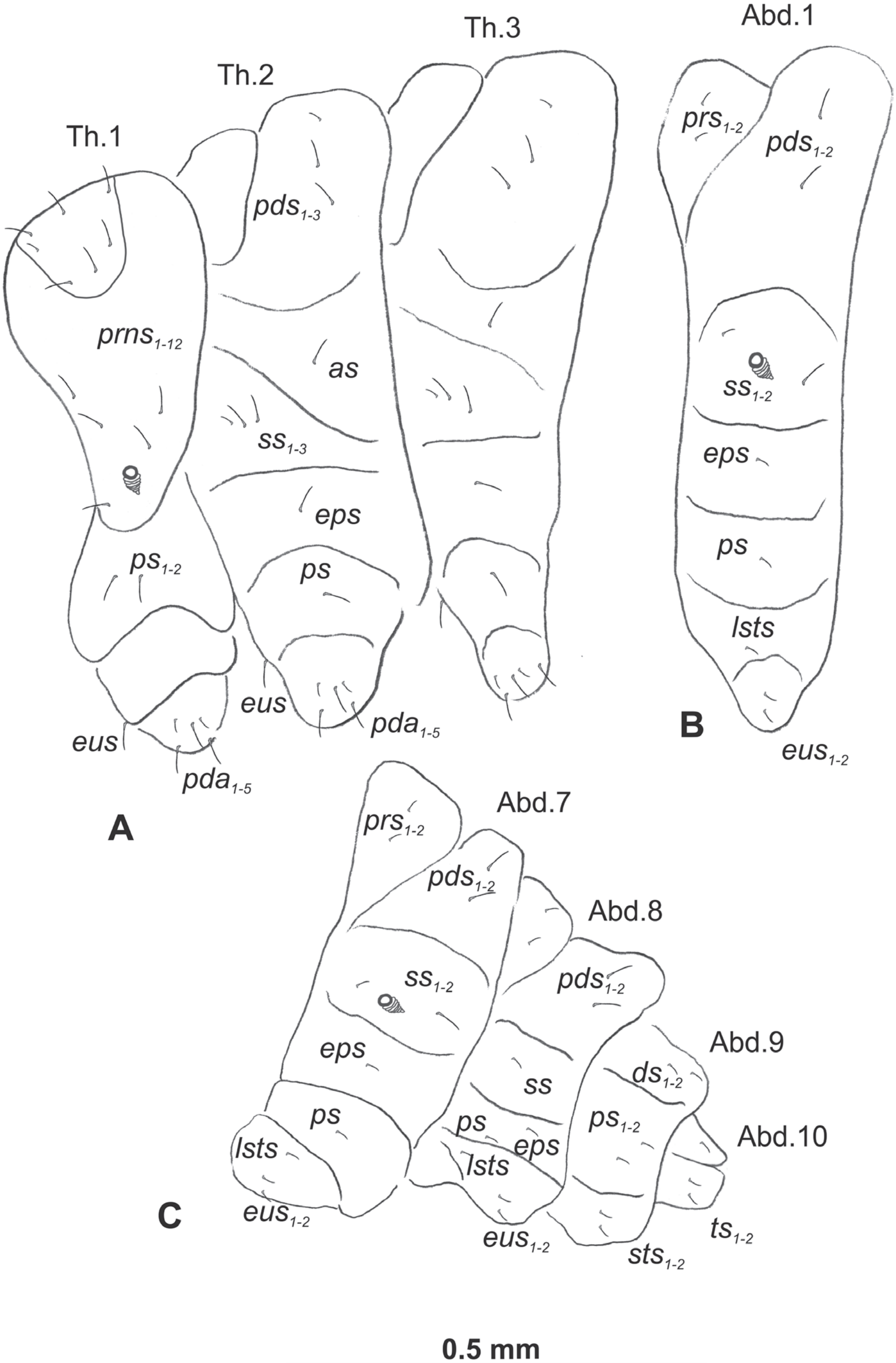

Figure 3. *Gymnetron tibiellum* Desbrochers des Loges mature larva, habitus **A** lateral view of thoracic segments **B** lateral view of abdominal segment I **C** lateral view of abdominal segments VI–X. Abbreviations: Th1–3 – numbers of thoracic segments, Ab1–10 – numbers of abdominal segments, setae: *as* – alar, *ds* – dorsal, *eps* – epipleural, *eus* – eusternal, *lsts* – laterosternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *ss* – spiracular, *ps* – pleural, *sts* – sternal, *ts* – terminal.

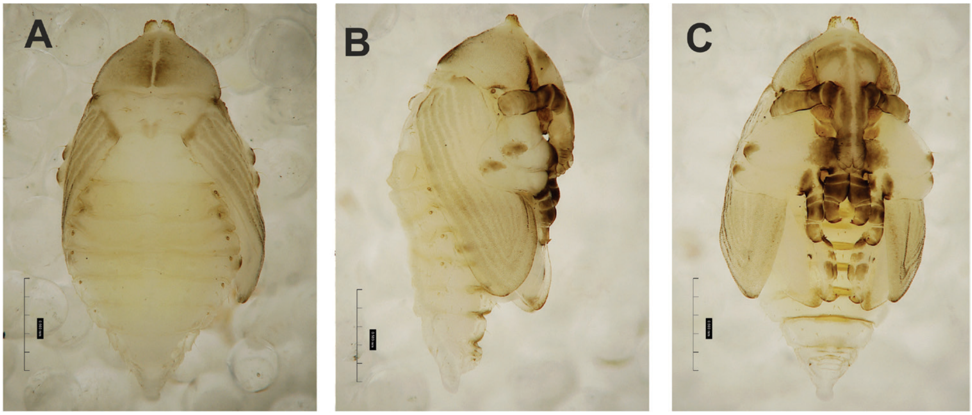

Figure 4. *Gymnetron tibiellum* Desbrochers des Loges pupa habitus **A** ventral view **B** lateral view **C** dorsal view. Scale bars: 0.5 mm.

Biological notes. The immature stages of *G. tibiellum* were collected from capsules of *Veronica anagallis-aquatica* L. Previously, nothing was known about the biology of this species. The adults are active from mid-April following the appearance of the host plants. Oviposition takes place from early June until mid-August. The presence of larvae inside the seed capsules is readily detected from the dark colour of the deposited frass. The biologies of *G. tibiellum* and *G. veronicae* are very similar but no competition between these two weevil species has been observed in over 500 dissected seeds capsules where they occur in syntopy.

Remarks and comparative notes. *Gymnetron tibiellum* is widely distributed in the south-eastern part of central Europe, Italy, the Balkans, Caucasus, Anatolia and the Middle East (Alonso-Zarazaga et al. 2017). The adults of this species are very closely related to *G. veronicae*, from which they differ by the shape of the rostra and the penis (Caldara 2008a). This close relationship was confirmed here by several characters which the immature stages have in common, although differences in several other characters of both larvae and pupae readily discriminate these two species.

Gymnetron veronicae (Germar, 1821)

Material examined. Serbia, Gornji Milanovac, Donja Vrbava, GPS 44°1.663'N, 20°34.496'E, 370 m, ex *Veronica anagallis-aquatica*, 20.06.2020, leg. Toševski (4 larvae and 4 pupae).

Description of mature larva (Figs 6A, B, 7A–F, 8A–C). ***Measurements*** (in mm). Body length: 2.16–3.00. The widest point in the body (meso- and metathorax) measures up to 1.00. Head width: 0.50–0.53.

General. Body elongate, slender, weakly curved, rounded in cross section (Fig. 6A).

Colouration. Head dark brown (Fig. 6B). All thoracic and abdominal segments white with numerous reddish or brown asperities (Fig. 6A).

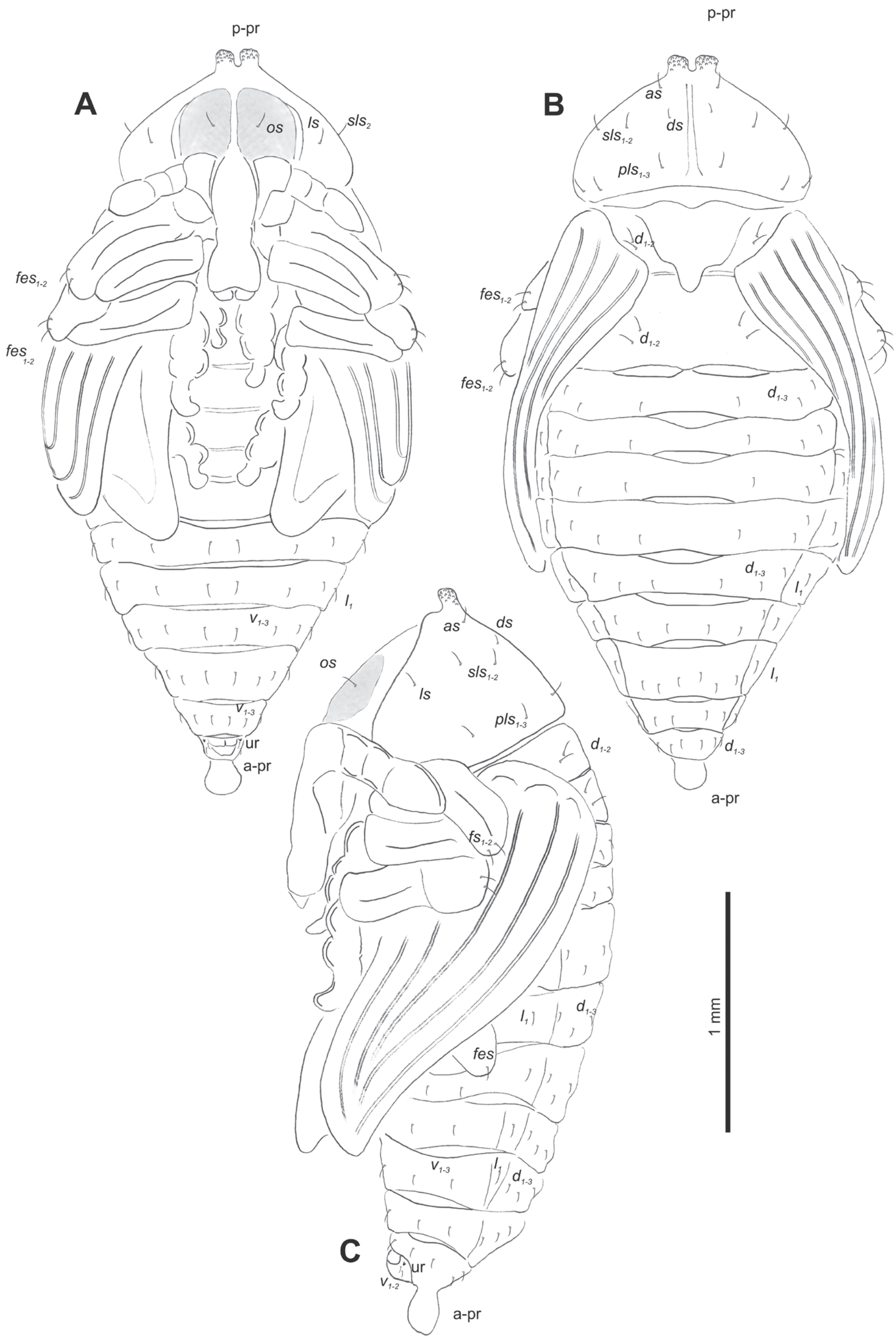

Figure 5. *Gymnetron tibiellum* Desbrochers des Loges pupa habitus **A** ventral view **B** dorsal view **C** lateral view. Abbreviations: a–pr – abdominal protuberances, p–pr – pronotal protuberances, ur – urogomphi; setae: *as* – apical, *d* – dorsal, *ds* – discal, *fes* – femoral, *l*, *ls* – lateral, *os* – orbital, *pls* – posterolateral, *sls* – superlateral, *v* – ventral.

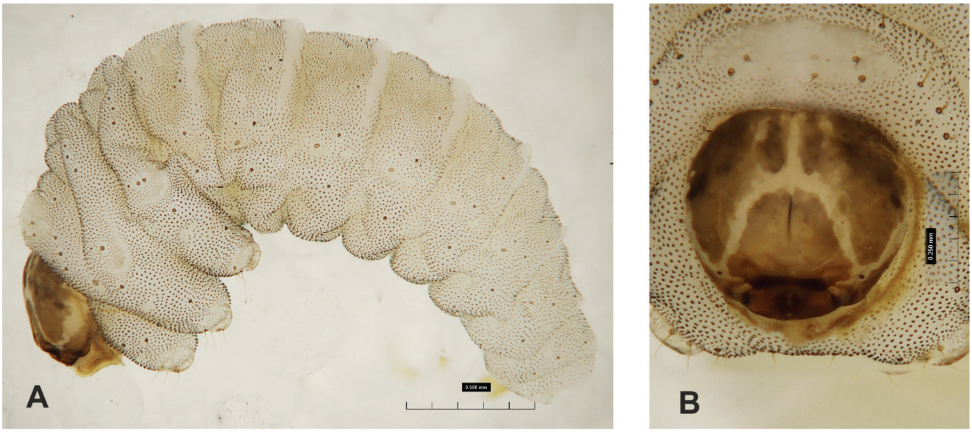

Figure 6. *Gymnetron veronicae* (Germar) mature larva **A** habitus **B** head, dorsal view. Scale bars: 0.5 mm (**A**); 0.25 mm (**B**).

Vestiture. Setae on body thin, orange, distinctly different in length (minute to very short or long).

Head capsule (Figs 6B, 7A). Head suboval, flattened laterally, endocarinal line present, clearly extending to half the length of frons. Frontal sutures on head very broad and distinct. Stemma, in the form of a very small pigmented spot with convex cornea. *Des*$_1$ long, located in middle of the central part of epicranium; *des*$_2$ short, placed medially; *des*$_3$ relatively long, located anteriorly on epicranium close to border with frontal suture; *des*$_4$ short, placed above frontal suture; *des*$_5$ long, located anterolaterally (Fig. 7A). *Fs*$_1$ short; *fs*$_2$ absent; *fs*$_3$ located medially; *fs*$_4$ short, located anteriorly; and *fs*$_5$ long, located anterolaterally, close to antenna (Fig. 7A). *Les*$_1$ and *les*$_2$ as long as *des*$_5$; one *ves* minute. Epicranial area with four postepicranial setae.

Antennae membranous and distinctly convex basal membranous article bearing one relatively long conical sensorium and six sensilla different in length (four basiconica and two ampullacea) (Fig. 7B).

Clypeus (Fig. 7C) ~ 3× as wide as long with two medium *cls*, located posterolaterally, without sensillum; fused to labrum.

Mouth parts. Labrum (Fig. 7C) ~ 4× as wide as long, three piliform *lms*, relatively long but of different lengths; *lms*$_1$ located anteromedially, *lms*$_2$ located partly close to clypeus, and *lms*$_3$ located anterolaterally, *lms*$_1$ and *lms*$_2$ relatively elongate, *lms*$_3$ short. Epipharynx (Fig. 7D) with two very long digitate *als*, almost identical in length; with three *ams* of different length, *ams*$_1$ and *ams*$_2$ piliform and short, *ams*$_3$ digitate and enlarged in middle; without *mes*; labral rods indistinct, irregular in shape. Mandibles (Fig. 7E) with two relatively long, piliform *mds*, located in distinct holes. Maxilla (Fig. 7F): stipes with one *stps*, two *pfs* and one minute *mbs* and one sensillum, *stps* and both *pfs* relatively long; mala with five medium, digitate *dms*; four *vms*, of different lengths, two setae very short, and two setae minute. Maxillary palpi with two palpomeres; length ratio of basal and distal palpomeres: 1:0.5. Praelabium (Fig. 7F) suboval-shaped, with one medium *prms*; ligula with sinuate margin and two very

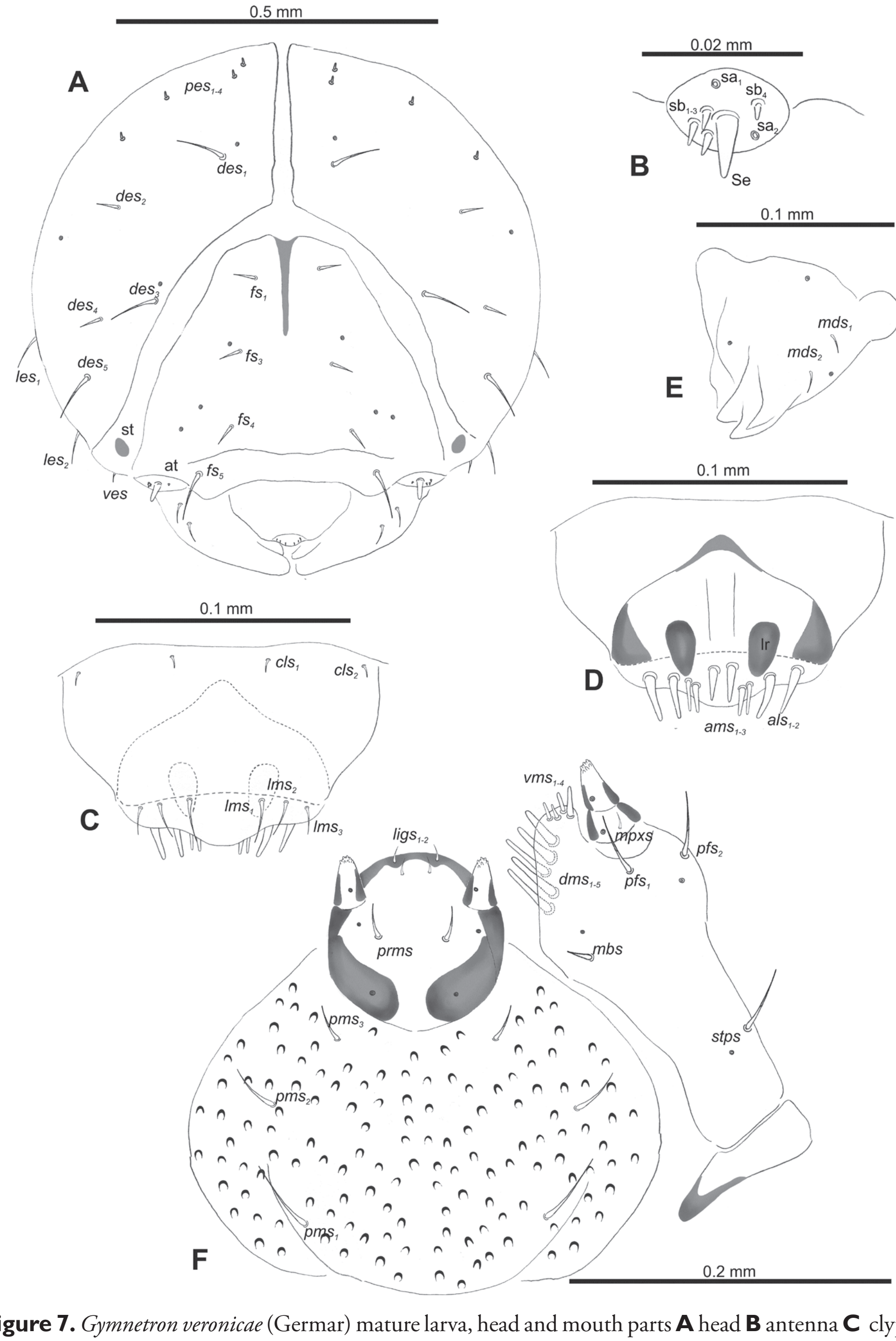

Figure 7. *Gymnetron veronicae* (Germar) mature larva, head and mouth parts **A** head **B** antenna **C** clypeus and labrum **D** epipharynx **E** left mandible **F** maxillolabial complex. Abbreviations: at – antenna, lr – labral rods, sa – sensillum ampullaceum, sb – sensillum basiconicum, Se – sensorium, st – stemma; setae: *als* – anteriolateral, *ams* – anteromedial, *cls* – clypeal, *des* – dorsal epicranial, *dms* – dorsal malar, *fs* – frontal epicranial, *les* – lateral epicranial, *ligs* – ligular, *lms* – labral, *mbs* – basioventral, *mds* – mandibular dorsal, *mpxs* – maxillary palps, *pes* – postepicranial, *pfs* – palpiferal, *pms* – postmental, *prms* – premental, *stps* – stipital, *ves* – ventral, *vms* – ventral malar.

short *ligs*; premental sclerite broad, well visible. Postlabium (Fig. 7F) with three *pms:* pms_1 very long; pms_2 short, located medially; pms_3 located laterally; membranous area densely and finely asperate.

Thorax. Prothorax (Fig. 8A) with seven long and one short *prns*, small pigmented dorsal sclerite present with three long *prns*, this sclerite subdivided into two triangular plates medially; two long *ps*; and two short to very short *eus*. Mesothorax (Fig. 8A) with two very short to minute *prs*; one short and two long *pds*; one long *as*; one long and two very short to minute *ss*; one long *eps*; one long *ps*; and two short *eus*. Chaetotaxy of metathorax (Fig. 8A) almost identical to that of mesothorax. Each pedal area of thoracic segments well separated, with three long and two very short to minute *pda*.

Abdomen. Spiracles on abdominal segments I–VI close to the anterior margin and functional, spiracles on abdominal segment VII not functional, and abdominal segment VIII with atrophied spiracles. Abdominal segments I–VII (Fig. 8B, C) with two minute *prs* (segment VII with one *prs*); one long and one minute *pds*; one long and one very short to minute *ss*; one long *eps*; one relatively long *ps*; one short *lsts*; and two very short and sometimes one additional minute *eus*. Abdominal segment VIII (Fig. 8C) with one minute *prs*; one long *pds*; one very short to minute *ss*; one long *eps*; one relatively long *ps*; one short *lsts*; and two very short and sometimes one additional minute *eus*. Abdominal segment IX (Fig. 8C) with one relatively long *ds*; one relatively long *ps*; and one short to very short *sts*. Abdominal segment X (Fig. 8C) with one very short seta (*ts*).

Description of pupa (Figs 9A–C, 10A–C). ***Measurements*** (in mm). Body length: 2.12–2.32. Body width: 1.25–1.23, Thorax width: 0.70–0.80.

Body. Brownish, pronotal protuberances (p-pr) sclerotized, covered with conical asperities; apical parts of femora, head, rostrum and pronotum darker than rest of body. Rostrum moderately slender. Pronotal protuberances almost completely fused. Pronotum twice as wide as long. Mesonotum slightly smaller than metanotum. Urogomphi short, conical, with sclerotized apices. Abdominal segment VIII with rounded, prominent abdominal protuberance dorsally (a-pr) (Fig. 10A–C).

Chaetotaxy. Sparse, setae short to medium, transparent. Head with one medium *os*. Rostrum without setae (Fig. 10B). Pronotum with two elongate *as*, one *ds*, one *sls*, and three *pls*, all of almost equal length. Dorsal parts of meso- and metathorax with three setae of various length, situated medially. Apex of femora with two medium-sized *fes* (Fig. 10A–C). Abdominal segments I–VIII with four medium to short setae placed in horizontal line medially. Each lateral part of abdominal segments I–VIII with two setae of various size. Ventral parts of abdominal segments I–VIII with three medium setae. Abdominal segment IX with two minute setae ventrally (Fig. 10A–C).

Biological notes. The larva was already known to feed on the ovary of *Veronica beccabunga* L, where it pupates and develops to the adult stage, and the adult was also collected on *V. anagallis-aquatica* L. and *V. scutellata* L. (Hoffmann 1958; Koch 1992; Sprick 1997). We can now confirm that at least *V. anagallis-aquatica* L. must be another host plant. The biology of this weevil species is the same as that of *G. tibiellum.*

Remarks and comparative notes. The adult of this species, widely distributed throughout Europe (Alonso-Zarazaga et al. 2017), is closely related to *G. tibiellum*, but with which it is sympatric only in south-eastern Europe. The two species differ mainly

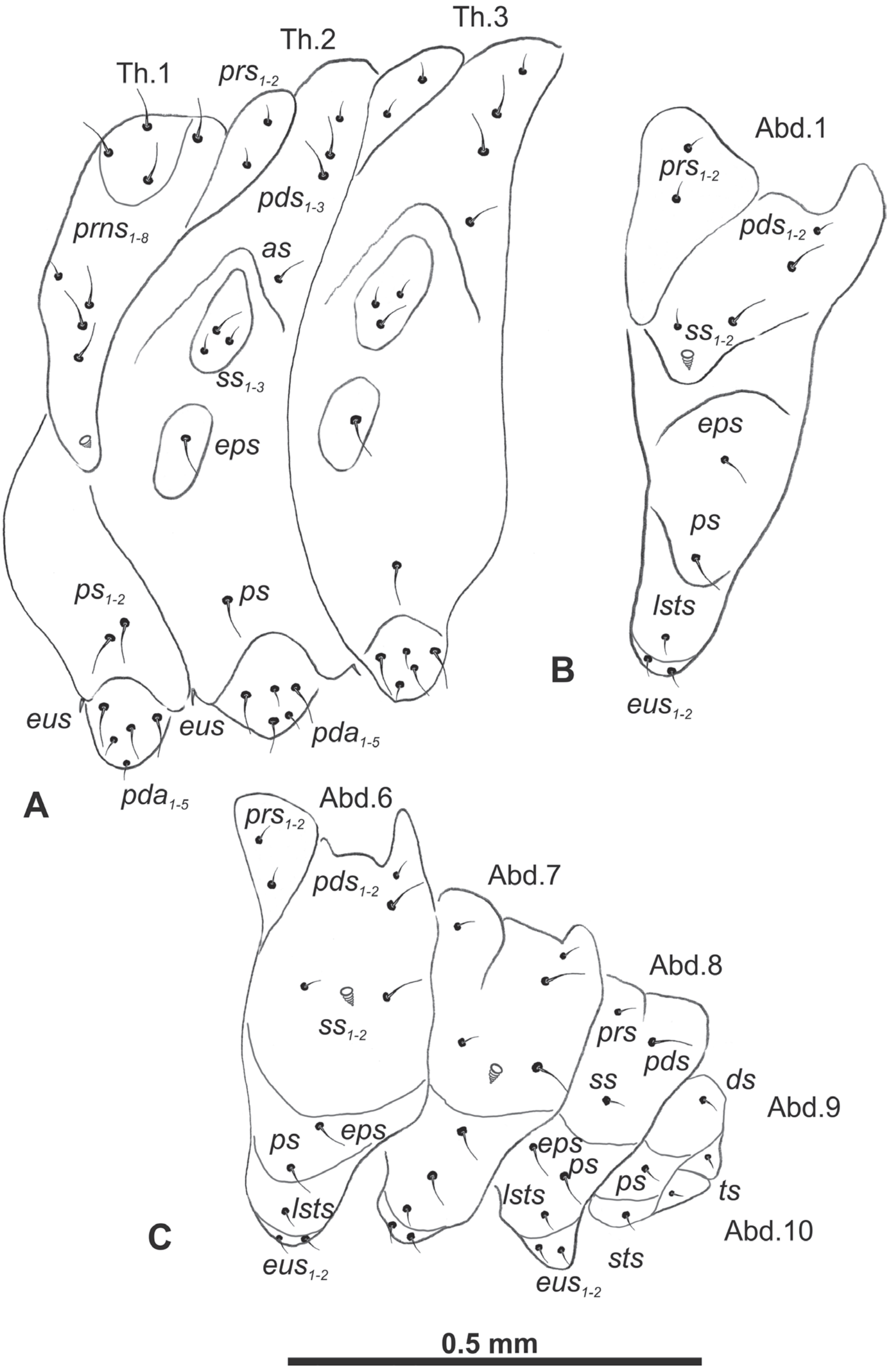

Figure 8. *Gymnetron veronicae* (Germar) mature larva, habitus **A** lateral view of thoracic segments **B** lateral view of abdominal segment I **C** lateral view of abdominal segments VI–X. Abbreviations: Th1–3 – numbers of thoracic segments, Ab1–10 – numbers of abdominal segments; setae: *as* – alar, *ds* – dorsal, *eps* – epipleural, *eus* – eusternal, *lsts* – laterosternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *ss* – spiracular, *ps* – pleural, *sts* – sternal, *ts* – terminal.

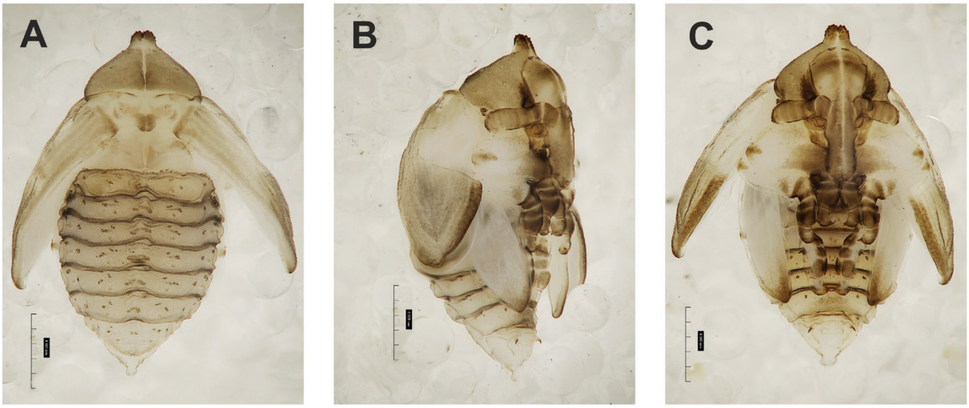

Figure 9. *Gymnetron veronicae* (Germar) pupa habitus **A** ventral view **B** lateral view **C** dorsal view. Scale bars: 0.5 mm.

in the shapes of the rostra and the penis. Examination of the larvae confirms the relationship between them: they share the praedorsal segment on the abdominal segments with two *pds*, the epicranium with fs_3 and the labral setae in one line. However, the larva of *G. veronicae* differs from that of *G. tibiellum* by the cuticle of the body covered with numerous reddish or brown asperities and setae emerging from black spots, the dark brown not pale yellow head, and the epipharynx with two (not three) *als* and three (not two) *ams*. The pupae also have many characters in common (see the key), but clearly differ by the number of setae *as*, *ls* and *sls* on the pronotum, those on the meso- and metathorax, and on the dorsal parts of abdominal segments I–VII.

Gymnetron rotundicolle Gyllenhal, 1838

Material examined. Serbia, Kalna, GPS 43°24.673'N, 22°25.737'E, 365 m, ex *Veronica hederophylla*, 20.06.2020, leg. Toševski (20 larvae); Serbia, Zemun, GPS 44°51.313'N, 20°22.625'E, 105 m, ex *V. opaca*, 19.06.2020, leg. Toševski (4 larvae and 2 pupae).

Description of mature larva (Figs 11A, B, 12A–F, 13A, B). ***Measurements*** (in mm). Body length: 2.20–2.33. The widest point in the body (meso- and metathorax) measures up to 0.86. Head width: 0.36–0.50.

General. Body relatively elongate, distinctly curved, rounded in cross section (Fig. 11A).

Colouration. Head pale yellow (Fig. 11B). All thoracic and abdominal segments white, cuticle smooth (Fig. 11A).

Vestiture. Setae on body thin, transparent, distinctly different in length (minute to very short or medium).

Head capsule (Figs 11B, 12A). Head suboval, endocarinal line present, shorter than half the length of frons. Frontal sutures on head of medium width, distinct. Stemma, in

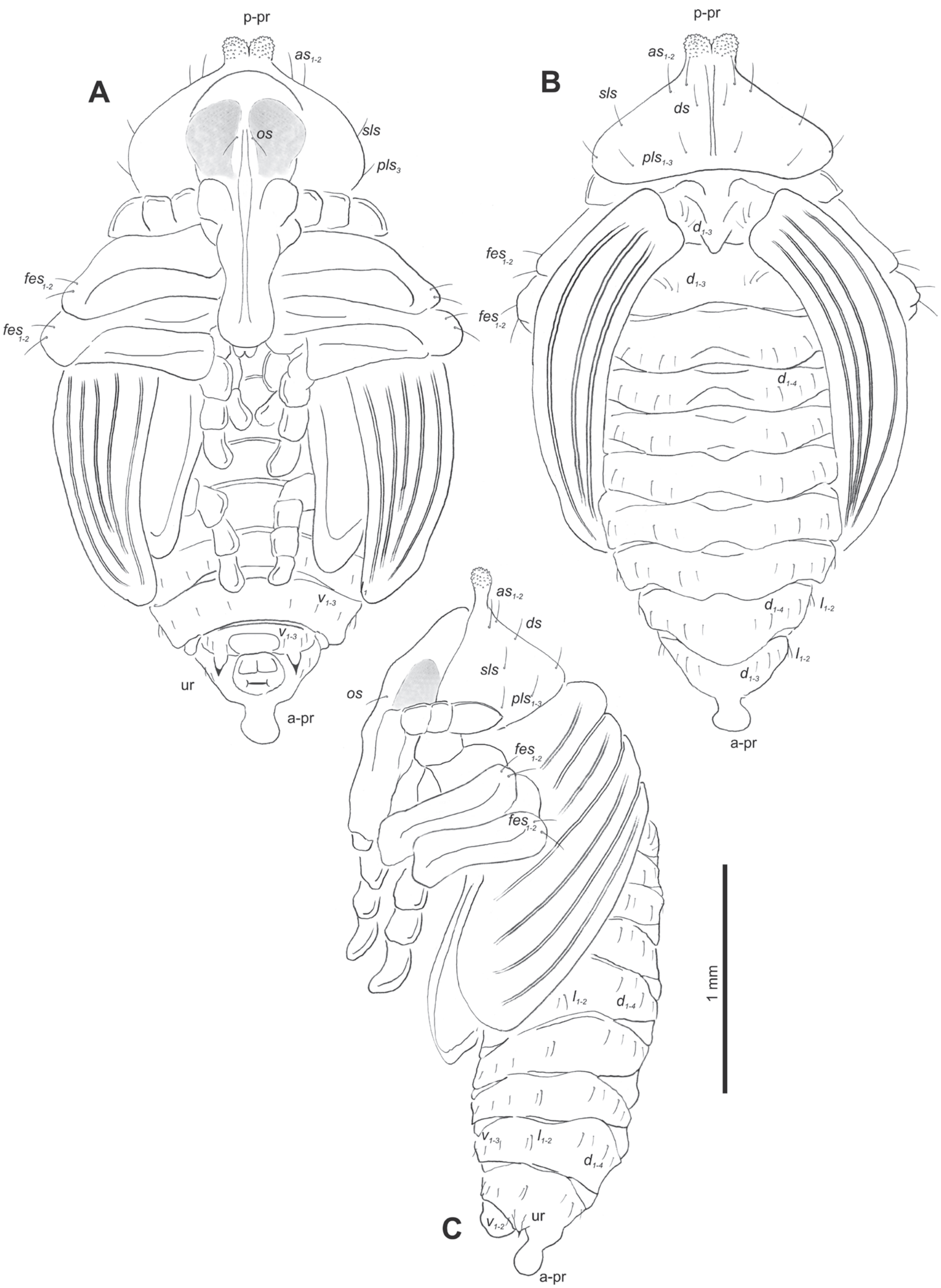

Figure 10. *Gymnetron veronicae* (Germar) pupa habitus **A** ventral view **B** dorsal view **C** lateral view. Abbreviations: a–pr – abdominal protuberances, p–pr – pronotal protuberances, ur – urogomphi; setae: *as* – apical, *d* – dorsal, *ds* – discal, *fes* – femoral, *l* – lateral, *os* – orbital, *pls* – posterolateral, *sls* – superlateral, *v* – ventral.

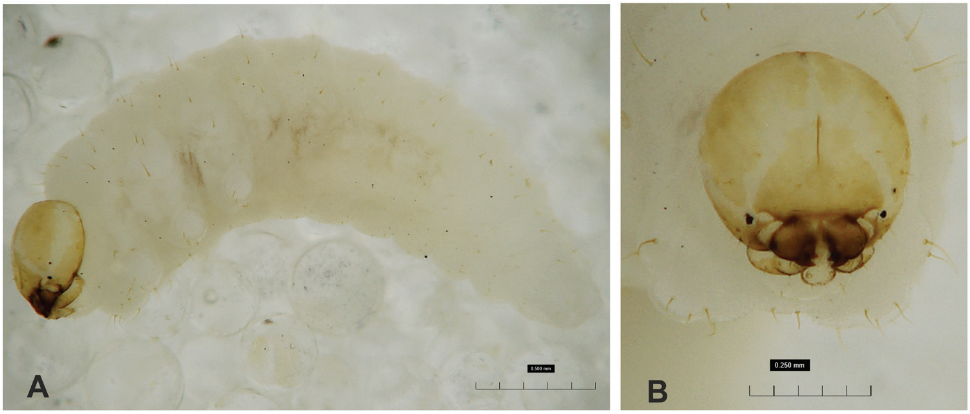

Figure 11. *Gymnetron rotundicolle* Gyllenhal mature larva **A** habitus **B** head, dorsal view. Scale bars: 0.5 mm (**A**); 0.25 mm (**B**).

form of distinct, black pigmented spot with convex cornea. Des_1 short, located in middle of central part of epicranium; des_2 short, located in middle of central part of epicranium; medium size des_3 located anteriorly on epicranium close to border with frontal suture; des_4 short, located between des_2 and des_3; des_5 of medium size, located anterolaterally (Fig. 12A). Fs_1 absent; fs_2 very short to minute, located medially; fs_3 absent; fs_4 medium, located anteriorly; and fs_5 relatively long, located anterolaterally, close to antenna (Fig. 12A). Les_1 and les_2 as long as des_5; two *ves* short. Epicranial area with four postepicranial setae (*pes*).

Antennae membranous and distinctly convex basal membranous article bearing one relatively long conical sensorium and three sensilla basiconica (Fig. 12B).

Clypeus (Fig. 12C) ~ 3× as wide as long with two relatively long *cls: cls_1* located posterolaterally, cls_2 located posteromedially, and one sensillum between setae; not fused with labrum.

Mouth parts. Labrum (Fig. 12C) ~ 3× as wide as long, with three piliform *lms*, relatively long, of almost equal length; lms_1 located posteromedially, close to clypeus, lms_2 located anteromedially, and lms_3 located anterolaterally. Epipharynx (Fig. 12D) with three very long digitate *als*, almost identical in length, two piliform *ams* almost equal in length and one *mes*; labral rods indistinct, enlarged anteriorly. Mandibles (Fig. 12E) with two relatively long, piliform *mds*, located in distinct holes. Maxilla (Fig. 12F): stipes with one *stps*, two *pfs*, one *mbs* and sensillum, *stps* and $pfs_{1–2}$ long, *mbs* very short; mala with five relatively long, digitate *dms*; four *vms*, different in length, one setae very short, and three setae minute. Maxillary palpi with two palpomeres; length ratio of basal and distal palpomeres: 1:0.5. Praelabium (Fig. 12F) oval, with one relatively long *prms*; ligula with sinuate margin and two very short *ligs* and one sensillum; premental sclerite broad, readily visible at sides but almost invisible in middle. Postlabium (Fig. 12F) with three *pms*, very long pms_2, and very short to short pms_1 and pms_3, all located laterally; membranous area sparsely and finely asperate.

Thorax. Prothorax (Fig. 13A) with six relatively long and one short to very short *prns*, pigmented dorsal sclerite present with four relatively long *prns*, this sclerite subdivided

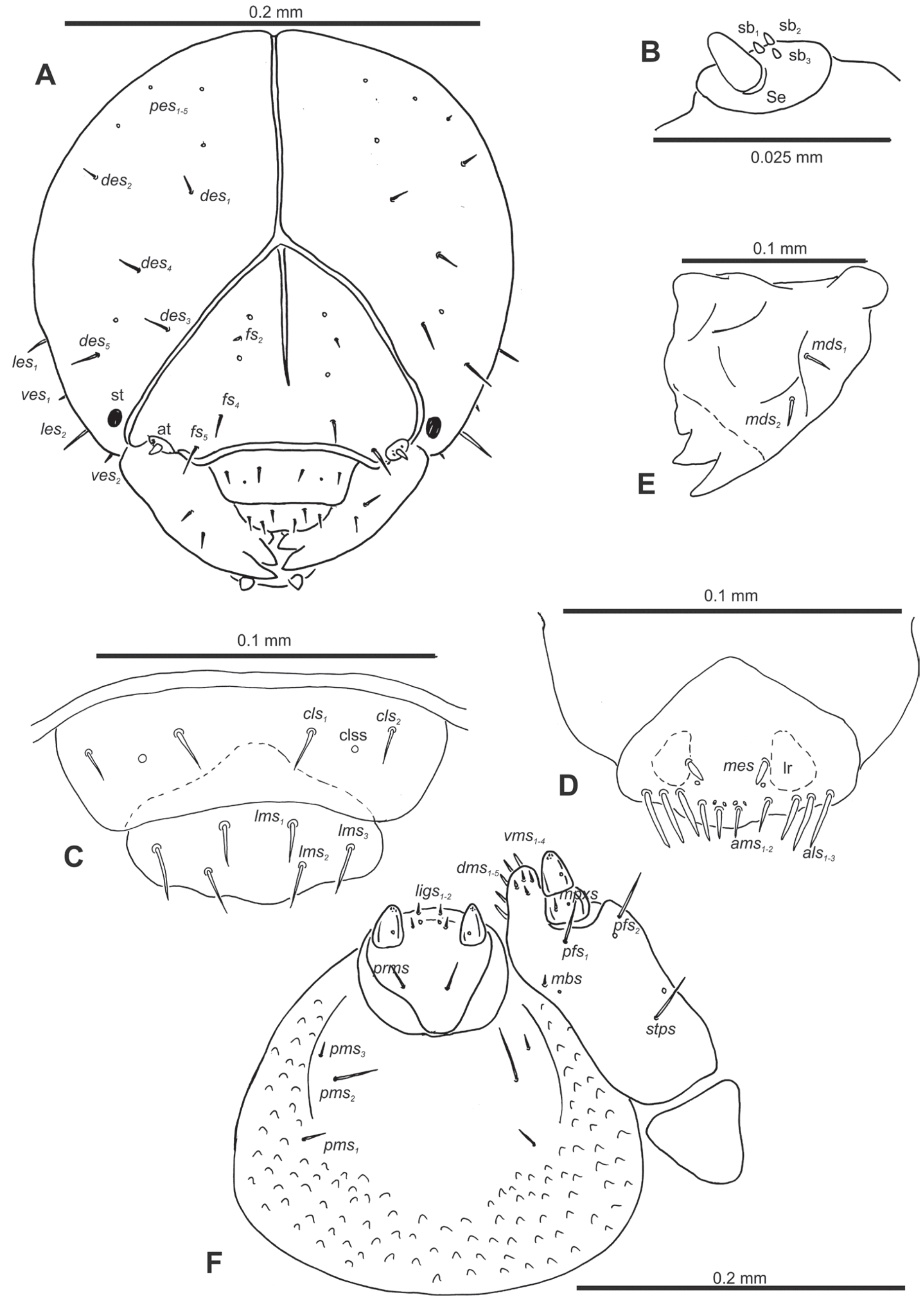

Figure 12. *Gymnetron rotundicolle* Gyllenhal mature larva, head and mouth parts **A** head **B** antenna **C** clypeus and labrum **D** epipharynx **E** left mandible **F** maxillolabial complex. Abbreviations: at – antenna, clss – clypeal sensillium, lr – labral rods, sb – sensillum basiconicum, Se – sensorium, st – stemma; setae: *als* – anteriolateral, *ams* – anteromedial, *cls* – clypeal, *des* – dorsal epicranial, *dms* – dorsal malar, *fs* – frontal epicranial, *les* – lateral epicranial, *ligs* – ligular, *lms* – labral, *mbs* – basioventral, *mds* – mandibular dorsal, *mes* – median, *mpxs* – maxillary palps, *pes* – postepicranial, *pfs* – palpiferal, *pms* – postmental, *prms* – premental, *stps* – stipital, *ves* – ventral, *vms* – ventral malar.

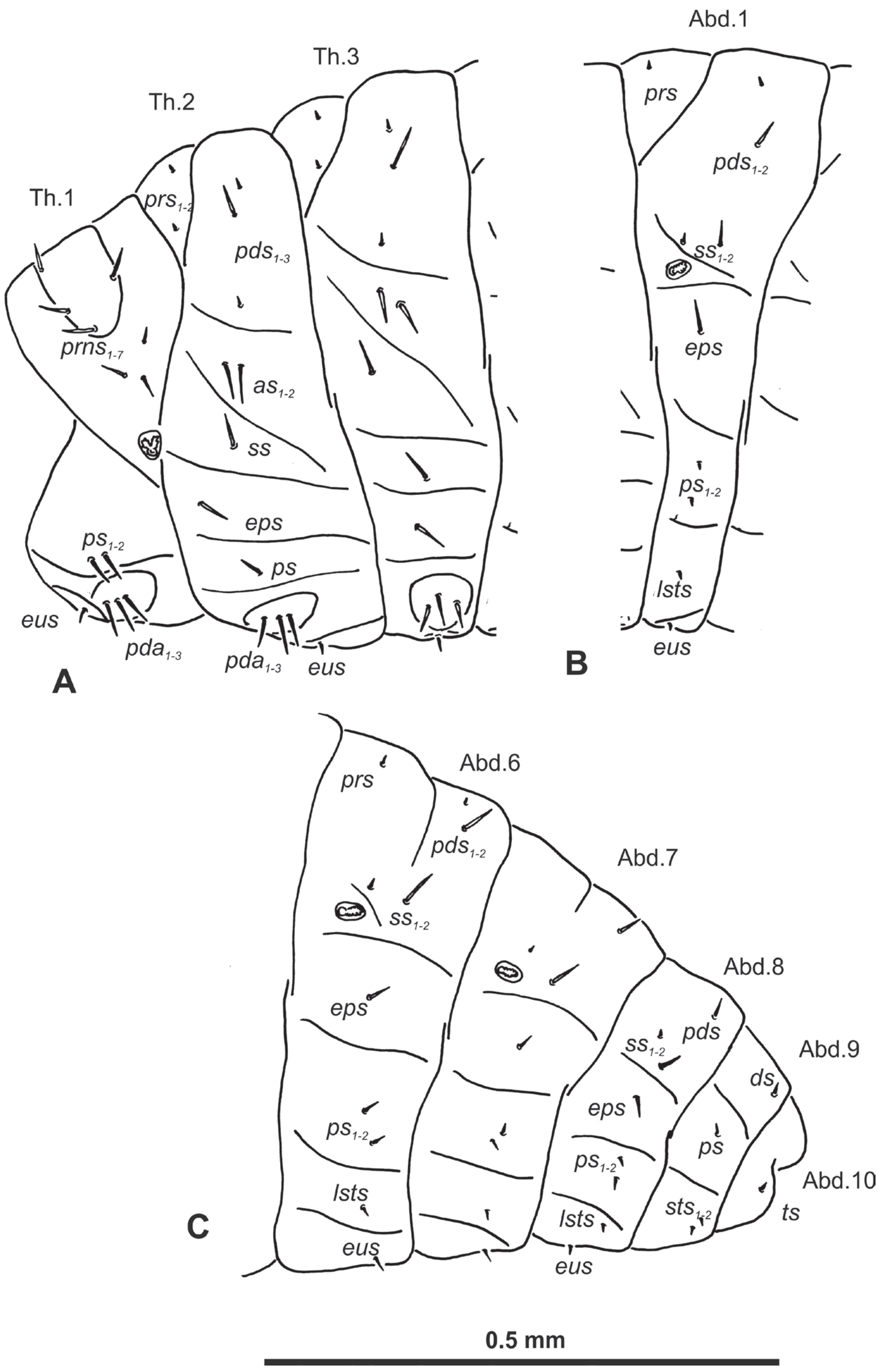

Figure 13. *Gymnetron rotundicolle* Gyllenhal mature larva, habitus **A** lateral view of thoracic segments **B** lateral view of abdominal segment I **C** lateral view of abdominal segments VI–X. Abbreviations: Th1–3 – numbers of thoracic segments, Ab1–10 – numbers of abdominal segments; setae: *as* – alar, *ds* – dorsal, *eps* – epipleural, *eus* – eusternal, *lsts* – laterosternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *ss* – spiracular, *ps* – pleural, *sts* – sternal, *ts* – terminal.

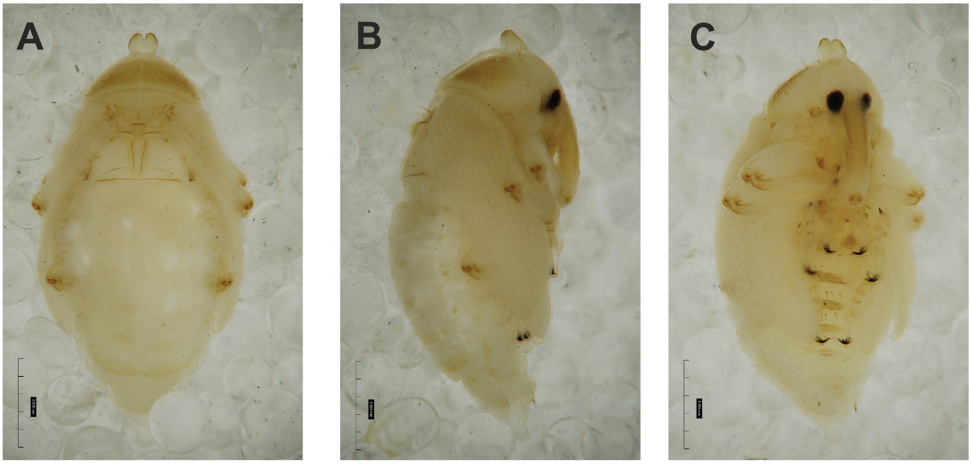

Figure 14. *Gymnetron rotundicolle* Gyllenhal pupa habitus **A** ventral view **B** lateral view **C** dorsal view. Scale bars: 0.5 mm.

into two triangular plates medially; two relatively long *ps*; and one short *eus*. Mesothorax (Fig. 13A) with two very short to minute *prs*, one relatively long and two short to very short *pds*; one relatively long *as*; two relatively long *ss*; one relatively long *eps*; one relatively long *ps*; and one short *eus*. Chaetotaxy of metathorax (Fig. 13A) almost identical to that of mesothorax. Each pedal area of thoracic segments well separated, with three long *pda*.

Abdomen. Spiracles on abdominal segments I–VI close to the anterior margin and functional, spiracles on abdominal segment VII not functional, and abdominal segment VIII with atrophied spiracles. Abdominal segments I–VI (Fig. 13B, C) with one very short to minute *prs*; one relatively long and one very short *pds*; one relatively long and one very short to minute *ss*; one relatively long *eps*; two very short *ps*; one very short *lsts*; and one very short to minute *eus*. Abdominal segments VII–VIII (Fig. 13C) without *prs*; with one relatively long *pds*; one very short to minute *ss*; one relatively long *eps*; two very short *ps*; one very short *lsts*; and one very short to minute *eus*. Abdominal segment IX (Fig. 13C) with one very short *ds*; one very short *ps*; and two very short *sts*. Abdominal segment X (Fig. 13C) with one very short to minute seta (*ts*).

Description of pupa (Figs 14A–C, 15A–C). ***Measurements*** (in mm). Body length: 2.20–2.37. Body width: 1.12–1.42, Thorax width: 0.70–0.85.

Body. Yellowish, pronotal protuberances (p-pr) weakly sclerotized, with serrated margins; apical parts of femora brownish. Rostrum slender. Pronotum twice as wide as long. Pronotal protuberances fused at basis. Mesonotum slightly smaller than metanotum. Urogomphi reduced, conical, with sclerotized apex. Abdominal segment VIII with rounded, prominent abdominal protuberance dorsally (a-pr) (Fig. 15A–C).

Chaetotaxy. Sparse, setae short to medium, transparent. Head with one short *os*. Rostrum without setae (Fig. 14B). Pronotum with two *as*, one *ds*, and three *pls* equal in length. Dorsal parts of meso- and metathorax with three setae of different length, situated medially. Apex of femora with one medium *fes* (Fig. 15A–C). Abdominal segments I–VIII with two short, equally long setae dorsally: one situated medially, the

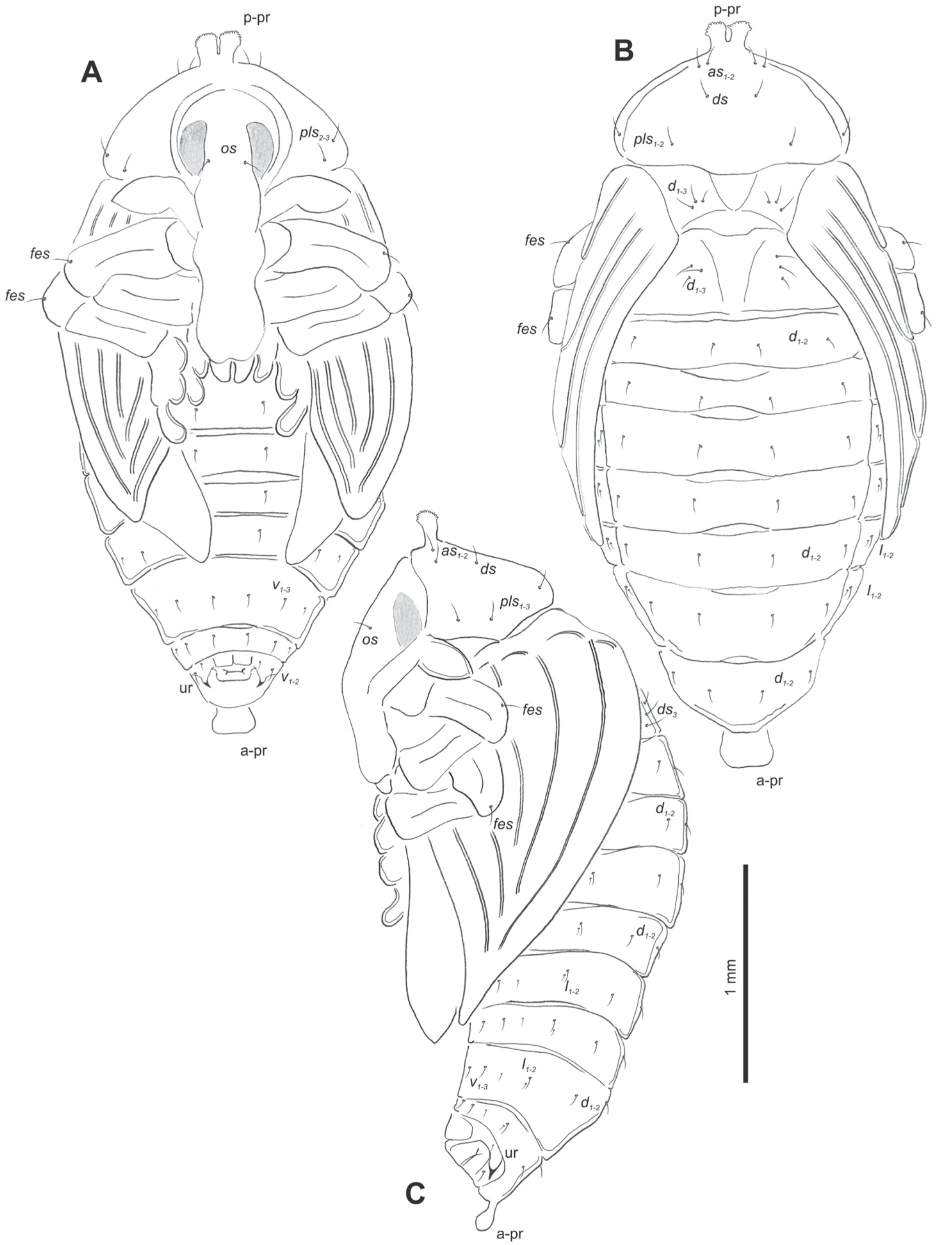

Figure 15. *Gymnetron rotundicolle* Gyllenhal pupa habitus **A** ventral view **B** dorsal view **C** lateral view. Abbreviations: a–pr – abdominal protuberances, p–pr – pronotal protuberances, ur – urogomphi; setae: *as* – apical, *d* – dorsal, *ds* – discal, *fes* – femoral, *l*, *ls* – lateral, *os* – orbital, *pls* – posterolateral, *v* – ventral.

other mediolaterally. All dorsal abdominal setae almost equal in length, short. Each lateral part of abdominal segments I–VIII with two setae of various length (one short, one minute). Ventral parts of abdominal segments I–VIII with three medium setae. Abdominal segment IX with two very short setae ventrally (Fig. 15A–C).

Biological notes. The adults of *G. rotundicolle* were previously recorded as collected on two species of *Veronica: V. persica* Poiret in Italy and Switzerland (Caldara 2008b; Germann et al. 2013), and *V. chamaedrys* L. in the Czech Republic and Slovakia (Krátký and Trnka 2012; Krátký 2013). The reports of *Veronica hederifolia* L. and *V. opaca* Fr. as host plants of this weevil are new data. The adults appear in early spring (mid-March), feeding on the upper leaves of newly growing shoots of the host. Oviposition takes place in the seed capsules, in which the larvae complete their development. The presence of larvae inside seed capsules can be detected from the dark colour of their frass.

Remarks and comparative notes. The first findings of this originally central Asian species in many countries of central and southern Europe (Italy, Switzerland, France, Germany, Czech Republic, Slovakia, Hungary, Poland) have been reported in many faunistic papers during the last 15 years (Strejček 2007; Caldara 2008b; Krátký and Trnka 2012; Krátký 2013; Germann et al. 2013; Reibnitz 2013; Podlussány et al. 2017; Wanat and Ruta 2018; Nolte and Haag 2019). These papers indicate with a high degree of certainty that this species only recently colonized areas where a few years ago it was absent, in contrast to its host plants (Caldara 2008b; Germann et al. 2013).

Gymnetron melanarium (Germar, 1821)

Material examined. Serbia, Pirot, Ponor, GPS 43°11.013'N, 22°25.067'E, 686 m, ex *Veronica austriaca* subsp. *jacquinii*, 20.06.2020, leg. Toševski (35 larvae and 11 pupae).

Description of mature larva (Figs 16A, B, 17A–F, 18A, B). ***Measurements*** (in mm). Body length: 2.33–2.66. The widest point in the body (meso- and metathorax) measures up to 1.00. Head width: 0.50–0.53.

General. Body elongate, slender, weakly curved, rounded in cross section (Fig. 16A).

Colouration. Head pale yellow (Fig. 16B). All thoracic and abdominal segments smooth (Fig. 16A).

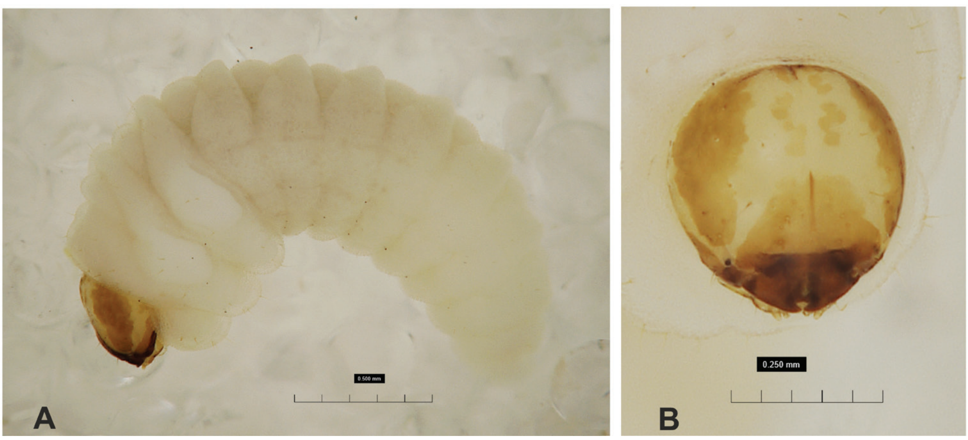

Figure 16. *Gymnetron melanarium* (Germar) mature larva **A** habitus **B** head, dorsal view. Scale bars: 0.5 mm (**A**); 0.25 mm (**B**).

Vestiture. Setae on body thin, yellow, distinctly different in length (minute to very short or long).

Head capsule (Figs 16B, 17A). Head almost oval, endocarinal line present, extending distinctly to 3/4 of the length of frons. Frontal sutures on head distinct. Stemma, in form of pigmented spot with convex cornea. Des_1 medium, located in middle of central part of epicranium; medium des_2; medium des_3 located anteriorly on epicranium, close to border with frontal suture; medium des_4; medium des_5 placed laterally (Fig. 17A). Fs_1 absent; fs_2 medium, located medially; fs_3 absent; fs_4 medium, located anteriorly; and fs_5 long, located anterolaterally, close to antenna (Fig. 17A). Les_1 medium and les_2 as long as des_5; single *ves* medium. Epicranial area with six postepicranial setae.

Antennae membranous and distinctly convex basal membranous article bearing one relatively long conical sensorium and four sensilla: three basiconica and single ampullaceum (Fig. 17B).

Clypeus (Fig. 17C) ~ 3× as wide as long with two relatively long *cls*, located posterolaterally, with single sensillum; fused to labrum.

Mouth parts. Labrum (Fig. 17C) ~ 3× as wide as long, with three piliform *lms*, relatively long, lms_3 slightly shorter than others; lms_1 located anteromedially, lms_2 located partly close to clypeus, and lms_3 located anterolaterally. Epipharynx (Fig. 17D) with three very long digitate *als*, almost identical in length; with two piliform *ams*, equal in length, and one short, digitate *mes*; labral rods indistinct, narrow. Mandibles (Fig. 17E) with two relatively long, piliform *mds*, located in distinct holes. Maxilla (Fig. 17F): stipes with one *stps*, two *pfs* and one sensillum, without *mbs*; *stps* and both *pfs* long; mala with five moderately elongate digitate *dms*; four *vms*, different in length, two setae short, and two setae very short. Maxillary palpi with two palpomeres; length ratio of basal and distal palpomeres: 1:1.2. Praelabium (Fig. 17F) oval, with one medium *prms*; ligula with rounded margin and two very short *ligs*; premental sclerite broad, well visible. Postlabium (Fig. 17F) with three *pms*, short pms_1, very long pms_2 and short pms_3, all located laterally; membranous area densely and distinctly asperate.

Thorax. Prothorax (Fig. 18A) with nine long and one minute *prns*; two long *ps*; and two very short *eus*. Mesothorax (Fig. 18A) with two minute *prs*; one medium and two long *pds*; one long *as*; two long and one minute *ss*; one long *eps*; one long *ps*; and one short *eus*. Chaetotaxy of metathorax (Fig. 18A) almost identical to that of mesothorax. Each pedal area of thoracic segments well separated, with one long, two medium and two very short to minute *pda*.

Abdomen. Spiracles on abdominal segments I–VI placed medially and functional, spiracles on abdominal segment VII not functional, and abdominal segment VIII with atrophied spiracles. Abdominal segments I–VI (Fig. 18B, C) with one minute *prs*; one long and one medium *pds*; one long and one very short to minute *ss*; one long *eps*; one relatively long *ps*; without *lsts* and two very short *eus*. Abdominal segments VII–VIII (Fig. 18C) without *prs*; one long and one medium *pds*; one very short to minute *ss*; one long *eps*; one long *ps*; and two very short *eus*. Abdominal segment IX (Fig. 18C) with one relatively long *ds*; one relatively long *ps*; and one medium *sts*. Abdominal segment X (Fig. 18C) with one very short seta (*ts*).

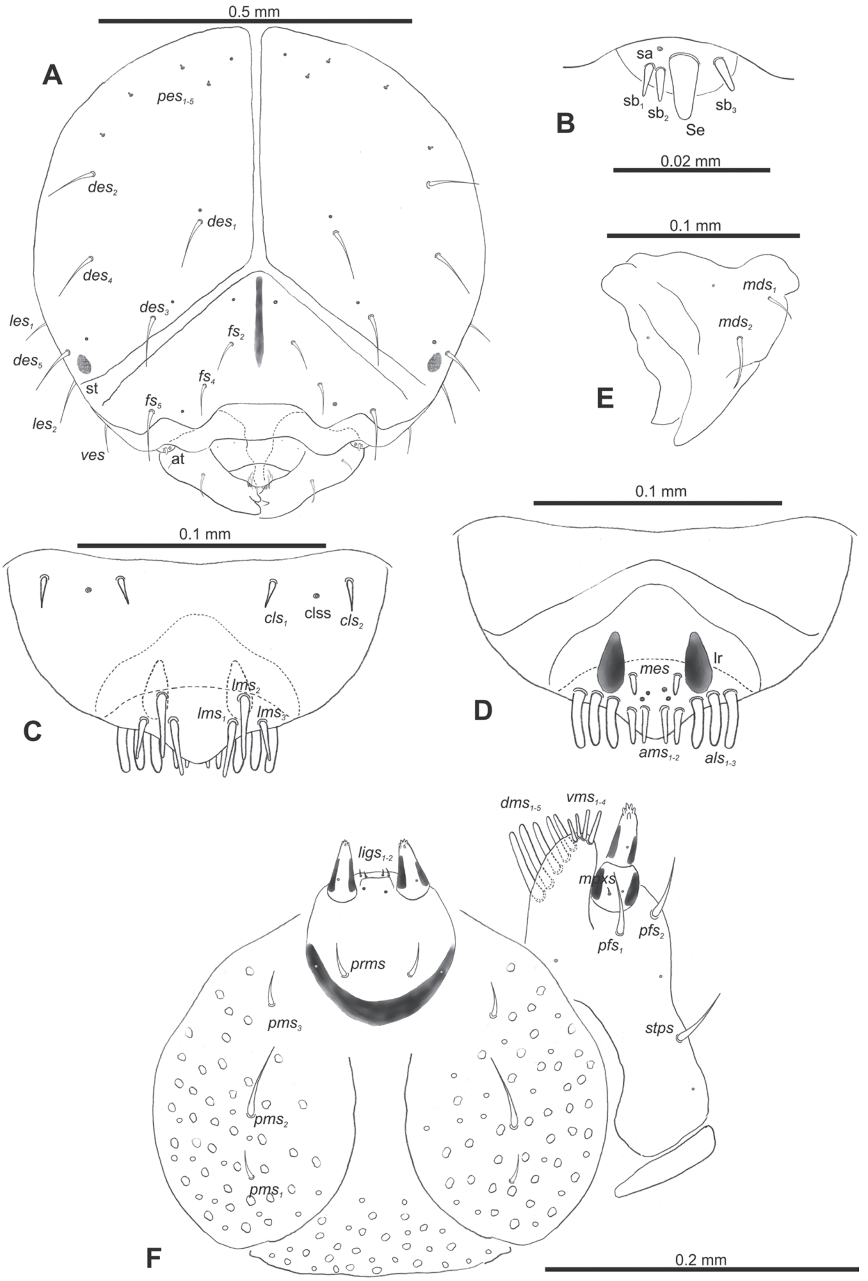

Figure 17. *Gymnetron melanarium* (Germar) mature larva, head and mouth parts **A** head **B** antenna **C** clypeus and labrum **D** epipharynx **E** left mandible **F** maxillolabial complex. Abbreviations: at – antenna, clss – clypeal sensillium, lr – labral rods, sa – sensillum ampullaceum, sb – sensillum basiconicum, Se – sensorium, st – stemma; setae: *als* – anteriolateral, *ams* – anteromedial, *cls* – clypeal, *des* – dorsal epicranial, *dms* – dorsal malar, *fs* – frontal epicranial, *les* – lateral epicranial, *ligs* – ligular, *lms* – labral, *mds* – mandibular dorsal, *mes* – median, *mpxs* – maxillary palps, *pes* – postepicranial, *pfs* – palpiferal, *pms* – postmental, *prms* – premental, *stps* – stipital, *ves* – ventral, *vms* – ventral malar.

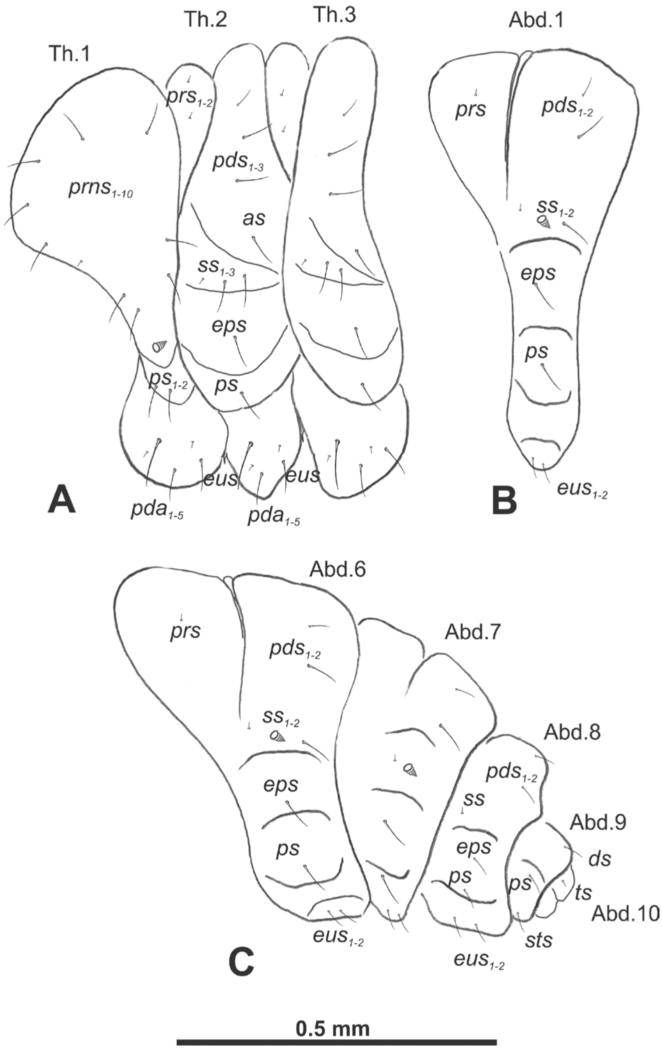

Figure 18. *Gymnetron melanarium* (Germar) mature larva, habitus **A** lateral view of thoracic segments **B** lateral view of abdominal segment I **C** lateral view of abdominal segments VI–X. Abbreviations: Th1–3 – numbers of thoracic segments, Ab1–10 – numbers of abdominal segments; setae: *as* – alar, *ds* – dorsal, *eps* – epipleural, *eus* – eusternal, *lsts* – laterosternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *ss* – spiracular, *ps* – pleural, *sts* – sternal, *ts* – terminal.

Description of pupa (Figs 19A–C, 20A–C). ***Measurements*** (in mm). Body length: 2.12–2.32. Body width: 1.25–1.32. Thorax width: 0.75–0.82.

Body. Yellowish, pronotal protuberances (p-pr) sclerotized, smooth; head, rostrum, antennae, dorsal parts of meso- and metanotum, and apical parts of femora brownish. Rostrum rather slender. Pronotal protuberances well separated. Pronotum 1.8× as wide as long. Mesonotum slightly smaller than metanotum. Urogomphi reduced, conical, with sclerotized apex. Abdominal segment VIII with conical abdominal protuberance dorsally (a-pr) having acute, sclerotized apex (Fig. 19A–C).

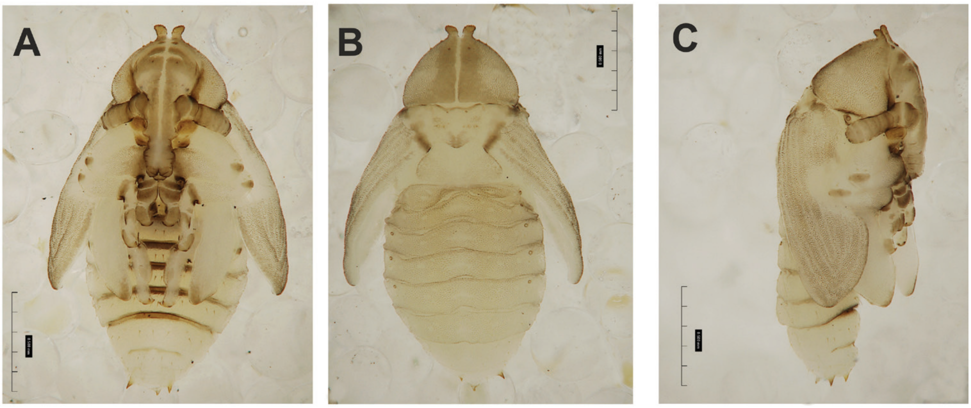

Figure 19. *Gymnetron melanarium* (Germar) pupa habitus **A** ventral view **B** lateral view **C** dorsal view. Scale bars: 0.5 mm.

Chaetotaxy. Sparse, setae rather short to moderately elongate, transparent. Head with two *os*, different in length. Rostrum with one *rs*. Setae on head and rostrum straight, as long as those on prothorax (Fig. 20B). Pronotum with two *as*, two *ls*, two *ds* and four *pls*; ds_{1-2} and ls_2 slightly shorter than other pronotal setae. Dorsal parts of meso- and metathorax with two setae placed medially. Apex of femora with two *fes* equal in length (Fig. 20A–C). Abdominal segments I–VIII with five short, equally long setae dorsally: first placed antero-medially, the others distributed in regular line along posterior margin of segment. All dorsal abdominal setae short, almost equal in length. Each lateral part of abdominal segments I–VIII with one elongated seta. Ventral parts of abdominal segments I–VIII with three medium setae. Abdominal segment IX with two very short setae ventrally (Fig. 20A–C).

Biological notes. Previously the larva of this species was observed on *Veronica serpyllifolia* L., on the stems where it produces a small uni- or bilocular gall in which metamorphosis takes place. The adult emerges from the gall at the end of summer and hibernates in the soil (Hustache 1931; Hoffmann 1958). The adult has also been collected on other *Veronica* species such as *V. agrestis* L., *V. austriaca* subsp. *austriaca* L., *V. chamaedrys* L., *V. officinalis* L, and *V. teucrium* (L.) D.A. Webb (Hoffmann 1958; Koch 1992; Sprick 1997). In Serbia, the development of *G. melanarium* is restricted to the seed capsules of *Veronica austriaca* subsp. *jacquinii* (Baumg.) Watzl, which is new information. Nearly 90% of the seed capsules are infested with one or two larvae. The larvae are seed feeders and development occurs in the basal part of the strongly flattened, glossy and glabrous seed capsules with no visible sign of larval presence. Oviposition takes place from mid-May onwards and the new generation of adults emerges during July.

Remarks and comparative notes. This species belongs to a group of very similar species characterized by slender subrectangular elytra, rostrum in lateral view tapered from the antennal insertion to the apex, and short protibiae in the female. There are no particular phylogenetic affinities with the adult (see Caldara 2008a) and pupal stages (abdominal protuberance short, triangular, head with 2 *os*) of the other species

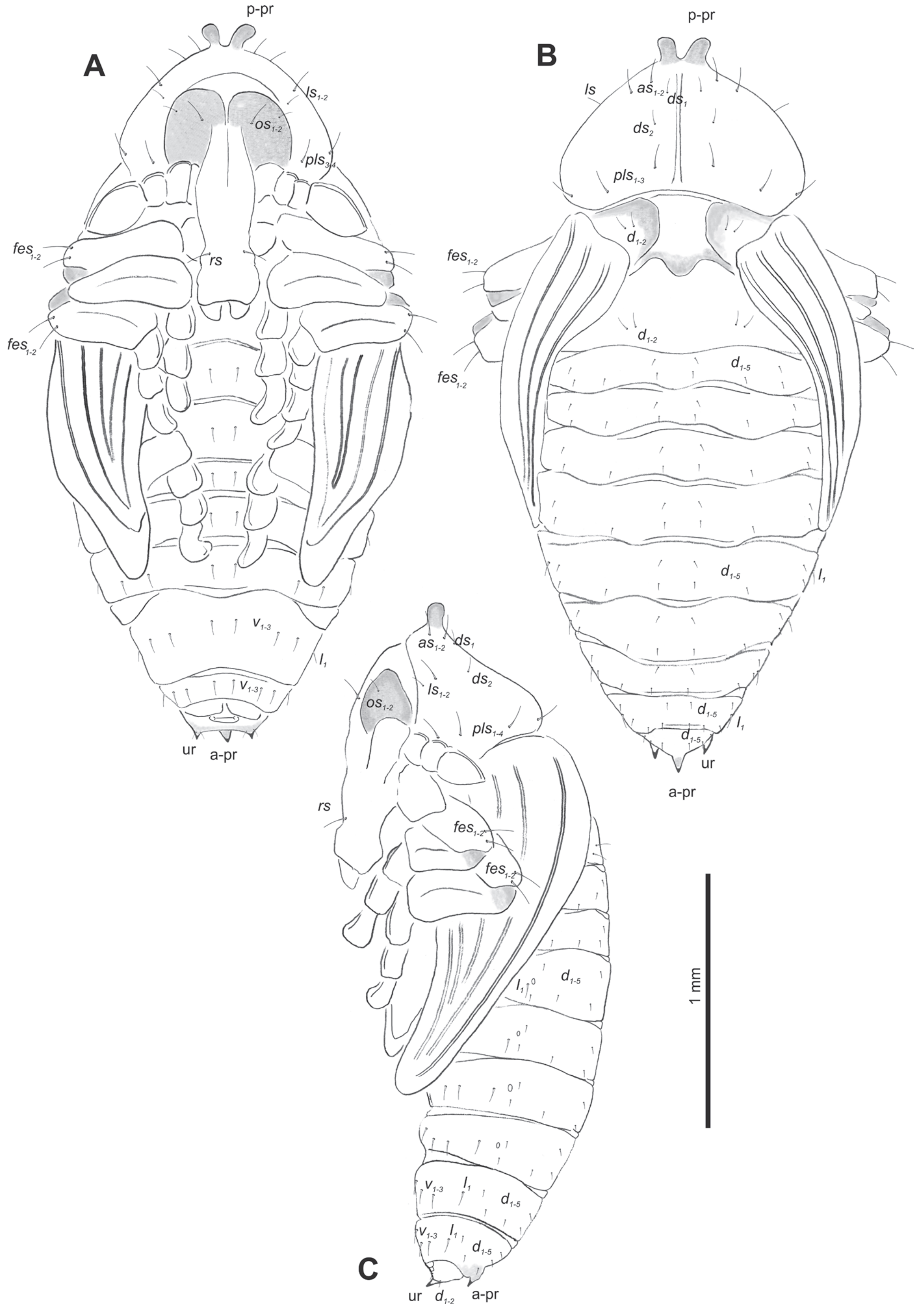

Figure 20. *Gymnetron melanarium* (Germar) pupa habitus **A** ventral view **B** dorsal view **C** lateral view. Abbreviations: a–pr – abdominal protuberances, p–pr – pronotal protuberances, ur – urogomphi; setae: *as* – apical, *d* – dorsal, *ds* – discal, *fes* – femoral, *l*, *ls* – lateral, *os* – orbital, *pls* – posterolateral, *rs* – rostral, *v* – ventral.

described here. By contrast, the larvae share several characters with *G. rotundicolle*, e.g., the praedorsal segment on abdominal segments with one *pds*, the epicranium lacking *fs*$_{3}$, and the conical layout of the labral setae.

Gymnetron villosulum Gyllenhal, 1838

Material examined. Serbia, Boljetin, GPS 44°30.973'N, 22°0.921'E, 139 m, ex gall *Veronica anagallis-aquatica*, 16.07.2012, leg. Toševski (3 larvae and 1 pupa).

Description of mature larva (Figs 21A, B, 22A–F, 23A–C). ***Measurements*** (in mm). Body length: 2.25–2.46. The widest point in the body (meso- and metathorax) measures up to 1.20. Head width: 0.40–0.51.

General. Body elongate, slender, weakly curved, rounded in cross section (Fig. 21A).

Colouration. Head dark brown (Fig. 21B). All thoracic and abdominal segments white with many reddish or brown asperities (Fig. 21A).

Vestiture. Setae on body thin, orange, distinctly different in length (minute to very short or long).

Head capsule (Figs 21B, 22A). Head suboval, flattened laterally, endocarinal line present, clearly extending to 1/3 of the length of frons. Frontal sutures on head very broad and distinct. Stemma, in the form of a very small pigmented spot with convex cornea. *Des*$_{1}$ short, located in middle of central part of epicranium; *des*$_{2}$ absent; relatively long *des*$_{3}$ located anteriorly on epicranium close to border with frontal suture; *des*$_{4}$ absent; *des*$_{5}$ long, located anterolaterally (Fig. 22A). *Fs*$_{1}$ absent; *fs*$_{2}$ relatively long, located medially; *fs*$_{3}$ absent; *fs*$_{4}$ relatively long, located anteriorly; and *fs*$_{5}$ long, located anterolaterally, close to antenna (Fig. 22A). *Les*$_{1}$ and *les*$_{2}$ as long as *des*$_{5}$; *ves* short. Epicranial area with two postepicranial setae.

Antennae membranous and distinctly convex basal membranous article bearing one relatively long conical sensorium and four sensilla basiconica (Fig. 22B).

Clypeus (Fig. 22C) ~ 3–4× as wide as long with two relatively long *cls*, located posterolaterally, without sensillum; fused to labrum.

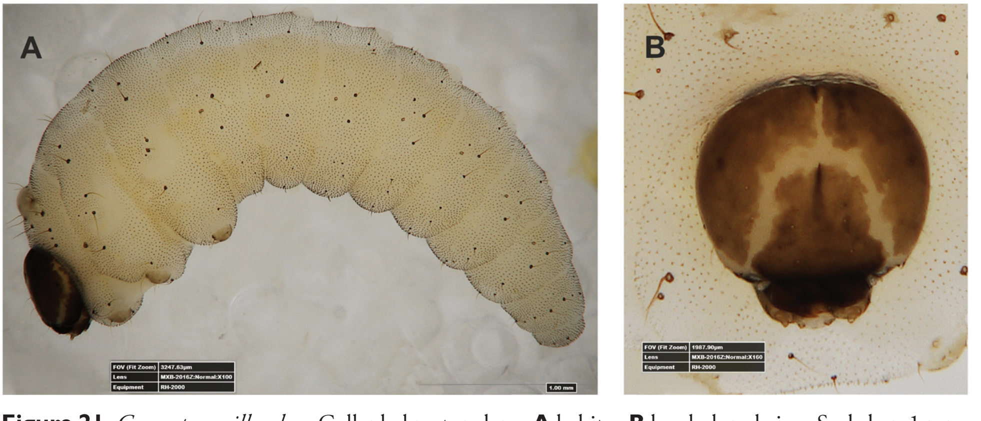

Figure 21. *Gymnetron villosulum* Gyllenhal mature larva **A** habitus **B** head, dorsal view. Scale bar: 1 mm.

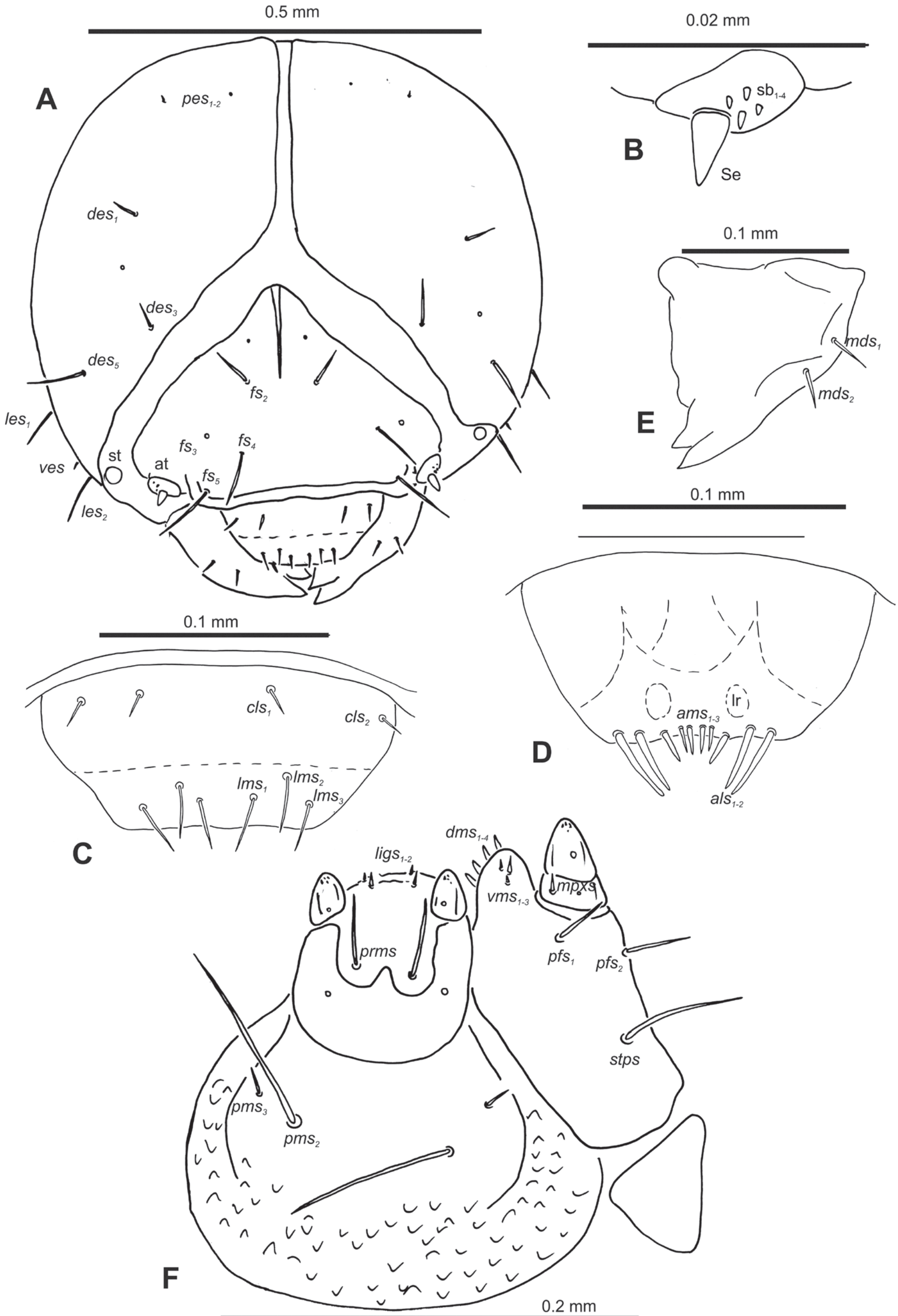

Figure 22. *Gymnetron villosulum* Gyllenhal mature larva, head and mouth parts **A** head **B** antenna **C** clypeus and labrum **D** epipharynx **E** left mandible **F** maxillolabial complex. Abbreviations: at – antenna, lr – labral rods, sb – sensillum basiconicum, Se – sensorium, st – stemma; setae: *als* – anteriolateral, *ams* – anteromedial, *cls* – clypeal, *des* – dorsal epicranial, *dms* – dorsal malar, *fs* – frontal epicranial, *les* – lateral epicranial, *ligs* – ligular, *lms* – labral, *mds* – mandibular dorsal, *mpxs* – maxillary palps, *pes* – postepicranial, *pfs* – palpiferal, *pms* – postmental, *prms* – premental, *stps* – stipital, *ves* – ventral, *vms* – ventral malar.

Mouth parts. Labrum (Fig. 22C) ~ 4× as wide as long, with three piliform *lms*, relatively long, almost of equal length; *lms*$_1$ located anteromedially, *lms*$_2$ partly located close to clypeus, and *lms*$_3$ located anterolaterally. Epipharynx (Fig. 22D) with two very long digitate *als*, almost identical in length; with three *ams* of different length, *ams*$_1$ and *ams*$_2$ piliform and short, digitate *ams*$_3$ and enlarged in middle; without *mes*; labral rods indistinct, irregular in shape. Mandibles (Fig. 22E) with two relatively long, piliform *mds*, located

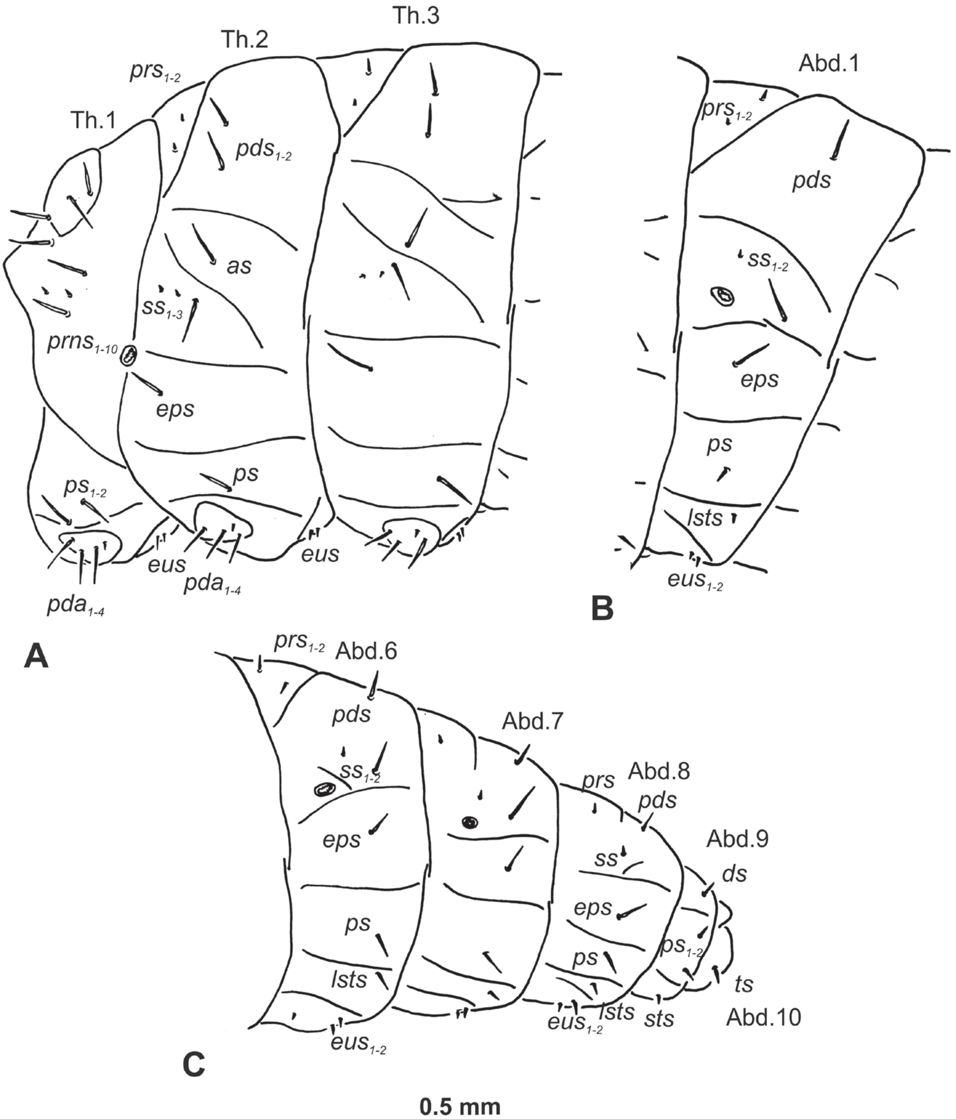

Figure 23. *Gymnetron villosulum* Gyllenhal mature larva, habitus **A** lateral view of thoracic segments **B** lateral view of abdominal segment I **C** lateral view of abdominal segments VI–X. Abbreviations: Th1–3 – numbers of thoracic segments, Ab1–10 – numbers of abdominal segments; setae: *as* – alar, *ds* – dorsal, *eps* – epipleural, *eus* – eusternal, *lsts* – laterosternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *ss* – spiracular, *ps* – pleural, *sts* – sternal, *ts* – terminal.

Figure 24. *Gymnetron villosulum* Gyllenhal pupa habitus **A** ventral view **B** dorsal view. Scale bars: 1 mm.

in distinct holes. Maxilla (Fig. 22F): stipes with one *stps*, two *pfs* and without *mbs* and sensillum, *stps* and *pfs*$_1$ long, *pfs*$_2$ relatively long; mala with four short digitate *dms*; three *vms*, different lengths, one seta very short, and two setae minute. Maxillary palpi with two palpomeres; length ratio of basal and distal palpomeres: 1:0.5. Praelabium (Fig. 22F) oval, with one long *prms*; ligula with sinuate margin and two very short *ligs*; premental sclerite broad, well visible. Postlabium (Fig. 22F) with two *pms*, *pms*$_1$ absent, short *pms*$_2$ located laterally and very long *pms*$_3$ located medially; membranous area sparsely and finely asperate.

Thorax. Prothorax (Fig. 23A) with six long and two very short to minute *prns*, small pigmented dorsal sclerite present with two long *prns*, this sclerite subdivided into two triangular plates medially; two long *ps*; and two short to very short *eus*. Mesothorax (Fig. 23A) with two very short to minute *prs*, two long *pds*; one long *as*; one long and two very short to minute *ss*; one long *eps*; one long *ps*; and two short *eus*. Chaetotaxy of metathorax (Fig. 23A) almost identical to that of mesothorax. Each pedal area of thoracic segments well separated, with three long and one very short to minute *pda*.

Abdomen. Spiracles on abdominal segments I–VI close to the anterior margin and functional, spiracles on abdominal segment VII not functional, and abdominal segment VIII with atrophied spiracles. Abdominal segments I–VI (Fig. 23B, C) with one short and one minute *prs*; one long *pds*; one long and one very short to minute *ss*; one long *eps*; one relatively long *ps*; one short *lsts*; and two very short and sometimes one additional minute *eus*. Abdominal segments VII–VIII (Fig. 23C) with one very short *prs*; one long *pds*; one long and one very short to minute *ss*; one long *eps*; one relatively long *ps*; one short *lsts*; and two very short and sometimes one additional minute *eus*. Abdominal segment IX (Fig. 23C) with one relatively long *ds*; two relatively long *ps*; and one short to very short *sts*. Abdominal segment X (Fig. 23C) with one very short seta (*ts*).

Description of pupa (Figs 24A–C, 25A–C). ***Measurements*** (in mm). Body length: 2.24–2.73. Body width: 1.30–1.55. Thorax width: 0.82–0.88.

Body. Brownish, pronotal protuberances (p-pr) sclerotized, smooth; head, rostrum and pronotum darker than rest of body. Rostrum moderately slender. Pronotal protu-

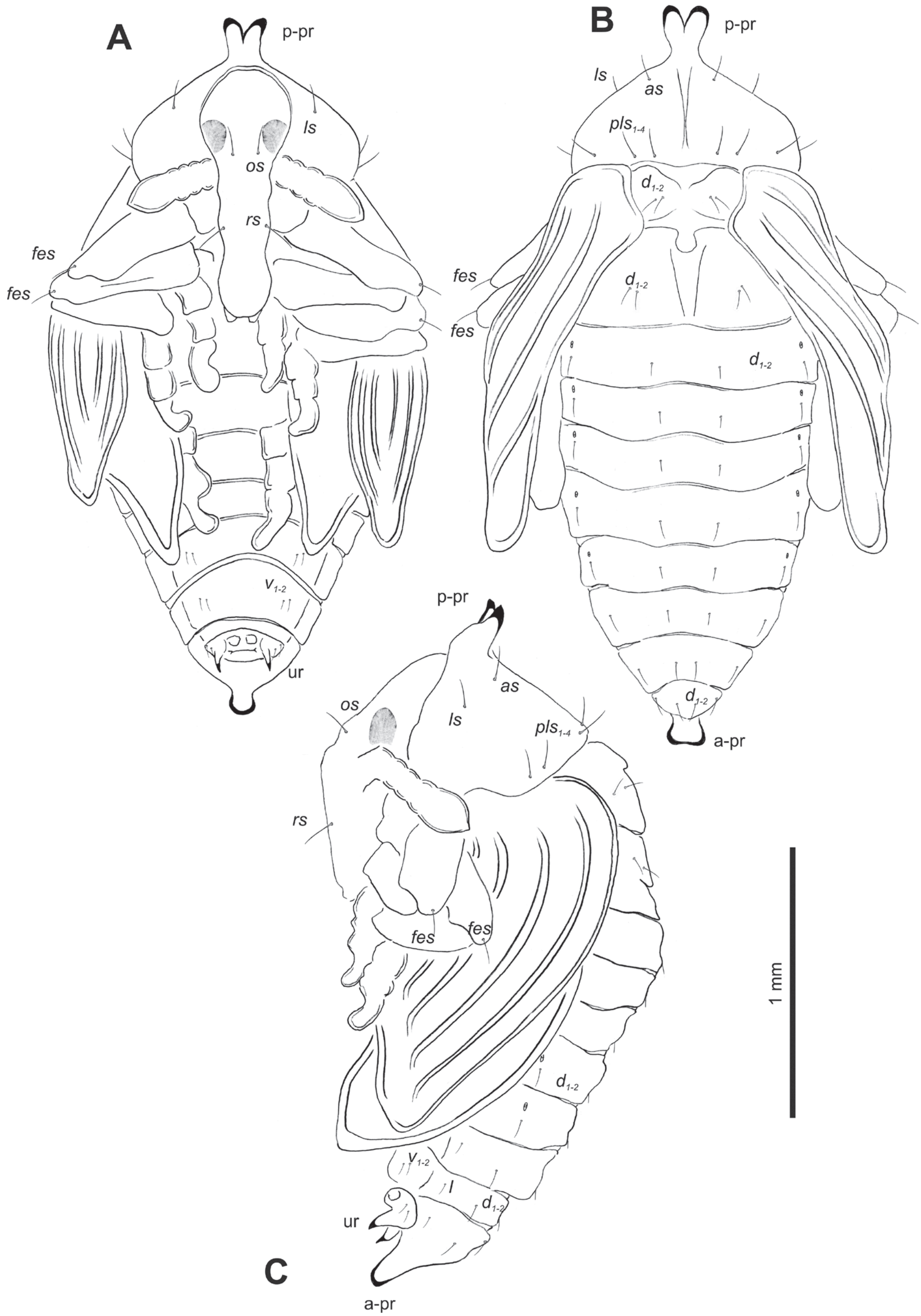

Figure 25. *Gymnetron villosulum* Gyllenhal pupa habitus **A** ventral view **B** dorsal view **C** lateral view. Abbreviations: a–pr – abdominal protuberances, p–pr – pronotal protuberances, ur – urogomphi; setae: *as* – apical, *d* – dorsal, *ds* – discal, *fes* – femoral, *l*, *ls* – lateral, *os* – orbital, *pls* – posterolateral, *rs* – rostral, *v* – ventral.

berances fused at basis. Pronotum 2.2× as wide as long. Mesonotum distinctly smaller than metanotum. Urogomphi short, conical, with sclerotized apices. Abdominal segment VIII with rounded, prominent abdominal protuberance dorsally (Fig. 25A, B).

Chaetotaxy. Sparse, setae short to medium, transparent. Head with one medium *os*. Rostrum with one *rs* (Fig. 25A). Pronotum with one elongate *as*, one *ls*, and four *pls* all almost equal in length. Dorsal parts of meso- and metathorax with two setae of various length, placed medially. Apices of femora with one medium-sized *fes* (Fig. 25A–C). Abdominal segments I–VIII with two medium-sized setae (one placed medially, the other laterally). Each lateral part of abdominal segments I–VIII with one medium-sized seta. Ventral parts of abdominal segments I–VIII with two medium-sized setae. Abdominal segment IX with two minute setae ventrally (Fig. 25A–C).

Biological notes. The host plants of this species are several *Veronica* species: *V. anagallis-aquatica* L., *V. anagalloides* Guss., *V. beccabunga* L., *V. catenata* Pennell, *V. scutellata* L. (Kleine 1910; Urban 1930; Hustache 1931; Hoffmann 1958; Sprick 1997). The adults appear on the host plants in May. The females oviposit during June in the ovarial tissue, inducing a bulbous gall in which the larva develops.

Remarks and comparative notes. This species is common in the whole of Europe and Anatolia. The adult is closely related to *G. miyoshii*, a vicariant species living in eastern Asia (Caldara 2008a; Alonso-Zarazaga et al. 2017). The immature stages confirm this relationship, as they share the postdorsal segment on the abdominal segments with one *pds* and the dorsal epicranium without des_4.

Key to the known mature larvae of *Gymnetron* species

The following key is based on the larvae of the five *Gymnetron* species described in this paper and one described by Jiang and Zhang (2015).

1	Postdorsal segment on abdominal segments with one *pds*. Dorsal epicranium without des_4. Postlabium with two *pms*	**2**
–	Postdorsal segment on abdominal segments with two *pds.* Dorsal epicranium with des_4. Postlabium with three *pms*	**3**
2	Pronotum with six *prns* (as *prns* and *dpls*). Des_1 short; des_2 short; des_3 long, fs_2 and fs_4 short. Head with three *pes*	***G. miyoshii***
–	Pronotum with ten *prns*. Des_1 medium; des_2 absent; des_3 medium, fs_2 and fs_4 medium. Head with two *pes*	***G. villosulum***
3	Praedorsal segment on abdominal segments with two *pds.* Epicranium with fs_3. Labral setae in one line	**4**
–	Praedorsal segment on abdominal segments with one *pds.* Epicranium without fs_3. Labral setae in a triangle	**5**
4	Body cuticle covered with numerous reddish or brown asperities, black spots at base of setae. Head dark brown. Epipharynx with two *als* and three *ams*	***G. veronicae***
–	Body cuticle smooth, setae without black spots at base. Head pale yellow. Epiharynx with three *als* and two *ams*	***G. tibiellum***

5 Pronotum with seven setae. Meso- and metathorax with two *as* and one *ss*. Pedal area with three *pda*. *Mbs* present .... ***G. rotundicolle***
– Pronotum with ten setae. Meso- and metathorax with one *as* and three *ss*. Pedal area with five *pda*. *Mbs* absent..................................... ***G. melanarium***

Key to pupae of known *Gymnetron* species

The following key is based on the pupae of the five *Gymnetron* species described in this paper.

1 Abdominal protuberance prominent, disc-shaped. Head with one *os* **2**
– Abdominal protuberance short, conical. Head with two *os*.... ***G. melanarium***
2 Pronotal protuberances with serrated margin. Rostrum without setae. Pronotum with one *ds* and two or three *pls*. Ventral parts of abdominal segment I–VII with three setae **3**
– Pronotal protuberances with smooth margin. Rostrum with one *rs*. Pronotum without *ds* and four *pls*. Ventral parts of abdominal segment I–VII with two setae .... ***G. villosulum***
3 Pronotum with three *pls*. Femora with two *fes*. Dorsal parts of abdominal segments I–VII with three or four setae **4**
– Pronotum with two *pls*. Femora with one *fes*. Dorsal parts of abdominal segments I–VII with two setae... ***G. rotundicolle***
4 Pronotum with one *as*, and one *ls*. Meso- and metathorax with two setae. Dorsal parts of abdominal segments I–VII with three setae....... ***G. tibiellum***
– Pronotum with two *as*, and without *ls*. Meso- and metathorax with three setae. Dorsal parts of abdominal segments I–VII with four setae.......... ***G. veronicae***

Discussion

Comparison with immature stages of known Mecinini

It has been suggested that the number of palpomeres of the labial palpi is one of the most important morphological characters of larvae in the Mecinini (Skuhrovec et al. 2018). Phylogenetically, the basal state in weevils is the presence of two palpomeres on the labial palpi (Marvaldi 1997). In *Mecinus* there are species in the plesiomorphic state (e.g., *Mecinus collaris* Germar, 1821; *Mecinus janthinus* group), but also such with one palpomere (Gosik et al. 2020). All the *Gymnetron* species examined here have one labial palpomere, as do the few species of *Rhinusa* described to date. In contrast, *Cleopomiarus* and *Miarus* generally have two palpomeres, although in some *Cleopomiarus* species the basal palpomere is not distinctly separated from the labium and can appear to be just a single palpomere (Skuhrovec et al. 2018).

Another crucial generic-specific character in Mecinini larvae is the number of air tubes of the thoracic and abdominal spiracles. In *Gymnetron* all the spiracles are unicameral (Jiang and Zhang 2015). In the larvae of *Mecinus* species this character has two states: (1) all spiracles unicameral, as in *Gymnetron* and (2) the thoracic spiracle bicameral and the abdominal ones unicameral, as in some *Rhinusa* (Anderson 1973; May 1993; Ścibior and Łętowski 2018; Gosik et al. 2020). In contrast, all known larvae of *Cleopomiarus* and *Miarus* species have bicameral spiracles on the thorax and abdomen (Skuhrovec et al. 2018).

Another debatable state in the larvae is the number of epipharyngeal setae (especially *ams* and *mes*), which has not yet been completely resolved in Curculionidae (Gosik and Skuhrovec 2011; Stejskal et al. 2014; Trnka et al. 2015). In the Mecinini there are three *als*, two or three *ams*, and none or one *mes*. In our view, the final decision regarding the number of each seta is important, but not crucial, and the comparison between groups/genera should be made together for all three kinds of these epipharyngeal setae in order to make fewer errors when creating a differential diagnosis for the genera in the tribe.

The last important characteristic observed within the Mecinini tribe is the integument of the body covered with distinct asperities, both in the larval and pupal stages (Skuhrovec et al. 2018). This feature is very variable within each genus, probably owing to the distinctive environmental conditions within plant tissues.

With regard to the pupae, an uncommon character is the presence of two more or less sclerotized pronotal prominences, which can be smooth or serrated. Moreover, these pronotal protuberances (p-pr) are divisible into two parts with or without a stem from the pronotum and may have conical asperities or serrated margins. These prominences are present in all the *Gymnetron* species studied here, but also in some *Rhinusa* and a few *Mecinus* (Gosik 2010). The evolutionary significance of this character, which disappears altogether in the adult, is unclear.

Differences between immatures at the species level

All the larvae and pupae of every species studied here, and also the three described by Jiang and Zhang (2015), have several characters distinguishing them from one another. These differences confirm that most of them belong to different groups, as suggested by the study of the adults (Caldara 2008a). Three species, very closely related on the basis of the adult morphology (*G. veronicae*, *G. tibiellum* and *G. auliense*), also have several characters in common in the larvae (presence of fs_3; pro- and postdorsal folds of abdominal segments I–VI (VIII) with two *prs* and two *pds*; labral setae in one line) and in the pupae (sclerotized pronotal protuberances covered with conical asperities). The other two related species, *G. villosulum* and *G. miyoshii*, resemble each other more than the other species (in the larvae des_4 and *mbs* absent, postdorsal segment on abdominal segments with one *pds*; in the pupae pronotal protuberances smooth). The other species do not show clear relationships with each other or with the group of *G. veronicae* and *G. villosulum*. Only *G. vittipenne* could be related to the *G. villosulum* group, as also shown by the phylogenetic tree of the adults reported by Caldara (2008a).

Biological and evolutionary considerations

This study confirms that all the Palaearctic species of the genus *Gymnetron* with known biologies live only on *Veronica*. No other species belonging to the Mecinini live on this genus of Plantaginaceae. All the species usually seem to feed on various species of this genus, partly unrelated to each other and belonging to different subgenera as currently considered (Albach et al. 2004). They feed on the ovary or the stem of the plant, sometimes forming more or less voluminous galls. A recent study of *Gymnetron* and *Rhinusa* indicated a strong phylogenetic signal with respect to host plants but a weaker one with respect to the particular plant structures occupied by the insects in question on different plant structures (Hernández-Vera et al. 2013).

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RESEARCH ARTICLE

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Two new species of the genus *Joeropsis* Koehler, 1885 (Isopoda, Asellota, Joeropsididae) from Korean waters

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Abstract
Two new species, *Joeropsis denticulatus* **sp. nov.** and *Joeropsis semicircularis* **sp. nov.** are reported from South Korea. *Joeropsis denticulatus* **sp. nov.** can be identified by the following character states: whole body has dark brown chromatophores dorsally, lateral margins of the cephalon are smooth and narrowing anteriorly, and basis of pereopods has serrated cuticular scales superiorly. *Joeropsis semicircularis* **sp. nov.** can be identified by the following character states: the cephalon, pereonite 4, and pleotelson have dark brown chromatophores dorsally, lateral margins of the cephalon are smooth and parallel each other, and flagellar article 1 of the antenna is swollen and semi-circular in shape.

Keywords
Isopoda, *Joeropsis*, morphology, new species, South Korea, taxonomy

Introduction

The genus *Joeropsis* Koehler, 1885 including 77 species is the largest genus in the family Joeropsididae Nordenstam, 1933 (Boyko et al. 2008). *Joeropsis* can be distinguished from other joeropsidid genera by having a laterally parallel body shape, a dorsally smooth or finely granular body surface, and a not medially expanded maxillipedal palp article 3 (Just 2001; Bruce 2015). Although, occasionally, the colour pattern fades of a body for old preserved specimens or shows intraspecific variations in some species, the pattern of the body has been recognized as an apparent character in *Joeropsis* taxonomy to distinguish species (Menzies 1951; Bruce 2015). Additionally, Bruce (2015) has recently mentioned that shapes of the cephalon, pseudorostrum, maxilliped, pleotelson, male pleopod 1, and uropods can be useful diagnostic characters in this genus.

The genus *Joeropsis* is common in shallow coastal waters, particularly, colonizing in coral reef habitats (Bruce 2009, 2015). The genus is known to be distributed worldwide and is well represented in tropical regions such as the Indo-West Pacific (Kensley and Schotte 2002; Bruce 2009, 2015). Although the genus represents the highest species diversity in the Pacific Ocean with 33 recorded species (Boyko et al. 2008), only nine species have been reported from the North Pacific (Miller 1941; Menzies 1951; Schultz 1966; Kensley 1989; Kussakin 1999; Nunomura 1999). In particular, our knowledge on the genus is relatively poor in the temperate Far East, and only four species have been recorded: *J. affinis* Kussakin, 1961 from the middle Kuril Islands, Russia; *J. lata* Kussakin, 1961 from the Western Kamchktka Shelf, Russia; *J. lobota* Richardson, 1899 from Osaka Bay, Japan; and *J. latiantennata* Nunomura, 1999 from the Shikine Island, Japan (Kussakin 1961; Nunomura and Nishimura 1976; Nunomura 1999). During surveys of Korean isopods, the authors found two apparently undescribed *Joeropsis* species from sublittoral habitats. Here, we provide detailed descriptions and illustrations of these two species.

Material and methods

Materials of *J. denticulatus* sp. nov. and *J. semicircularis* sp. nov. were collected from eight sampling stations of the sublittoral zones in Korean waters using a Smith-McIntyre grab and SCUBA diving (Fig. 1; Table 1). The substrate was gravel mud flat with depths of 10 to 30 m. Collected material was sorted using a sieve with a 1 mm mesh size and immediately fixed with 94% ethyl alcohol. After transferring this material to the laboratory, observation was conducted under a dissecting microscope (Olympus SZH-ILLD) and a compound microscope (Olympus BX50). Measurements and drawings of specimens were carried out with the aid of a drawing tube. Terminology for body and appendage morphology follows Bruce (2009, 2015). Drawings were digitally scanned, inked, and arranged using a tablet and Adobe Illustrator CS6 as described by Coleman (2003, 2009). Examined materials in this study were deposited at the National Institute of Biological Resource (**NIBR**) and Chosun University in South Korea.

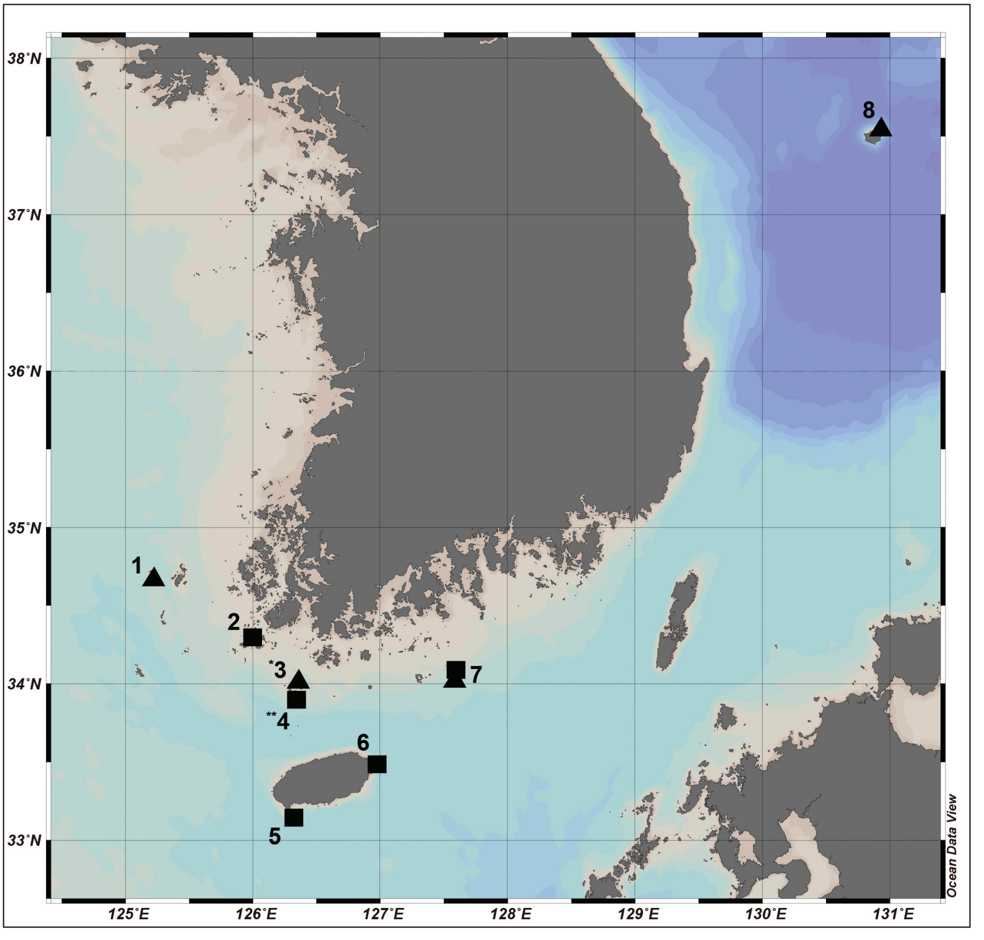

Figure 1. Map of the sampling stations of *J. denticulatus* sp. nov. (filled square, ■) and *J. semicircularis* sp. nov. (filled triangle, ▲). Station numbers of sampling localities (also type localities) are listed in Table 1.

Table 1. Sampling stations of the two new species in Korean waters.

No.	Locality	Geographical Coordinates	Depth (m)	Collecting method	Date
1	Jeollanam-do, Sinan-gun, Heuksan-myeon, Hondo-ri, Hongdo Island	34°40'09"N, 125°10'59"E	10	SCUBA diving	19 Jun. 2018
2	Jeollanam-do, Sinan-gun, Jangsan-myeon, Baegyado Island	34°22'24"N, 126°00'15"E	10	SCUBA diving	12 Apr. 2018
*3	Jeju-do, Jeju-si, Chuja-myeon, Chujado Island	33°59'08"N, 126°19'08"E	10	SCUBA diving	06 Jul. 2019
**4	Jeju-do, Jeju-si, Chuja-myeon, Chujado Island	33°55'18"N, 126°19'27"E	20	Smith-McIntyre grab	17 Apr. 2019
5	Jeju-do, Seoqwipo-si, Daejeong-eup	33°11'24"N, 126°16'08"E	30	Smith-McIntyre grab	31 Jan. 2018
6	Jeju-do, Jeju-si, Udo-myeon, Udo Island	33°31'38"N, 126°57'14"E	15	Smith-McIntyre grab	17 Apr. 2019
7	Jeollanam-do, Yeosu-si, Samsan-myeon, Sangbaeckdo Island	34°03'15"N, 127°35'00"E	15	SCUBA diving	28 Jun. 2017
8	Gyeongsangbuk-do, Ulleung-gun, Buk-myeon, Cheonbu-ri, Gwaneumdo Islet off Ulleungdo Island	37°32'43"N, 130°55'22"E	20	SCUBA diving	19 Jun. 2016

*, type locality of *Joeropsis semicircularis* sp. nov.; **, type locality of *J. denticulatus* sp. nov.

Taxonomy

Order Isopoda Latreille, 1817
Suborder Asellota Latreille, 1802
Superfamily Janiroidea G.O. Sars, 1897
Family Joeropsididae Nordenstam, 1933

Genus *Joeropsis* Koehler, 1885

Joeropsis Koehler, 1885: 7; Kensley and Schotte 1989: 87; Wilson 1997: 86; Kussakin 1999: 12; Just 2001: 304; Kensley and Schotte 2002: 1428.
Jæropsis: Richardson 1905: 476; Stebbing 1905: 50.
Jaeropsis: Nordenstam 1933: 191; Menzies and Barnard 1959: 10; Menzies 1962: 64; Menzies and Glynn 1968: 76.
Iaeropsis: Nierstrasz 1941: 288 (unjustified emendation).

Type species. *Joeropsis brevicornis* Koehler, 1885 by original designation.

Diagnosis. Body smooth, rarely with sculpture dorsally, laterally parallel. Pseudorostrum with overhanging apex. Eyes positioned dorsolaterally. Mandibles with evenly spaced cusps; spine row consisting of long setae. Maxilliped, endite reaching end of palp article 3; palp article 3 lacking medial lobe. Pereopod 1 with 2 claws and pereopods 2–7 with 2 or 3 claws. Pleopod 2 with a few short simple setae distally in females. Pleopod 3, exopod obliquely articulated between articles (Just 2001; Bruce 2015).

Remarks. The genus *Joeropsis* can be differed from other joeropsidid genera by having a dorsally smooth or finely granular body (vs. coarsely granular and nodular in *Rugojoeropsis* Just, 2001) and parallel lateral body shape (vs. converging posteriorly in *Scaphojoeropsis* Just, 2001) (Bruce 2015). The colour pattern of a body can be distinguishable to easily separate members of the genus (Bruce 2015). Additionally, the morphology of the cephalon, pseudorostrum, antennae, maxilliped, pleotelson, and male pleopod 1 can be the most diagnostic characters for *Joeropsis* species (Kensley and Schotte 2002; Bruce 2009, 2015).

Joeropsis denticulatus sp. nov.

http://zoobank.org/0835482B-A1B9-4B6C-A73A-53BC7DAE399A
Figs 2A, 3–5

Material examined. ***Holotype*, designated here:** South Korea • 1 ♂ (5.0 mm); Jeju-do, Jeju-si, Chuja-myeon, Chujado Island; 33°55'18"N, 126°19'27"E; 20 m; 17 Apr. 2019; Smith-McIntyre grab; NIBRIV0000862803.

***Paratypes*:** 2 ♂♂ (4.2, 4.8 mm), 3 ♀♀ (3.6, 3.8, 3.8 mm); same data as for holotype; NIBRIV0000896084.

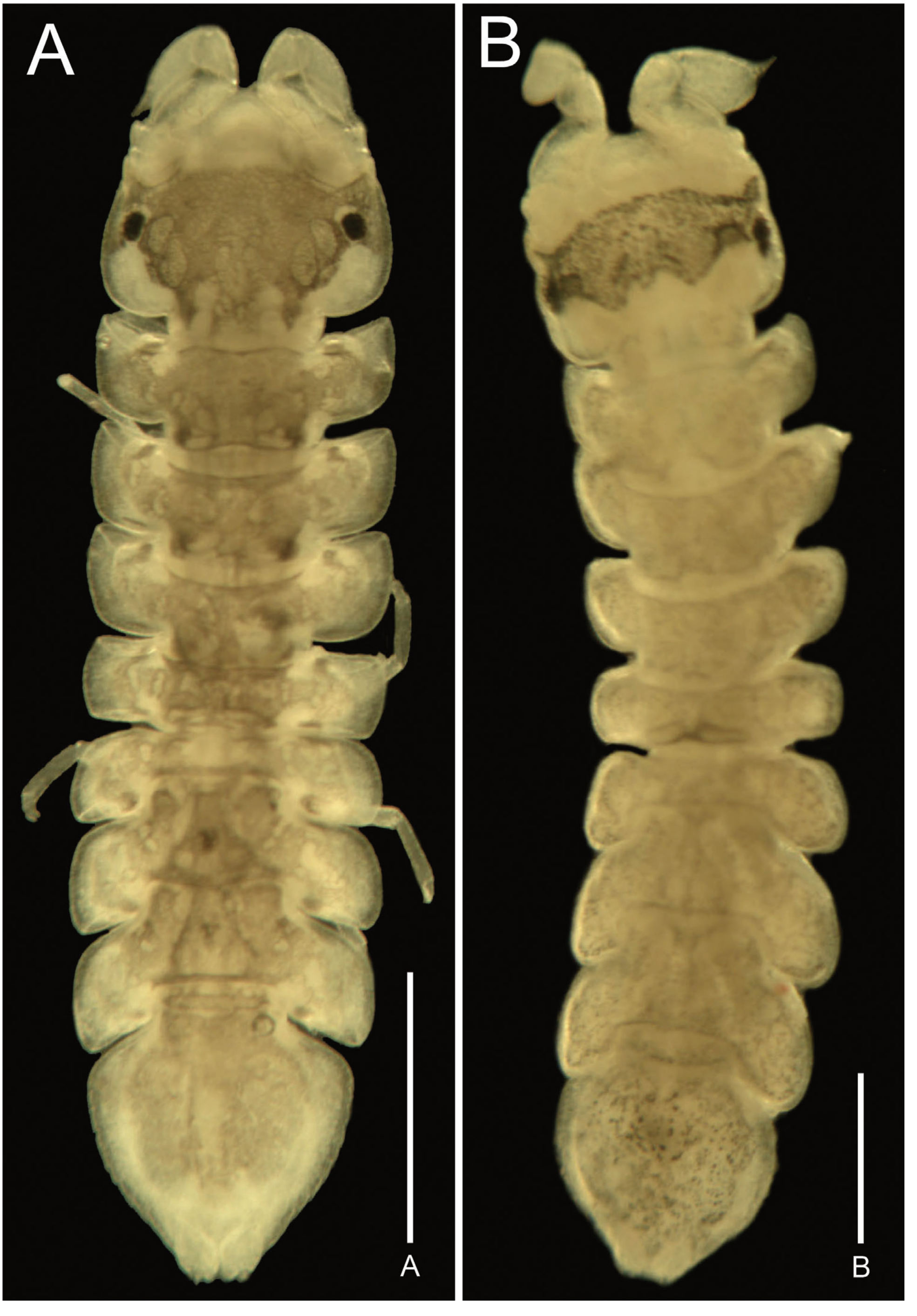

Figure 2. Photographs of two new species of *Joeropsis*: **A** *J. denticulatus* sp. nov., one of paratypes (NIBRIV0000896084), dorsal view **B** *J. semicircularis* sp. nov., one of paratypes (NIBRIV0000896085), dorsal view. Scale bars: 10 mm (**A**); 5 mm (**B**).

Additional material. South Korea • 1 ♂; Jeju-do, Jeju-si, Udo-myeon, Udo Island; 33°31'38"N, 126°57'14"E; 17 Apr. 2019; 15 m; Smith-McIntyre grab • 5 ♂♂, 4 ♀♀; Jeju-do, Seoqwipo-si, Daejeong-eup; 33°11'24"N, 126°16'08"E; 31 Jan. 2018; 30 m; Smith-Mclntyre grab; NIBRIV0000862803 • 1 ♂; Jeollanam-do, Sinan-gun, Jangsan-myeon, Baegyado Island; 34°22'24"N, 126°00'15"E; 12 Apr. 2018; 10 m; SCUBA diving • 1 ♂; Jeollanam-do, Yeosu-si, Samsan-myeon, Sangbaeckdo Island; 34°03'15"N, 127°35'00"E; 15 m; 28 Jun. 2017; SCUBA diving.

Etymology. The specific name, *denticulatus*, is derived from the Latin word *denticulatus*, meaning "with small teeth". This name refers to pereopods possessing serrate cuticular scales.

Description of holotype male. ***Body*** (Figs 2A, 3A) almost 3.9 × longer than width; dorsal surface matte, smooth, without setae. ***Cephalon*** 0.7 × as long as wide; lateral margins narrowing anteriorly; eyes positioned sublaterally, globular, dark brown, dorsally bulging. ***Pseudorostrum*** (Fig. 3B) 0.7 × as long as proximal wide, narrowing anteriorly; apex rounded. ***Pereonites*** not compact; lateral margins smooth. ***Pleotelson*** ~ 1.0 × longer than greatest width, shield-shaped, tapering distally; caudomedial lobe subacute, tapering distally; lateral margins slightly convex, with 8 spines.

Antennula (Fig. 3C), peduncular article 1 rectangular, 1.4 × longer than width, with serrate cuticular scales distally, 5 simple setae along with lateral margin, 1 penicillate seta distally, and 5 penicillate setae medially; article 2 oblong, 0.5 × as long as article 1, with 1 simple seta and 2 penicillate setae distally, and cuticular scales laterally; article 3 oblong, 0.6 × as long as article 2, with 2 simple setae laterally and 3 simple setae distally; flagellar article 1 almost 0.5 × as long as peduncular article 3, with 1 penicillate seta and 1 simple seta distally; article 2 ~ 2.0 × longer than flagellar article 1, with 2 simple setae and 2 aesthetascs distally, and 1 simple seta laterally; article 3 minute, with 4 simple setae, 1 penicillate seta, and 1 aesthetasc on distal end. ***Antenna*** (Fig. 3D, E) with 10 flagellar articles; peduncular article 3 with 1 process on medial margin; article 5 1.4 × longer than articles 1–4 combined, with serrate lateral cuticular scales and 1 medial process proximally; article 6 0.7 × as long as article 5, widening distally, with serrate cuticular scales, 3 penicillate setae, and several simple distal setae; flagellum with numerous simple setae; flagellar article 1 elongate ovoid, 1.8 × longer than remaining articles combined, 1.3 × longer than peduncular article 6, with cuticular scales laterally.

Mandibles (Fig. 3F, G), molar process distal half finely serrated; incisor with 5 cusps; palp article 2 with serrate setae distally; palp article 3 with serrate setae along with lateral margin. ***Left mandible*** (Fig. 3F) with a protrusion between incisor and molar process; spine row composed of 12 serrate setae. ***Right mandible*** (Fig. 3G), spine row consisting of 10 serrate setae. ***Maxillula*** (Fig. 3H), mesial lobe with 3 robust simple setae and several fine setae distally; lateral lobe with 12 strongly serrate robust setae and several fine setae on distal region. ***Maxilla*** (Fig. 3I), mesial lobe shorter than other lobes, with 4 simple setae distally and fine setae along with medial margin; mesial and outer lobes with 4 serrate setae distally. ***Maxilliped*** (Fig. 3J, K), endite expanding half of palp article 4, with several short simple setae on medial surface and 2 coupling

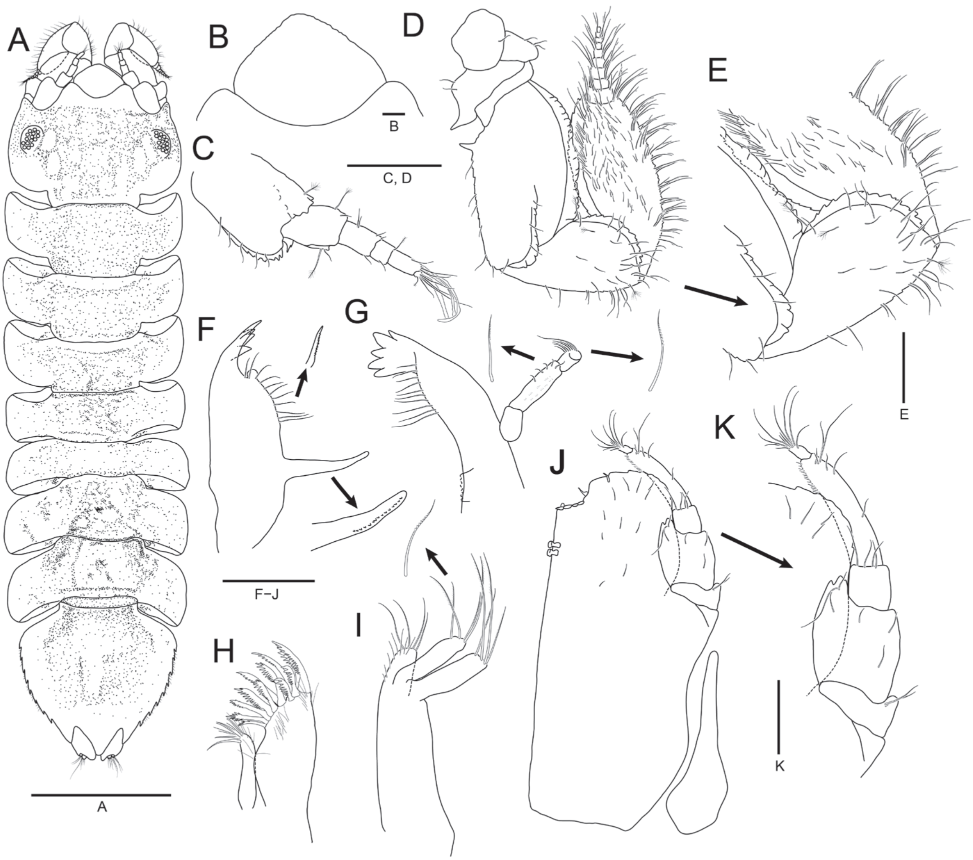

Figure 3. *Joeropsis denticulatus* sp. nov., holotype, male **A** habitus, dorsal view **B** pseudorostrum **C** antennula **D** antenna **E** detail of peduncular articles 5 to flagellar article 1 **F** left mandible **G** right mandible **H** maxillula **I** maxilla **J** maxilliped **K** detail of maxillipedal palp. Scale bars: 1 mm (**A**); 0.2 mm (**C, D, F–J**); 0.1 mm (**E, K**); 0.05 mm (**B**).

hooks on medial distal end; distal region of endite rounded and serrated while concave medially, with 4 medial tubercular robust setae; palp article 1 with 2 simple setae distally, article 2 2.8 × longer than article 1, with distally bifid mesial lobe, article 3 square, 0.4 × as long as article 2, with several simple setae distally, article 4 3.0 × longer than article 3, with fine setae on medial margin and several setae laterally, article 5 0.2 × as long as article 4, with several simple setae on distal end; epipod 3.4 × longer than basal width, tapering distally.

Pereopods (Fig. 4A–G), basis and ischium with serrated cuticular scales superodistally; carpus with slightly serrated cuticular scales inferodistally; propodus with 2–4 robust setae inferiorly and numerous short simple setae along with inferior margin. ***Pereopod 1*** (Fig. 4A), basis with 1 penicillate seta superiorly; ischium subequal to basis in length, narrowing proximally; merus 0.6 × as long as ischium; carpus 1.7 × longer than merus; propodus 0.9 × as long as carpus, with 1 penicillate seta on superior distal

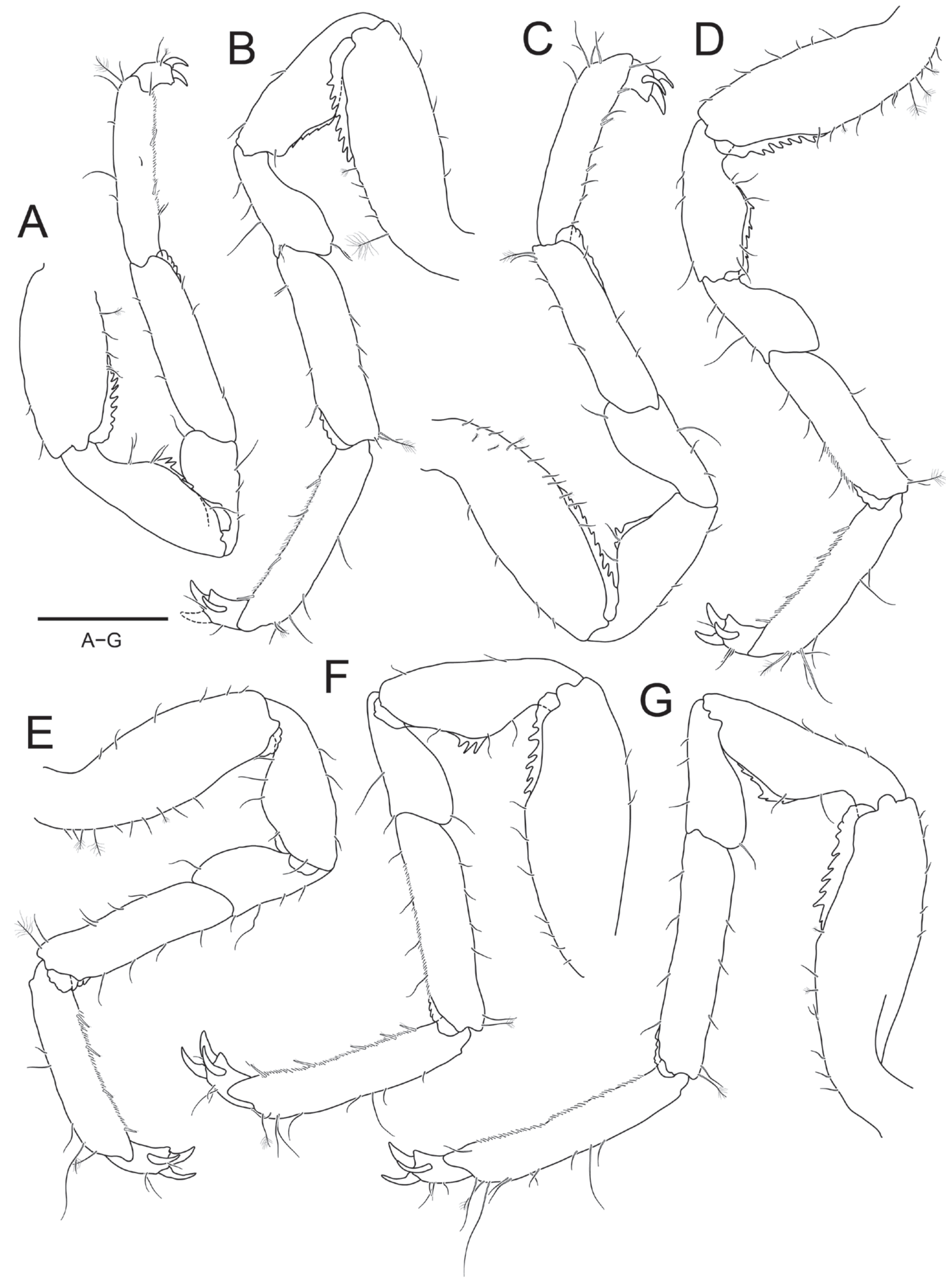

Figure 4. *Joeropsis denticulatus* sp. nov., holotype, male **A** pereopod 1 **B** pereopod 2 **C** pereopod 3 **D** pereopod 4 **E** pereopod 5 **F** pereopod 6 **G** pereopod 7. Scale bar: 0.2 mm.

angle; dactylus 0.2 × as long as propodus, with 2 claws and 1 penicillate seta distally. ***Pereopods 2–7*** (Fig. 4B–G) similar to each other; basis longer than ischium, with 0–2 penicillate setae on superior margin; ischium convex superomedially; carpus ~ 2.0 × longer than merus, with 1 penicillate seta superodistally; propodus similar to carpus in length, with 1 penicillate seta superodistally; dactylus ~ 0.2 × as long as propodus, with 3 claws distally.

Pleopod 1 (Fig. 5A) 2.6 × longer than greatest width, slightly concave laterally, narrowing distally; distolateral lobe projected, extending distally; apical lobe rounded, with marginal simple setae distally. ***Pleopod 2*** (Fig. 5B), protopod 2.7 × longer than mid-width, concave distolaterally bearing cuticular scale-setae, with subacute distal end; endopod positioned at 0.7 length of protopod from proximal region; exopod curved outwardly; appendix masculina reaching distal end of protopod, tapering distally. ***Pleopod 3*** (Fig. 5C), endopod 2.1 × longer than width, with 3 plumose setae distally; exopod with cuticular scale-setae along with lateral margin, first article 3.8 × longer than width; second article 0.4 × longer first article. ***Pleopod 4*** (Fig. 5D), endopod 2.2 × as long as wide, tapering distally; exopod vestigial. ***Pleopod 5*** (Fig. 5E) without exopod; endopod 2.0 × as long as wide, tapering distally.

Uropods (Figs 3A, 5F), protopod extending beyond margin of pleotelson, with strongly produced distal end, serrated medial margin, and 5 simple setae on distal region; endopod with 2 penicillate setae and several simple setae distally; exopod smaller than endopod, with several simple setae distally.

Description of female. Female similar to male. ***Pleopod 2*** (Fig. 5G) 1.4 × longer than greatest width, tapering distally, with fine setae on distal region; apex subacute, with 2 simple setae.

Size. Males 4.2–5.0 mm, mean 4.7 mm (n = 3); females 3.6–3.8 mm, mean 3.7 mm (n = 3); all from type series.

Colour pattern. Whole body is covered with dark brown chromatophores (Figs 2A, 3A).

Variation. The colour pattern of the body varies between individuals, especially on pereonite 5. Dark brown chromatophores are occasionally faint or not observable on it.

Distribution. South Korea (southern coast of the Korean Peninsula).

Remarks. *Joeropsis denticulatus* sp. nov. can be identified by the following character states: (1) whole body has chromatophores dorsally; (2) lateral margins of the cephalon are smooth and narrowing anteriorly; and (3) basis of pereopods has serrated cuticular scales superiorly.

Among the total of 77 species, *Joeropsis denticulatus* sp. nov. is similar to five *Joeropsis* species in having the laterally smooth and narrowing cephalon, anteriorly rounded pseudorostrum, medially lobed maxillipedal palp article 2, laterally serrated pleotelson, and medially serrated uropods: *J. adusta* Bruce, 2015; *J. affinis* Kussakin, 1961; *J. brevicornis* Koehler, 1885; *J. dubia* Menzies, 1951; and *J. salvati* Müller, 1989. Among them, *J. denticulatus* sp. nov. most closely resembles *J. dubia* in terms of pereopods with serrated cuticular scales on ischium, but the former can be distinguished from the latter by having pereopod 1 bearing serrated cuticular scales on the basis (vs. lacking serrated cuticular scales in the latter) and distally rounded pleopod 1 in males (vs. distally triangular in the latter) (Menzies 1951; Kussakin 1999). The new species can be distinguished from the remaining four species in terms of maxillipedal palp article 2 (having distally bifid medial lobe vs. having not in the latter species) and pereopods (having serrated cuticular scales on

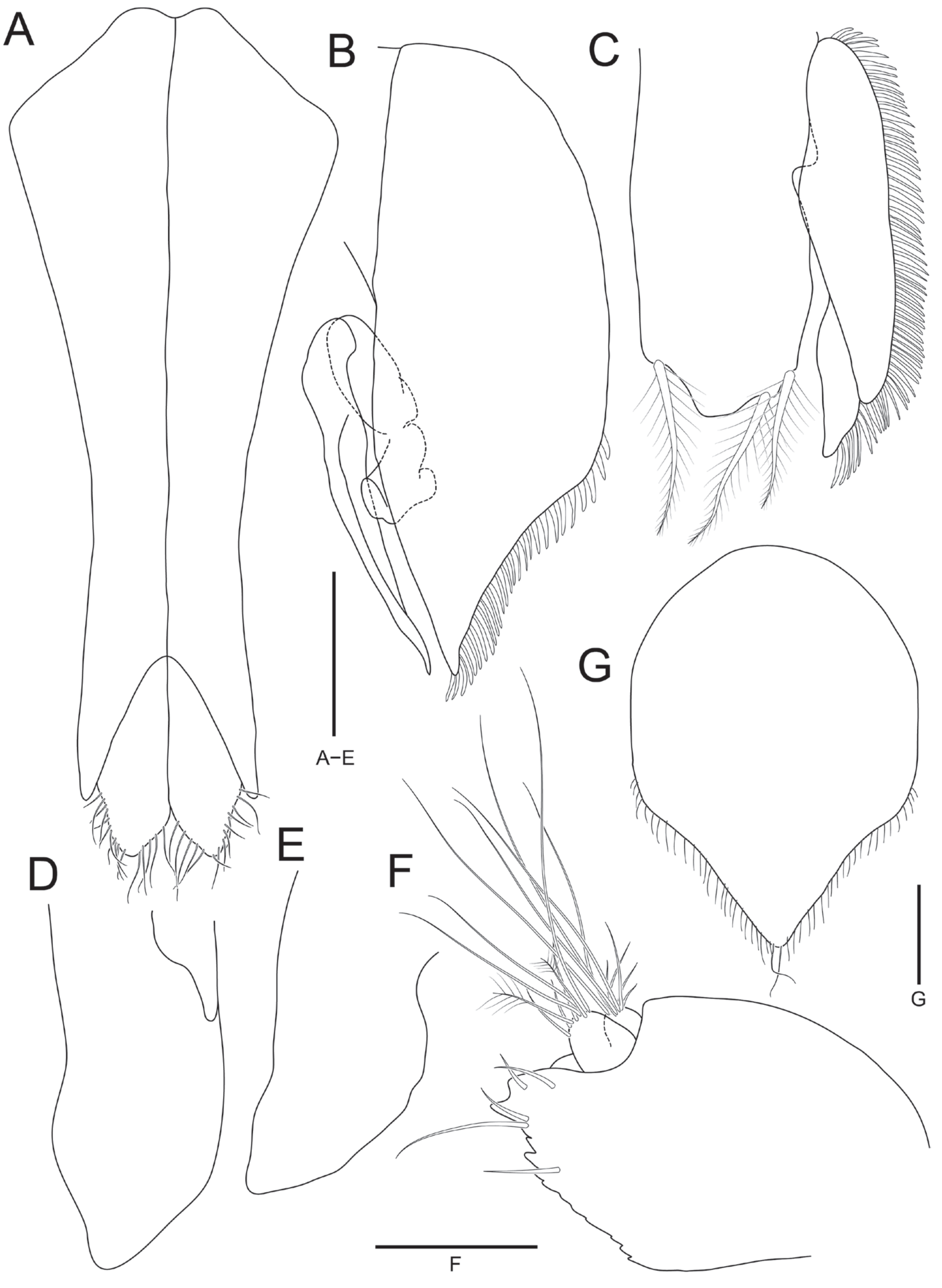

Figure 5. *Joeropsis denticulatus* sp. nov., holotype, male **A** pleopod 1 **B** pleopod 2 **C** pleopod 3 **D** pleopod 4 **E** pleopod 5 **G** uropod. Paratype, female: **F** pleopod 2. Scale bars: 0.2 mm (**A–E, G**); 0.1 mm (**F**).

the basis in the former vs. lacking in the latter species) (Koehler 1885; Bocquet and Lemercier 1958; Amar 1961; Kussakin 1961, 1999; Kensley 1975; Müller 1989; Bruce 2015). A detailed comparison of *Joeropsis* species mentioned above is provided in Table 2.

Table 2. Comparison of diagnostic characters among *Joeropsis* species.

Species	Cephalon, lateral margins	Pseudorostrum, apex	Antenna, flagellar article 1	Maxilliped, medial lobe in palp article 2	Pleotelson, lateral margins	Uropod, medial margin
J. denticulatus sp. nov.	Anteriorly narrowing/ smooth	Rounded	Not swollen	Present	Serrated	Serrated
J. semicircularis sp. nov.	Anteriorly narrowing/ smooth	Rounded	Not swollen	Present	Serrated	Serrated
J. adusta	Anteriorly narrowing/ smooth	Rounded	Not swollen	Present	Serrated	Serrated
J. affinis	Anteriorly narrowing/ smooth	Rounded	Not swollen	Present	Serrated	Serrated
J. brevicornis	Anteriorly narrowing/ smooth	Rounded	Not swollen	Present	Serrated	Serrated
J. dubia	Anteriorly narrowing/ smooth	Rounded	Not swollen	Present	Serrated	Serrated
J. salvati	Anteriorly narrowing/ smooth	Rounded/ concave	Not swollen	Present	Serrated	Serrated
J. dollfusi	Parallel/ smooth	Rounded	Not swollen	Absent	Serrated	Serrated
J. latiantennata	Parallel/ smooth	Rounded	Swollen	Absent	Serrated	Not serrated
J. stebbingi	Parallel/ smooth	Rounded	Not swollen	Absent	Serrated	Serrated
J. wolffi	Parallel/ smooth	Rounded	Not swollen	Absent	Serrated	Serrated

Joeropsis semicircularis sp. nov.

http://zoobank.org/2585142C-F02D-4951-B429-DF2321053C65

Figs 2B, 6–8

Material examined. ***Holotype*, designated here:** South Korea • 1 ♂ (3.7 mm); Jeju-do, Jeju-si, Chuja-myeon, Chujado Island; 33°59'08"N, 126°19'08"E; 10 m; 06 Jul. 2019; SCUBA diving; NIBRIV0000862804.

***Paratypes*:** 3 ♂♂ (3.7, 4.0, 4.0 mm), 6 ♀♀ (3.3, 3.4, 3.5, 3.5, 3.6, 3.7 mm), same data as holotype; NIBRIV0000896085.

Additional material. South Korea • 1 ♂; Jeollanam-do, Sinan-gun, Heuksan-myeon, Hondo-ri, Hongdo Island; 34°40'09"N, 125°10'59"E; 10 m; 19 Jun. 2018; SCUBA diving • 1 ♂, 1 ♀; Jeollanam-do, Yeosu-si, Samsan-myeon, Sangbaeckdo Island; 34°03'15"N, 127°35'00"E; 15 m; 28 Jun. 2017; SCUBA diving • 1 ♂, 4 ♀♀; Gyeongsangbuk-do, Ulleung-gun, Buk-myeon, Cheonbu-ri, Gwaneumdo Islet off Ulleungdo Island; 37°32'43"N, 130°55'22"E; 20 m; 19 Jun. 2016; SCUBA diving.

Etymology. The specific name, *semicircularis* is derived from the combination of Latin words *semis*, meaning "a half", and *circularis*, meaning "round". This name refers to the first flagellar article of the antenna that is semi-circular in shape.

Description of holotype male. ***Body*** (Figs 2B, 6A) almost 4.4 × longer than width; dorsal surface matt and smooth, without setae. ***Cephalon*** 0.8 × as long as wide; lateral margins parallel. ***Pseudorostrum*** (Fig. 6B) 0.7 × as long as proximal wide, narrowing anteriorly; apex rounded and rough. Eyes positioned sublaterally, bulging. ***Pereonites*** not compact, widely spaced, with smooth lateral margins. ***Pleotelson*** (Fig. 6C) 1.1 × longer than width, almost globular, tapering on posterior region; lateral margin serrated, with simple setae; caudomedial lobe rounded distally.

Antennula (Fig. 6D), peduncular article 1 square to globular, with cuticular scales along with outer margin; article 2 subsquare, 0.3 × as long as peduncular article 1, with 3 penicillate setae, 2 simple setae, and serrated cuticular scales distally; article 3 0.8 × as long as article 2; flagellar article 1 0.6 × as long as peduncular article 3, with 1 penicillate seta distally; article 2 1.8 × longer than flagellar article 1, with simple setae distally; article 3 minute, with 2 aesthetascs and simple setae on distal end. ***Antenna*** (Fig. 6E, F) composed of 6 peduncular articles and 5 flagellar articles; peduncular article 3 with 1 process on medial margin, article 5 about 1.7 × longer than articles 1–4 combined, with cuticular scales laterally, and 2 simple setae and 2 penicillate setae distally; article 6 0.7 × as long as article 5, with cuticular scales along with distolateral margin; flagellum with numerous simple setae; flagellar article 1 semi-circular, 3.8 × longer than flagellar articles 2–5 combined, 1.3 × longer than peduncular article 6, with cuticular scales on convex margin.

Mandibles (Fig. 6G, H), molar process finely serrate in distal half; spine row with 11 serrate setae in left mandible but 10 in right mandible, and incisor with 5 cusps; palp article 2 with 6 serrate setae distally, article 3 with 10 serrate setae along with lateral margin. ***Maxillula*** (Fig. 6I) inner lobe with 3 robust simple setae and several fine setae distally; outer lobe with 12 strongly serrate robust setae and 2 simple setae distally. ***Maxilla*** (Fig. 6J), inner lobe shorter than 2 outer lobes, with 4 simple setae distally and several fine setae laterally; mesial and outer lobes with 4 serrate setae on distal end, respectively. ***Maxilliped*** (Fig. 6K, L), endite almost 1.1 × longer than greatest width, reaching proximal third of palp article 4, truncated distally; distal margin with 4 tubercular robust and 2 short simple setae medially; medial margin with 3 coupling hooks distally; palp article 2 2.4 × longer than article 1, distomedial margin produced, with 3 simple setae distally; article 3 almost 0.5 × as long as article 2, with 3 setae distally; article 4 1.4 × longer than article 3, 2.8 × as long as wide, tapering distally, with 4 simple setae distally and 1 simple seta laterally; article 5 minute, with 6 simple setae distally; epipod ~ 4.3 × longer than basal width; tapering distally; apex subacute.

Pereopods (Fig. 7A–G), basis and ischium with cuticular scales on superodistal end; carpus with cuticular scales inferodistally and numerous short simple setae on inferodistal end; propodus with 2–4 robust setae and numerous short simple setae along with inferior margin. ***Pereopod 1*** (Fig. 7A), basis 2.7 × longer than width, with 1 simple seta on inferior margin; ischium 0.8 × as long as basis; merus 0.6 × as long as ischium, narrowing proximally; carpus 1.6 × longer than merus; propodus 1.2 × longer than carpus, with 1 penicillate seta superiorly; dactylus 0.3 × as long as propodus, with 2 claws on distal end. ***Pereopods 2–7*** (Fig. 7B–G) similar to each other; basis with penicillate setae and simple setae on both lateral margins; ischium ~ 0.8 × as long as basis, convex on superior margin; merus 0.6 × as long as ischium, tapering proximally; carpus subequal to propodus in length, with penicillate setae superodistally; propodus with 1 penicillate seta on superior margin; dactylus with 3 claws and few simple setae distally.

Pleopod 1 (Fig. 8A) 2.3 × longer than greatest width; lateral margins concave; distolateral lobe pointed, not extending distally; apical lobe rounded, with several simple setae. ***Pleopod 2*** (Fig. 8B), protopod 2.3 × longer than greatest width, concave on subapical region, acute distally, with several fine setae on subapical region; endopod positioned at 0.6 length of protopod from proximal region; exopod curved outwardly; appendix masculina acute, extending to apex of protopod. ***Pleopod 3*** (Fig. 8C), endopod 2.1 × longer than half-width, with 3 plumose setae distally; exopod composed of 2 articles, with cuticular scale-setae along with lateral margin, subacute distally. ***Pleopod 4*** (Fig. 8D), endopod 1.5 × longer than greatest width, truncated distally;

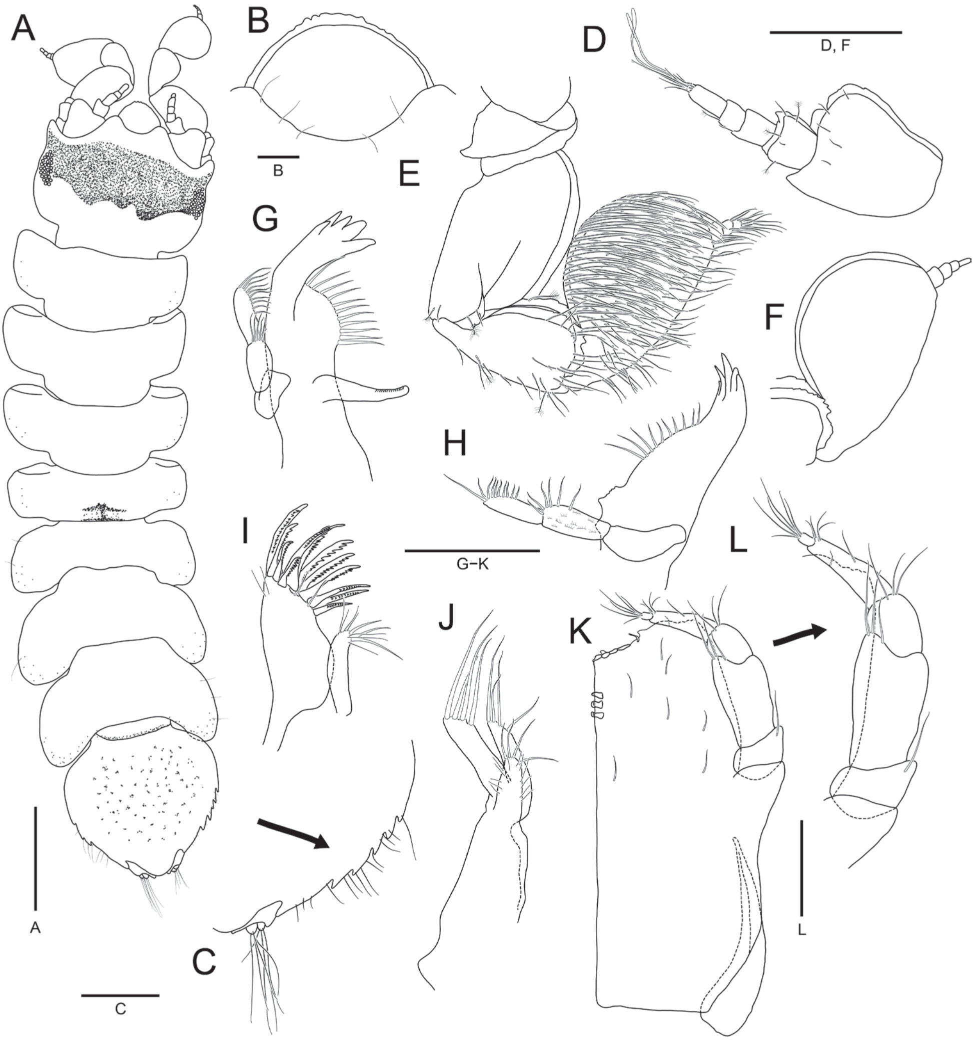

Figure 6. *Joeropsis semicircularis* sp. nov., holotype, male **A** habitus, dorsal view **B** pseudorostrum **C** lateral margin of pleotelson **D** antennula **E** antenna **F** flagellar articles of antenna except for setation **G** left mandible **H** right mandible **I** maxillula **J** maxilla **K** maxilliped **L** detail of maxillipedal palp. Scale bars: 0.5 mm (**A**); 0.2 mm (**C–K**); 0.1 mm (**L**); 0.05 mm (**B**).

exopod vestigial. ***Pleopod 5*** (Fig. 8E) without exopod; endopod 1.9 × longer than basal width, truncated distally.

Uropods (Figs 6A, 8F), protopod extending to distal end of pleotelson, medial margin slightly serrated; distomedial end strongly produced and acute, with 3 simple dorsal setae; endopod with 1 penicillate seta and several simple setae distally; exopod smaller than endopod, with several long simple setae distally.

Description of female. Female similar to male. ***Pleopod 2*** (Fig. 8G) 1.2 × longer than greatest width, globular, narrowing proximally, tapering distally; apex broadly rounded, with 4 simple setae apically.

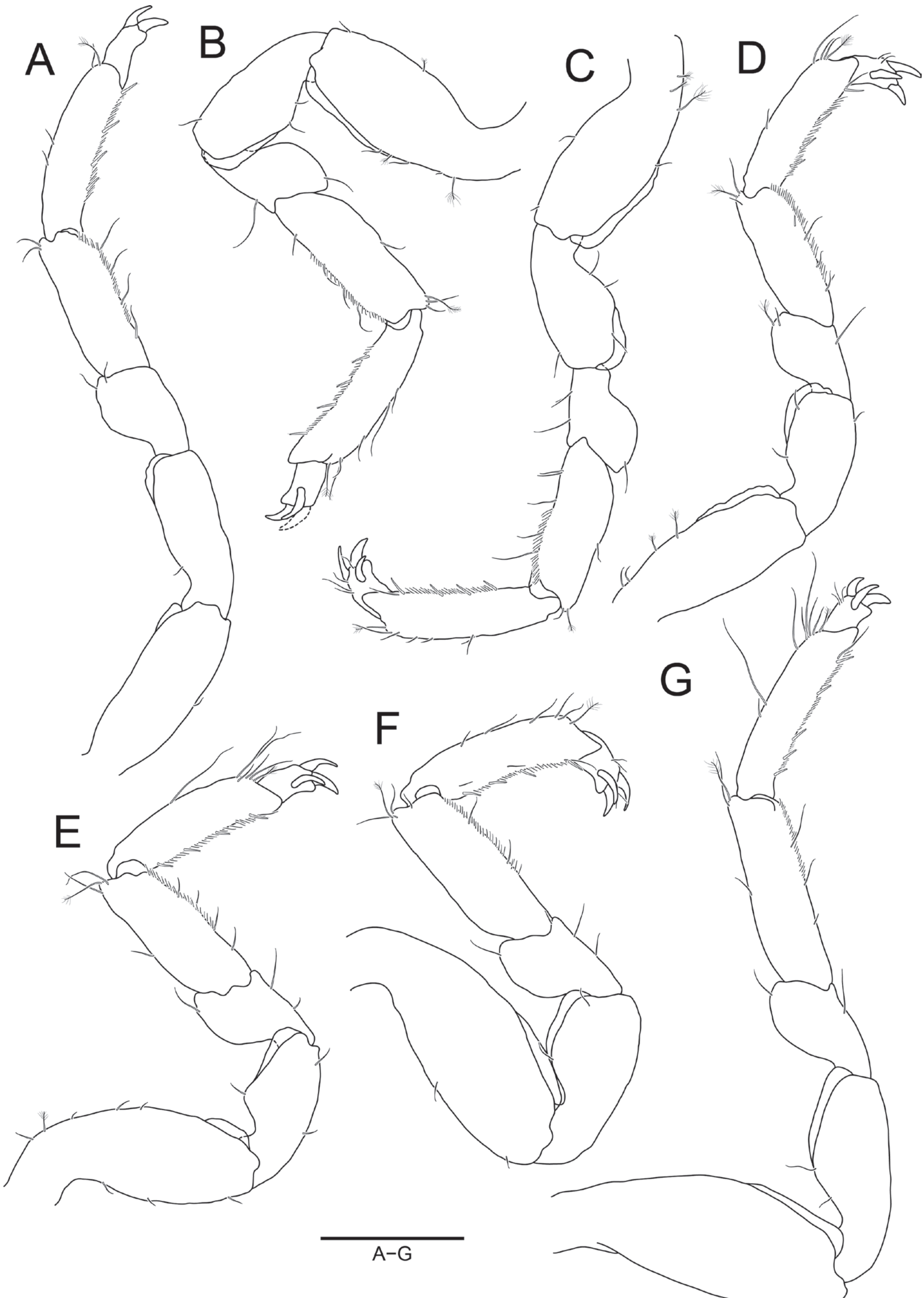

Figure 7. *Joeropsis semicircularis* sp. nov., holotype, male **A** pereopod 1 **B** pereopod 2 **C** pereopod 3 **D** pereopod 4 **E** pereopod 5 **F** pereopod 6 **G** pereopod 7. Scale bar: 0.2 mm.

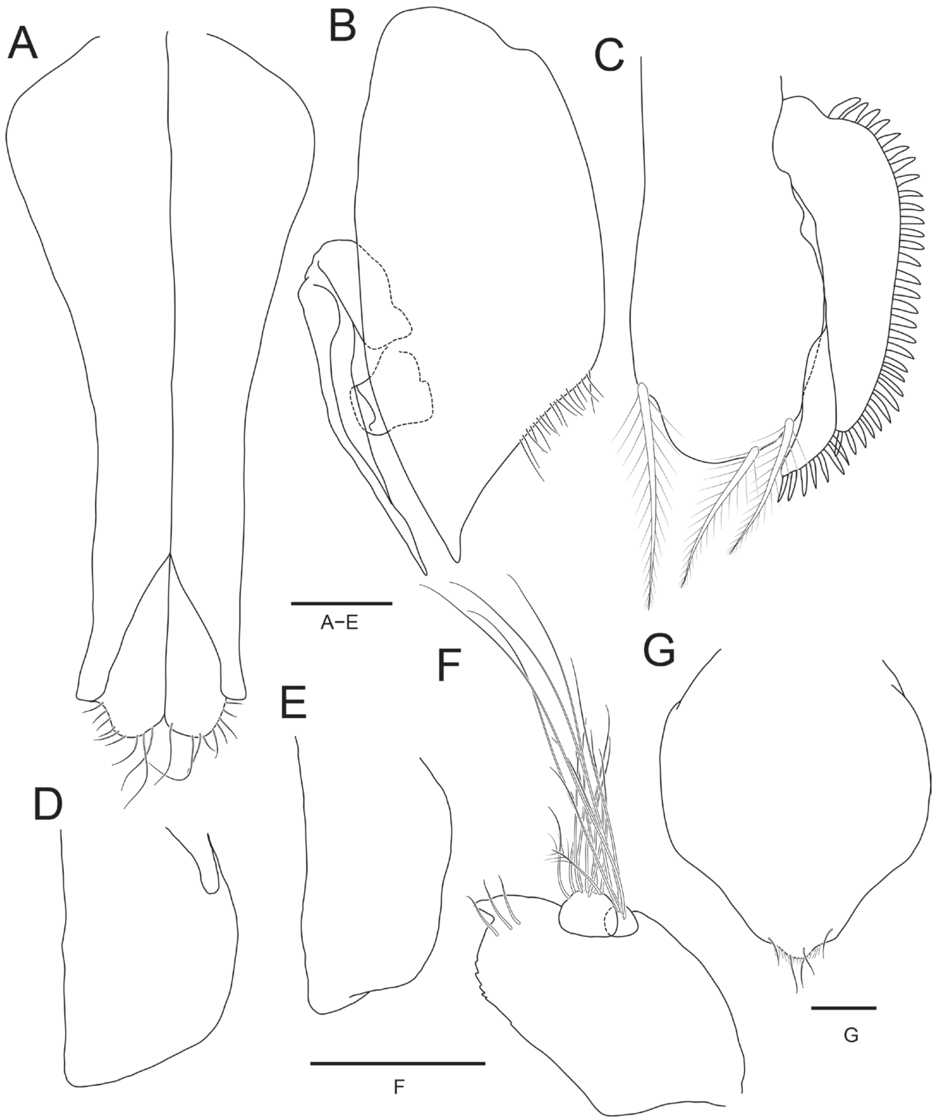

Figure 8. *Joeropsis semicircularis* sp. nov., holotype, male **A** pleopod 1 **B** pleopod 2 **C** pleopod 3 **D** pleopod 4 **E** pleopod 5 **F** uropod. Paratype, female **G** pleopod 2. Scale bars: 0.1 mm.

Size. Males 3.7–4.0 mm, mean 3.9 mm (n = 4); females 3.3–3.7 mm, mean 3.5 mm (n = 6); all from type series.

Colour pattern. The cephalon has a transverse dark brown band of chromatophores across the middle of the cephalon. Pereonite 4 and pleotelson are also covered with chromatophores, but indistinct (Figs 2B, 6A).

Variation. The colour pattern of chromatophores varies according to individual. On the cephalon, a transverse dark brown band is always distinct and regular, while on pereonite 4 or pleotelson, the chromatophores are occasionally varied according to the individuals.

Distribution. South Korea (southern coast of the Korean Peninsula and East Sea).

Remarks. *Joeropsis semicircularis* sp. nov. can be identified by the following features: (1) the body has dark brown chromatophores on the cephalon, pereonite 4, and pleotelson; (2) lateral margins of the cephalon are smooth and parallel; and (3) the first flagellar article of the antenna is swollen and semi-circular in shape.

Joeropsis semicircularis sp. nov. resembles four known species by having the cephalon laterally smooth and parallel, the pseudorostrum not concave or pointed distally, maxillipedal palp article 2 lacking medial lobe, and the pleotelson and uropods both laterally serrated: *J. dollfusi* Norman, 1899; *J. latiantennata* Nunomura, 1999; *J. stebbingi* Kensley, 1975; and *J. wolffi* Müller, 1991 (Koehler 1885; Norman 1899; Amar 1961; Kensley 1975; Müller 1991; Nunomura 1999). Among these species, *J. semicircularis* sp. nov. is most similar to *J. latiantennata* by having swollen and semicircular-shaped first flagellar article of the antenna (Nunomura 1999). However, the former differs from the latter by the following characteristic features: (1) the dactylus of pereopods 2–7 has three claws (vs. two claws in the latter); (2) the second peduncular article of the antenna has a process on medial margin (vs. has not in the latter); and (3) the fourth peduncular article of the antenna is not serrated (vs. serrated in the latter) (Nunomura 1999). The new species can be easily distinguishable from the remaining three species by having swollen and semi-circular-shaped first antennal flagellar article (Koehler 1885; Norman 1899; Amar 1961; Kensley 1975; Müller 1991). A detailed comparison of *Joeropsis* species mentioned above is provided in Table 2.

Key to known *Joeropsis* species in the Far East

1	Cephalon with anteriorly narrowing lateral margins	**2**
–	Cephalon with parallel lateral margins	**5**
2	Lateral margins of cephalon serrated	***J. lata***
–	Lateral margins of cephalon not serrated	**3**
3	Antennal peduncular articles 3 and 5 each with a process on medial margin	***J. denticulatus* sp. nov.**
–	Antennal peduncular articles 3 and 5 without any processes	**4**
4	Maxillipedal palp article 2 with medial lobe	***J. affinis***
–	Maxillipedal palp article 2 without medial lobe	***J. lobota***
5	Peduncular article 5 of antenna serrated on outer margin	***J. latiantennata***
–	Peduncular article 5 of antenna not serrated on outer margin	***J. semicircularis* sp. nov.**

Acknowledgements

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RESEARCH ARTICLE

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A new species and a newly recorded subgenus of *Lipotriches* Gerstaecker, 1858 (Hymenoptera, Apoidea, Halictidae, Nomiinae) from China

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Abstract

Two Chinese species of the genus *Lipotriches* Gerstaecker, 1858 are treated in this paper. *Lipotriches* (*Lipotriches*) *guihongi* Zhang & Niu, **sp. nov.** is recognized as a new species and *Lipotriches* (*Maynenomia*) *nanensis* (Cockerell, 1929) is a new species and subgenus record for China. The number of Chinese species of the subfamily Nomiinae and genus *Lipotriches* are updated to 47 and 15, respectively.

Keywords

Anthophila, Apiformes, bee pollinator, description, morphology, taxonomy

Introduction

The genus *Lipotriches* (subfamily Nomiinae) was described by Gerstaecker (1858) with *Lipotriches abdominalis* as the type species, including more than 340 species (Ascher and Pickering 2021). *Lipotriches* has a high diversity of species occurring throughout the Old World (Africa, Asia and Australia). Bee species of this genus are important pollinators for plants, especially for grasses (Pauly 2014a). Over the last few decades, various groups and species in this genus have been revised (Pauly 1984a, 2009, 2014a, b; Astafurova and Pesenko 2005; Michener 2007; Huang 2008; Niu et al. 2018). However, much more taxonomic work is needed for this group, especially in Asia.

In general, the body of *Lipotriches* species is relatively slender compared to most other nomiine species (Pauly 1990; Michener 2007). Morphological identification of the subgenus within *Lipotriches* strongly relies on adult characters: especially the pronotum with continuous, or medially, or laterally notched transverse carina in both sexes, and the basitibial plate of females with a carina only along the posterior margin (Michener 2007; Huang 2008). Pauly (1990) separated *Lipotriches* into several genera, such as *Austronomia* Michener, 1965, *Afronomia* Pauly, 1990, *Macronomia* Cockerell, 1917, and *Trinomia* Pauly, 1980. Later, Michener (2007) revised all the above groups as subgenera of the genus *Lipotriches*, dividing *Lipotriches* into nine subgenera in total.

Pauly (1984b) described *Maynenomia* as a genus with *Nomia maynei* Cockerell, 1937 as the type species. Subsequently, he described nine new species and transferred five *Nomia* species to this group, giving a total of 15 species of *Maynenomia* in Africa and Asia (Pauly 2009). Michener (2007) treated *Maynenomia* as a subgenus within the genus *Lipotriches*, and suspected this subgenus probably to be a synonym of the subgenus *Austronomia.* While Pauly treated *Maynenomia* at genus level, based on its "oval" head shape, we follow Ascher and Pickering (2021) and Michener (2007) in treating *Maynenomia* as a subgenus within *Lipotriches*.

Herein, we reported two Chinese species of the genus *Lipotriches*, including one newly described species and one newly recorded species. To date, the Chinese species of subfamily Nomiinae is increased to 47 in total (Niu et al. 2018; Zhang et al. 2020).

Materials and methods

In this study, a total of 50 specimens were examined, all of them were deposited in the Collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**IZCAS**). The specimens were examined with Nikon SMZ 1500 stereomicroscope. Photographs were taken with Nikon D7000 digital camera and were stacked with Helicon Focus and Zerene Stacker. Final images were edited for clarity and mounted into plates by Photoshop CS6.

The morphological terminology follows Pesenko (1983) and Michener (2007) in this study. Absolute measurements were taken in millimeters (mm) for body length. The following abbreviations are used: BL, body length which was measured from basal antennal socket to the metasomal apex; HL, head length which represented the widest point of the head in frontal view; T1–5, the first to fifth metasomal terga; S1–8, the first to eighth metasomal sterna; F1–11, the first to eleventh flagellar segments. We measured the punctation density, punctation diameter (d) and the space between them (i), such as i = 1d or i<d.

Taxonomy

Genus *Lipotriches* Gerstaecker, 1858

Subgenus *Lipotriches* Gerstaecker

Lipotriches Gerstaecker, 1858: 460. Type species: *Lipotriches abdominalis* Gerstaecker, 1857 = *Sphecodes cribrosa* Spinola, 1843, monobasic.

Rhopalomelissa Alfken, 1926: 267. Type species: *Rhopalomelissa xanthogaster* Alfken, 1926, by designation of Sandhouse (1943: 596).

Nomia (*Epinomia*) Alfken, 1939: 113, not Ashmead, 1899. Type speies: *Nomia andrenoides* Vachal, 1903 = *Nomia andrei* Vachal, 1897, by original designation.

Alfkenomia Hirashima, 1956: 33, replacement for *Epinomia* Alfken, 1939. Type species: *Nomia andrenoides* Vachal, 1903 = *Nomia andrei* Vachal, 1897, autobasic.

Rhopalomelissa (*Lepidorhopalomelissa*) Wu, 1985: 58. Type species: *Nomia burmica* Cockerell, 1920, by original designation.

Rhopalomelissa (*Trichorhopalomelissa*) Wu, 1985: 58. Type species: *Rhopalomelissa hainanensis* Wu, 1985, by original designation.

Rhopalomelissa (*Tropirhopalomelissa*) Wu, 1985: 58. Type species: *Rhopalomelissa nigra* Wu, 1985, by original designation.

Diagnosis. Small-sized, body length about 5–12 mm; metasoma slender, with petiolate, T1 longer than broad in male (most species); pronotum with continuous or medially or laterally transverse carina or lamella anterior to the scutum; metasoma partly or wholly red for some species (i.e., *Lipotriches floralis*, *Lipotriches esakii* and *Lipotriches mediorufa*).

Lipotriches (*Lipotriches*) *guihongi* Zhang & Niu, sp. nov.

http://zoobank.org/F11C65CF-98CB-4016-8AE6-4D101D75D5E8

Figs 1, 2

Type material. ***Holotype*:** China: 1♂, Xizang, Jilong County, Jilong Town, Jipu Village, 28°37'N, 85°32'E, 2744 m, 9 Aug. 2019, Dan Zhang, Qing-Tao Wu leg. ***Paratypes*:** 5♀21♂, Jilong County, Jilong Town, Jipu Village, 28°37'N, 85°32'E, 2744m, 7–9 Aug. 2019, Dan Zhang, Qing-Tao Wu leg.; 16♀1♂, Xizang, Jilong County, Jilong Town, Xinjiang Village, 28°22'N, 85°21'E, 2727m, 6 Aug. 2019, Dan Zhang, Qing-Tao Wu leg.

Diagnosis. Males of *L. guihongi* sp. nov. differ from other species of subgenus *Lipotriches* by the following combination of features: mesoscutum, metapostnotum and center disc of metasomal terga with dense and large punctures (Fig. 1c, d), S4 with dense short white hairs (Fig. 1f); S5 with a pair of circular protruding thickness on the disc, a pair of triangular feathery bristles connected on the apical margin (Fig. 1g);

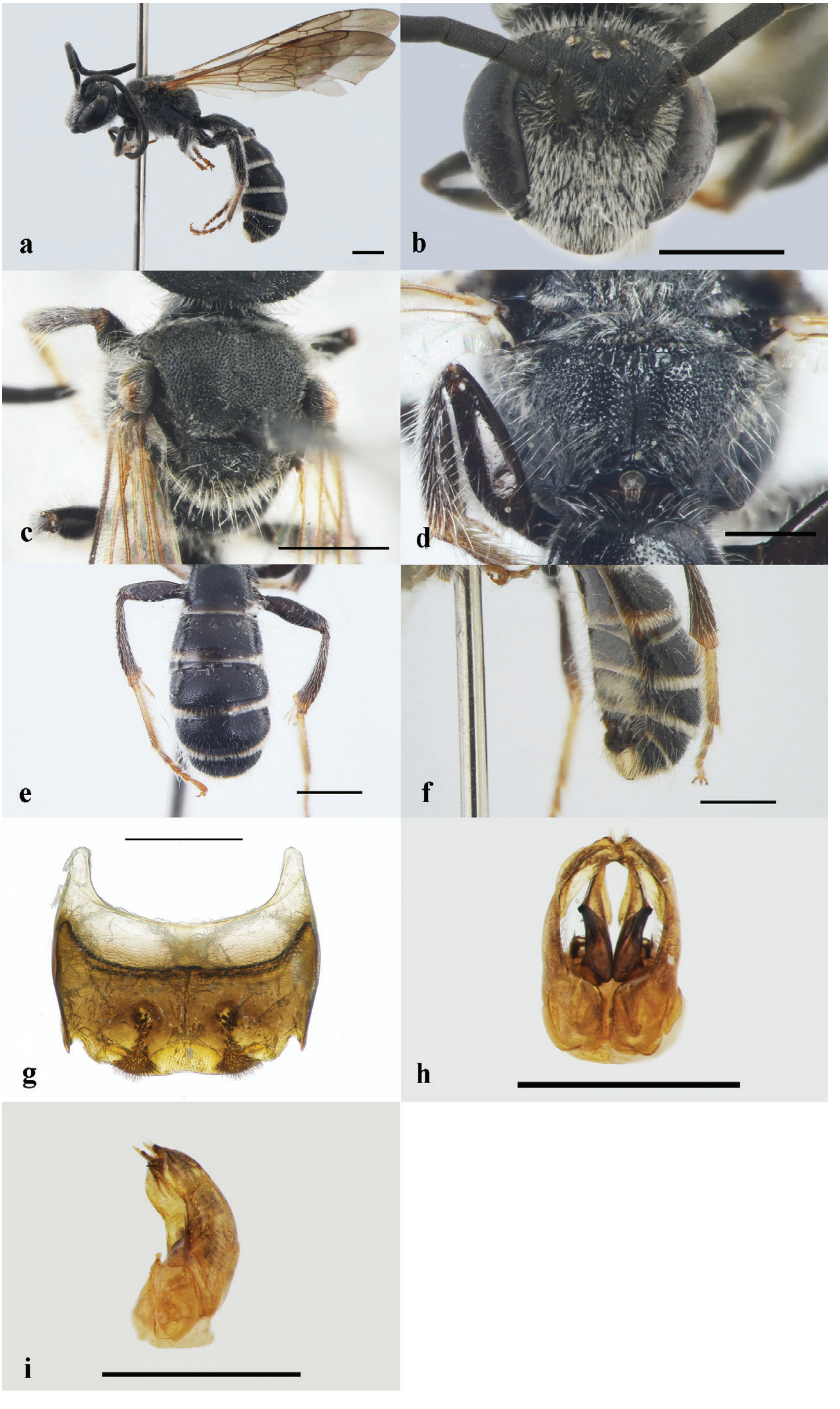

Figure 1. *Lipotriches* (*Lipotriches*) *guihongi* Zhang & Niu sp. nov., male **a** habitus in lateral view **b** head in frontal view **c** mesoscutum in dorsal view **d** propodeum in posterior view **e** metasoma in dorsal view **f** metasoma in lateral view **g** S5 in dorsal view **h** genitalia in dorsal view **i** genitalia in lateral view. Scale bars: 1 mm (**a–f**); 0.5mm (**g–i**).

L. guihongi is most similar to *Lipotriches yasumatsui* Hirashima, 1961 and *Lipotriches ceratina* (Smith,1857), however, the male of the new species can be distinguished from the two latter by a pair of large, dense, erect and brownish longitudinal tufted hairs on S5. In addition, S5 structure of *L. guihongi* sp. nov. is similar to *L. acanthospermi* Pauly, 2014b. We have found that the both species have dense tomentum on S4 and a pair triangular feathery bristles on the apical margin of S5, while the latter lacks a pair of circular protruding thickness on the disc of S5, and has only been found in Africa.

Description. Male (measurements are only from the holotype). BL = 8 mm (Fig. 1a), body black. ***Head.*** HL: HW = 0.89, head broader than long (Fig. 1b); clypeus broader than long (Fig. 1b); paraocular area with dense large punctures (i = 0.1–0.2d; Fig. 1b); vertex with sparser large punctures (i = 0.5–1d; Fig. 1b); vertex behind shiny; posterior margin of vertex rounded (Fig. 1a, b); mandible blackish-brown; frons with dense and minute punctures, medial frontal line smooth (Fig. 1b); antenna reaching the posterior margin of T1; F1–11 almost equal in length, nearly 2.3 times as long as broad (Fig. 1a, b); ocelli normal (Fig. 1b). ***Mesosoma***. Mesoscutum, scutellum, and metanotum dull, without reflections (Fig. 1c). Mesoscutum with large and mostly confluent punctures (i = 0.2–0.3d; Fig. 1c); metanotum normal, without process, with large punctures which are sparser than punctures on the mesoscutum (Fig. 1c); posterior surface of propodeum with more larger and denser (i = 0.1–0.2d) punctures than those on the mesosoma (Fig. 1d); metapostnotum shiny, with broad longitudinal wrinkles (Fig. 1d); fore wing with three submarginal cells, the 1st and 3rd submarginal cell nearly equal in length, almost two times as long as 2nd submarginal cells; tegula oval, yellow-brown, not enlarged (Fig. 1c); femur and tibia black (Fig. 1a); basitarsus, mediotarsus yellow-brown with tarsal claw (Fig. 1f); hind femur and tibia normal, not enlarged (Fig. 1c). ***Metasoma***. Surface of metasomal terga shiny, center of disc with dense punctures (i = 0.2–0.3d), apical of disc with sparser punctures than on the center (i = 0.5–1d); apical margin of T1–5 transparent (Fig. 1e, f); S5 with a pair of circular protruding thickness on the disc, a pair triangular feathery bristles on the apical margin connected (Fig. 1g); gonostylus as shown in Fig. 1h (in dorsal view) and Fig. 1i (in lateral view). ***Pubescence***. Clypeus, supraclypeal area and frons with white setae (Fig. 1a, b); scutellum with sparse long yellowish hairs (Fig. 1c); metanotum with dense pale tomentum (Fig. 1c); upper lateral surface of propodeum with sparse long white hairs (Fig. 1d); legs with sparse white hairs (Fig. 1a, d–f); apical area of metanotum with sparse long hairs (Fig 1c); apical margin of T1–4 with white hair band, interrupted in middle (Fig. 1e); S4 covered with dense pale tomentum (Fig. 1f).

Female. BL = 10–12 mm. Similar to male, except the following: metapostnotum with punctures sparser (i = 0.4–0.5d) and smaller than male's (Fig. 2d); head, mesosoma and metasoma with sparse yellowish hairs (Fig. 2b); T1–2 with densely and minutely punctures (i = 0.2–0.3d; Fig. 2d).

Etymology. The name "*guihongi*" is dedicated to Prof. Hong Gui. He is a famous entomologist in China, who advised and encouraged Chao-Dong Zhu to continue his study on insects.

Floral association. Unknown.

Distribution. China (Xizang).

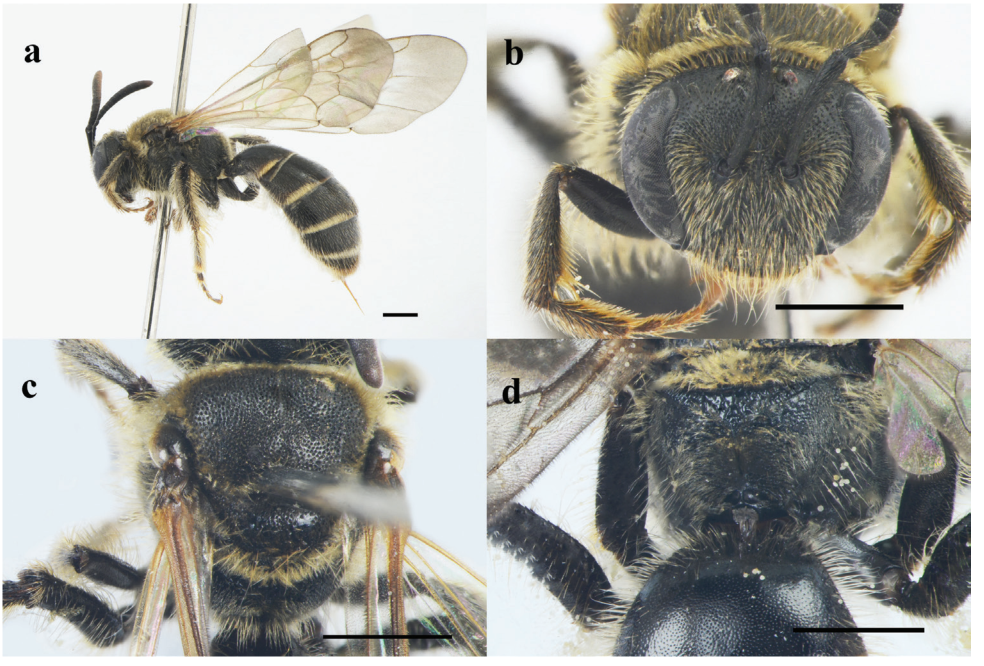

Figure 2. *Lipotriches* (*Lipotriches*) *guihongi* Zhang & Niu sp. nov., female **a** habitus in lateral view **b** head in frontal view **c** mesoscutum in dorsal view **d** propodeum in posterior view. Scale bars: 1 mm.

Subgenus *Maynenomia* Pauly, 1984

Maynenomia Pauly, 1984b: 698. Type species: *Nomia maynei* Cockerell, 1937 = *Nomia testacea* Friese, 1914, by original designation.

Diagnosis. Glossa slender; apical of basitibial plate opened, delimited on both sides in female; scape short, not reaching median ocellus in females.

Distribution. China (Yunnan); India (Uttarakhand); Indonesia; Laos; Malawi; Myanmar; South Africa; Tanzania; Thailand.

Lipotriches (*Maynenomia*) *nanensis* (Cockerell, 1929)
Fig. 3

Nomia nanensis Cockerell, 1929:133, ♀. Holotype, ♀, Thailande, Nan, USNM.
Maynenomia nanensis (Cockerell, 1929): Pauly 2009.

Material examined. China: 2♀, Yunnan, Xishuangbanna, Naban River, 22°04'N, 100°22'E, 1303 m, 16 Jun. 2014, Xiu-wei Liu leg..

Diagnosis. T1–2 mainly reddish, and T2 with large black spot at each side basally (Fig. 3e, f); legs reddish except fore femur black (Fig. 3c); mandibles subapically red,

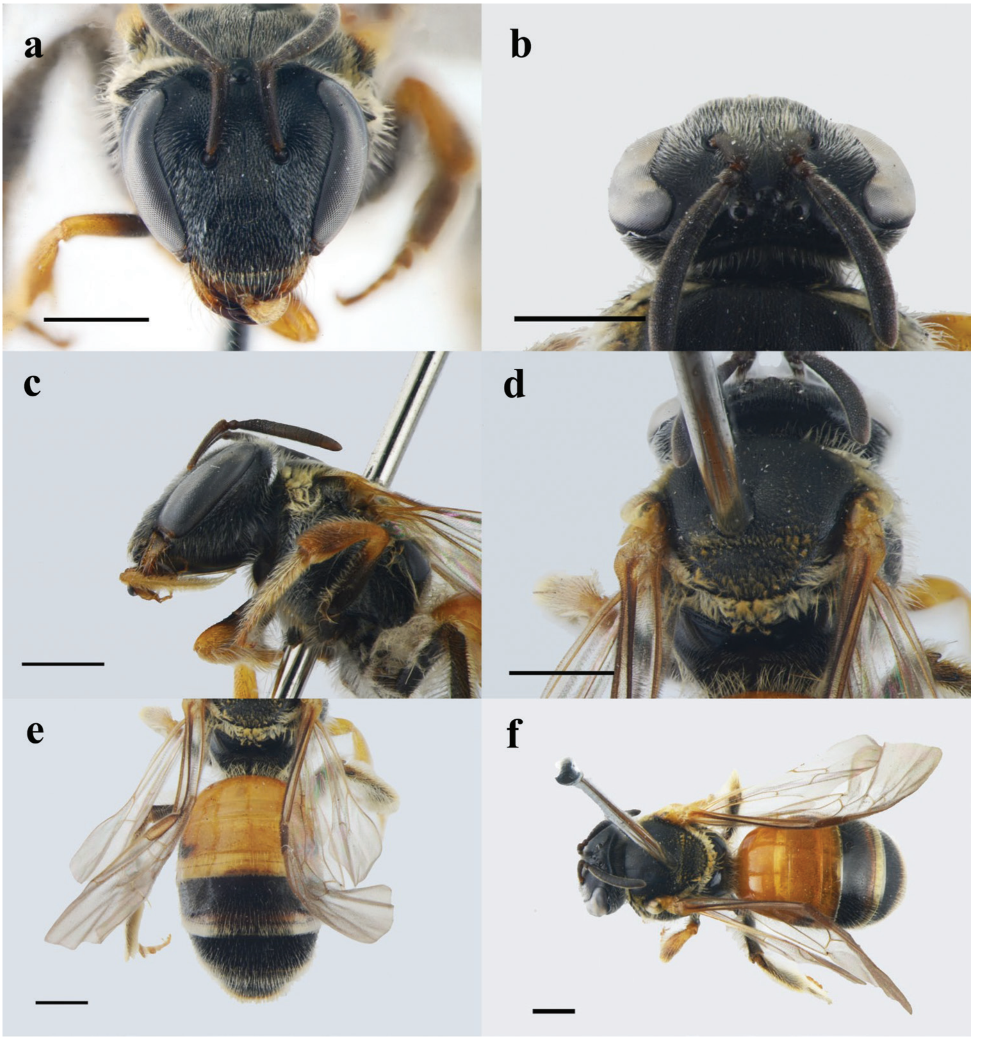

Figure 3. *Lipotriches* (*Maynenomia*) *nanensis*, female **a** head in frontal view **b** head in dorsal view **c** habitus in lateral view, showing the glossa **d** mesoscutum in dorsal view **e** metasoma in dorsal view **f** habitus in dorsal view. Scale bars: 1mm.

and apically black (Fig. 3c, f); hind tibia with basitibial plate (Fig. 3f); mesoscutum, scutellum and propodeum dull (Fig. 3d); mesoscutum with extremely dense and minute punctures (Fig. 3d); posterior surface of propodeum almost without punctures (Fig. 3d, e); metanotum with dense pale ochreous tomentum (Fig. 3d, e); surface of metasomal terga highly polished, with extremely sparse and minute punctures (Fig. 3e, f).

Distribution. China (Yunnan); India (Maharashtra); Laos; Myanmar; Thailand.

Remark. This species was recorded from China for the first time in this study, increasing the number of Chinese species of *Lipotriches* and Nomiinae to 15 and 47, respectively.

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Flospes gen. nov. (Orthoptera, Trigonidiidae, Trigonidiinae), a genus of swordtail crickets from China, with two new species and new combinations

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Abstract
We propose the genus *Flospes* **gen. nov.** for two new species, *Flospes guangxiensis* **sp. nov.** and *Flospes viridipennis* **sp. nov.**, obtained from Guangxi and Hainan provinces, China, respectively, based on male genitalia traits. Three other species with similar genitalia are placed in the new genus: *Flospes fujianensis* (Wang et al., 1999), **comb. nov.**, *Flospes hainanensis* (He et al., 2010), **comb. nov.**, and *Flospes denticulatus* (Liu & Shi, 2011), **comb. nov.** The new species are described, illustrated, and their ranges are given.

Keywords
Grylloidea, new genus, silent crickets, taxonomy, Trigonidiini

Introduction

There are 49 genera and 658 species in the Trigonidiinae (Orthoptera, Trigonidiidae) (Cigliano et al. 2021). In recent years, male genitalia have been used to identify crickets. It used to be relatively uncommon, but people loved to utilize acoustical structures to identify Trigonidiinae species (e.g., if the tegmen had a mirror or stridulatory vein and whether the tympanum was present) (Chopard 1936, 1951, 1969; Otte and Alexander 1983). Otte (2006) even speculated that classifying them by genital characteristics would result in a jumble of taxa. In our research, however, we discovered considerable intraspecific differences in these traits. Genitalia morphology is a crucial characteristic for delimiting genera of Grylloidea, just as it is for other taxa (Gorochov 2015; Gorochov et al. 2018). As a result, we handle trigonidiine taxa by concentrating on male genitalia and propose a new genus for two new species (*Flospes* gen. nov., *Flospes guangxiensis* sp. nov., and *Flospes viridipennis* sp. nov.).

Three more species should also be added to the new genus. According to the same kind of male genitalia when the genus was formed, *Amusurgus hainanensis* (= *Sectus hainanensis*) He et al., 2010 was included in *Sectus* Ma and Pan (2019). Due of its similar appearance to *S. hainanensis*, He et al. (2020) placed *Amusurgus fujianensis* (= *Sectus fujianensis*) (Wang et al. 1999) in the same genus. However, both *S. hainanensis* and *S. fujianensis* were found to be comparable to the new genus in terms of male genitalia or appearance in this study. For example, the epiphallus of *S. fujianensis* has lateral lobes, as in the new genus, while the type species of *Sectus* does not. *Metiochodes denticulatus* Liu & Shi, 2011 was formerly classified as a species of the genus *Metiochodes* Chopard, 1932, but its male genitalia matches that of the new genus. As a result, these species are here classified in *Flospes* gen. nov.: *Flospes hainanensis* comb. nov., *Flospes fujianensis* comb. nov., and *Flospes denticulatus* comb. nov.

Materials and methods

Specimens were firstly preserved in ethanol during fieldwork and then pinned and dry to be maintained in the laboratory. Photographs of specimens were obtained using a VHX-6000 Super-high magnification lens zoom 3D microscope (Keyence, Osaka, Japan). We dissected male genitalia from softened specimens and cleaned using aqueous protease, and made photomicrographs of genitalia using ToupCam Digital camera and bundled software (ToupTek, Hangzhou, China). Terminology used to describe the male genitalia follows Desutter-Grandcolas (1987). The specimens are deposited at the Museum of Flora and Fauna of Shaanxi Normal University, Xi'an, China (**SNNU**).

Measurements

All specimens were measured using a ToupCam Digital camera and bundled software (ToupTek, Hangzhou, China). All the measurements are in millimeters (mm).

Abbreviations

BL body length (from head to apical hindwing);
PL pronotal length;
TL tegmen length;
HFL hind femur length,
OL ovipositor length;
ep lb epiphallic lateral lobe;
ecp ectoparamere;

ecp ub	upper branch of ectoparamere;	**ec ap**	ectophallic apodeme;
ecp lb	lower branch of ectoparamere;	**en ap**	endophallic apodeme.
r	rami;		

Taxonomy

Subfamily Trigonidiinae Saussure, 1874
Tribe Trigonidiini Saussure, 1874

Genus *Flospes* Ma & He, gen. nov.
http://zoobank.org/33ADF11D-F7A6-4886-8061-42AB035ED6A6
Chinese name: 花蛉蟋属

Type species. *Amusurgus fujianensis* (=*Flospes fujianensis*).

Etymology. The genus name "Flospes" is a Latin word (= flower), which refers to the colorful body of the members of the genus (the fore and median femora are proximally black and distally white, the hind femur bears a dark brown band, and the cercus is black and white).

Diagnosis. Head almost as wide as anterior margin of pronotum. Frons slightly convex. Maxillary palpi black and white. Tegmen similar in both sexes (male lack of stridulatory apparatus). The internal tympanum large and long-oval, and the external one replaced by a small pit. The hind tibia bears three pairs of dorsal spurs. The legs and cercus black and white. The lateral lobes of epiphallus rod-like and ectoparamere enormously enlarged (much wider than epiphallic lateral lobe). The apex of female ovipositor expanded, blade-like and reddish brown.

Remarks. Similar to *Amusurgus*, the members of them are silent, pubescent and bearing rod-like epiphallic lateral lobes, but the species of the new has colorful legs and cercus, as well as ectoparamere that is enormously enlarged and almost membranous. The new genus is distinguished from *Sectus* by the absence of stridulatory apparatus and the presence epiphallic lobes. It differs from the genus *Metiochodes* Chopard, 1932 in that its ectoparamere is enlarged and membranous.

Key to known species of *Flospes* (male adults)

1 Veins green (Fig. 9) .... ***Flospes viridipennis* sp. nov.**
– Veins yellow (Fig. 5)... **2**
2 Epiphallus very short, almost without lateral lobe ...***Flospes hainanensis* comb. nov.**
– Epiphallus normal, bearing conspicuous lateral lobes and dorsally viewed as following (Figs 8, 12) **3**
3 Epiphallic lateral lobe apically acute ....***Flospes denticulatus* comb. nov.**
– Epiphallic lateral lobe apically blunt..**4**
4 Ectoparamere apically rounded .... ***Flospes fujianensis* comb. nov.**
– Ectoparamere apically rectangular ....***Flospes guangxiensis* sp. nov.**

Flospes denticulatus comb. nov.

Chinese name: 锯齿花蛉蟋

Metiochodes denticulatus Liu & Shi, 2011: 2

Holotype information. Type locality: China. Guizhou, Rongjiang, Xiaodanjiang. Deposited at Hebei University Museum (HBUM), Hebei, China (not examined).

Distribution (Fig. 1). China (Guizhou).

Remarks. This species was initially arranged in the genus *Metiochodes*, and its features of appearance and male genitalia are consistent with the characteristics of the new genus.

Flospes fujianensis comb. nov.

Chinese name: 福建花蛉蟋
Figs 1–4

Amusurgus fujianensis Wang, Zheng & Wu, 1999: 114
Amusurgus (*Paranaxipha*) *fujianensis* (= *Sectus fujianensis*), He et al. 2010: 60; He et al. 2020:126. misidentification of *F. viridipennis* sp. nov.

Materials examined. **China:** 3 males, 3 females; Guangdong, Nanling National Nature Reserve, bush leaves, 24.93°N, 113.04°E, 5.VIII.2019, Zhixin He & Tao Zhang, sweep net, leg. (SNNU).

Redescription. Male (Figs 2A, 4A, C, E, G). Body size small, pubescent. Head small, slightly broader than anterior margin of pronotum. Frons slightly narrower than antennal scape. Eyes large and strongly protruding to sides. Clypeus narrow, upper margin straight, and lower margin medially convex. Labrum shield-like, medially plump, and apically concave. Three apical joints of maxillary palpi distinctly elongate, and fifth joint apically truncated. Pronotum transverse, anterior margin straight, and posterior margin slightly and medially convex. Tegmina pubescent. Six primary veins staggered with numerous transverse veins between them. Visible part of hindwing is half length of tegmen. Internal tympanum large and long-oval, and external one replaced by a small pit. Hind tibia bearing three pairs of dorsal spurs.

Genitalia (Fig. 3A–C). Lateral lobes of epiphallus stick-like, apically blunt, and almost straight in dorsal view. Ectoparamere spoon-like, with sclerotized margin and membranous remainder portion. Rami very short. Ectophallic and endophallic apodemes greatly surpass the rami.

Female (Figs 2B, 4B, D, F). Resembles male. Longitudinal veins of tegmen parallel, with a few pale transverse veins forming several rectangular cells (filled with brown). Ovipositor not surpassing hindwings. Dorsal and ventral margins of basal ovipositor

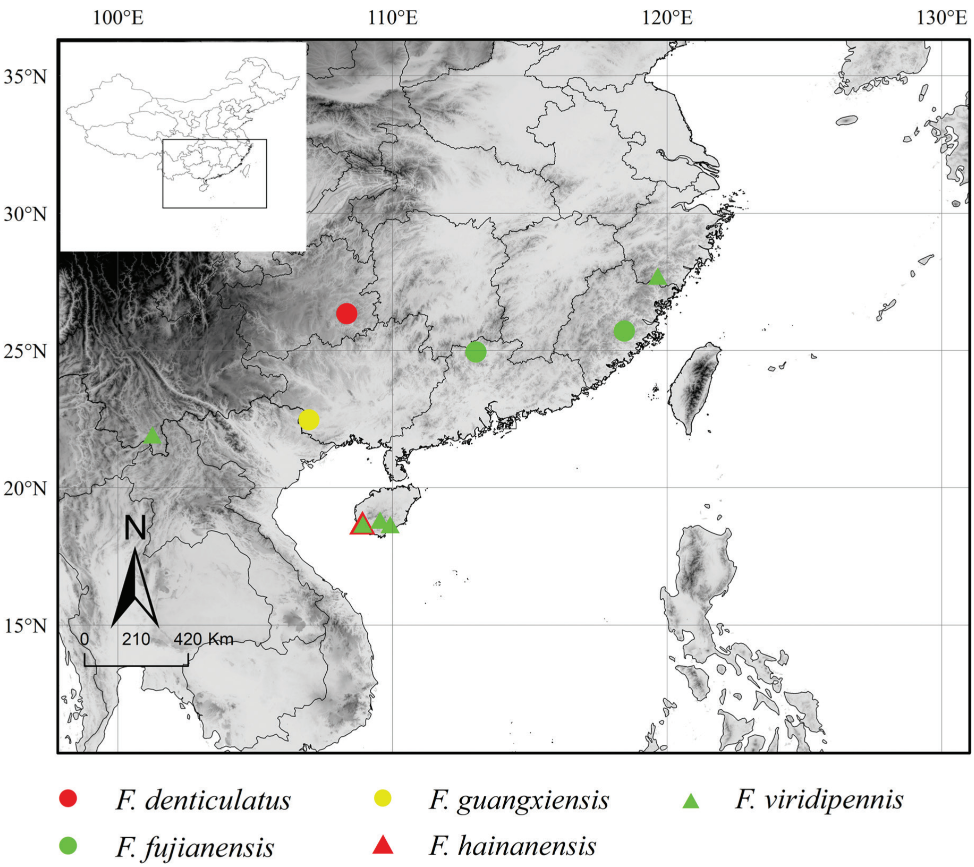

Figure 1. Distribution of *Flospes* species in China.

smooth and faintly narrowing, and both margins of apical part slightly denticulated and apically bent upwards.

Coloration. Body yellowish-brown. Pronotum brown. Fore and middle femur darkly colored. Hind femur bearing two dark bands (middle one and apical one). Tarsus darkly color. Cercus black and white.

Measurements. Male: BL 5.08–5.73, PL 0.66–0.75, TL 4.00–4.60, HFL 4.22–4.69. Female: BL 5.61–6.42, PL 0.90–1.04, TL 4.28–4.77, HFL 4.59–5.11, OL 2.40–2.74.

Distribution (Fig. 1). China (Fujian, Guangdong).

Remarks. This species was first described from Fujian Province, China. Its primary characteristics are body brown, leg and cercus black and white, tegmen brown, and armed with rod-like lateral lobe on the epiphallus and an enormously enlarged, rounded ectoparamere. He et al. (2010) described some specimens found in Hainan, Zhejiang, and Yunnan provinces as *A. fujianensis*, but these specimens bear a greenish-brown

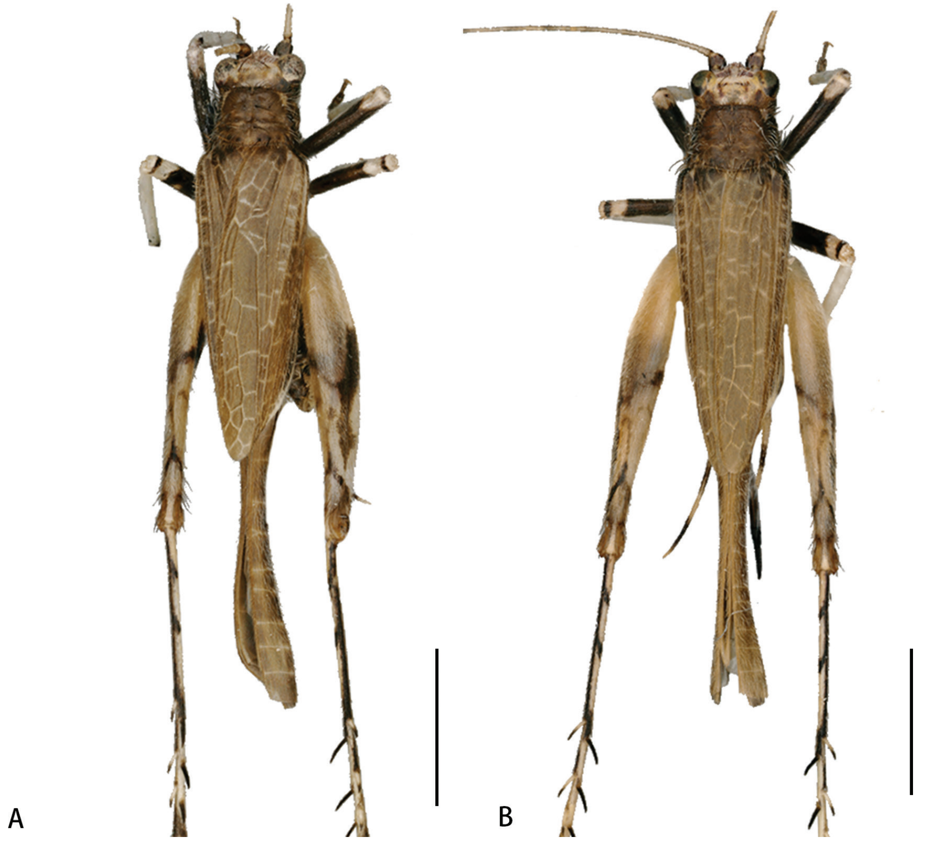

Figure 2. Habitus photographs of *Flospes fujianensis* **A** male **B** female. Scale bar: 2 mm

Figure 3. Male genitalia of *Flospes fujianensis* **A** dorsal view **B** lateral view **C** ventral view.

tegmen and squared ectoparamere. We checked specimens collected from Hainan Province and discovered that they are consistent with the description of "*A. fujianensis*" in He et al. (2010). Our specimens from Guangdong Province are consistent with the original description of *A. fujianensis* by Wang et al. (1999). As a result, we redescribe *A. fujianensis* here from our Guangdong specimens and judge that "*A. fujianensis*" of He et al. (2010) is a misidentification (see Remarks below under *Flospes viridipennis* He & Ma, sp. nov.).

Figure 4. *Flospes fujianensis* comb. nov. **A** lateral view of male **B** lateral view of female **C** male tegmen **D** female tegmen **E** face in anterior view **F** female ovipositor in lateral view **G** lateral view of hind femur. Scale bars: 0.5mm.

***Flospes guangxiensis* He & Ma, sp. nov.**
http://zoobank.org/185101ED-7820-41C2-84BA-B22DA49EE4E6
Chinese name: 广西花蛉蟋
Figs 1, 5–8

Type materials. *Holotype*. China: Male, Guangxi, Longzhou, Nonggang National Nature Reserve, bush leaves, 2.X.2021, 22.46°N, 106.96°E, Zhixin He & Ning Wang, sweep net, leg. ***Paratypes*.** 1 male, 2 females, same data as holotype (SNNU).

Description. Male (Figs 5A, 6A, 7A, C, E, G). Body size small. Head small, slightly broader than anterior of pronotum. Frons as wide as antennal scape. Eyes large and protruding laterally. Three apical joints of maxillary palpi distinctly elongate, and the fifth joint apically truncated. Pronotum transverse, posterior margin broader than the anterior one. Tegmen extending over abdominal apex, and bearing six staggered primary veins with many transverse veins between them. The visible part of hindwing half length of tegmen. Internal tympanum large and long-oval, and external one shaped like a small pit. The hind tibia bears three dorsal spurs on each side.

Figure 5. Habitus (alive) of *Flospes guangxiensis* sp. nov. on a leaf **A** male **B** female.

Genitalia (Fig. 8A–C). Lateral lobes of epiphallus stick-like, apically blunt, and inward curved in dorsal view. Ectoparamere roughly rectangular with the marginal part sclerotized and the remainders membranous. Ectophallic and endophallic apodemes short and not surpass rami.

Female (Figs 5B, 6B, 7B, D, F). Resembles male but slightly smaller. Longitudinal veins of tegmen parallel and producing rectangular cells (fill with dark brown) with a few pale transverse veins. Ovipositor not surpassing hindwings. Dorsal and ventral margins of the basal of ovipositor smooth and faintly narrowing, and both margins of apical part slightly denticulated and apically curved upwards.

Coloration. Body yellowish-brown. Pronotum dark brown. Most of the fore and middle femur darkly colored, but with apex pale. Hind femur medially bears a dark brown band. Tarsus darkly colored. Cercus black and white.

Measurements. Male: BL 5.68–5.93, PL 0.82–0.91, TL 4.22–4.64, HFL 3.82–4.21. Female: BL 5.87–6.21, PL 0.76–0.82, TL 4.21–4.43, HFL 4.07–4.33, OL 2.25–2.51.

Etymology. The name refers to the province of China where the type locality is located.

Distribution (Fig. 1). China (Guangxi).

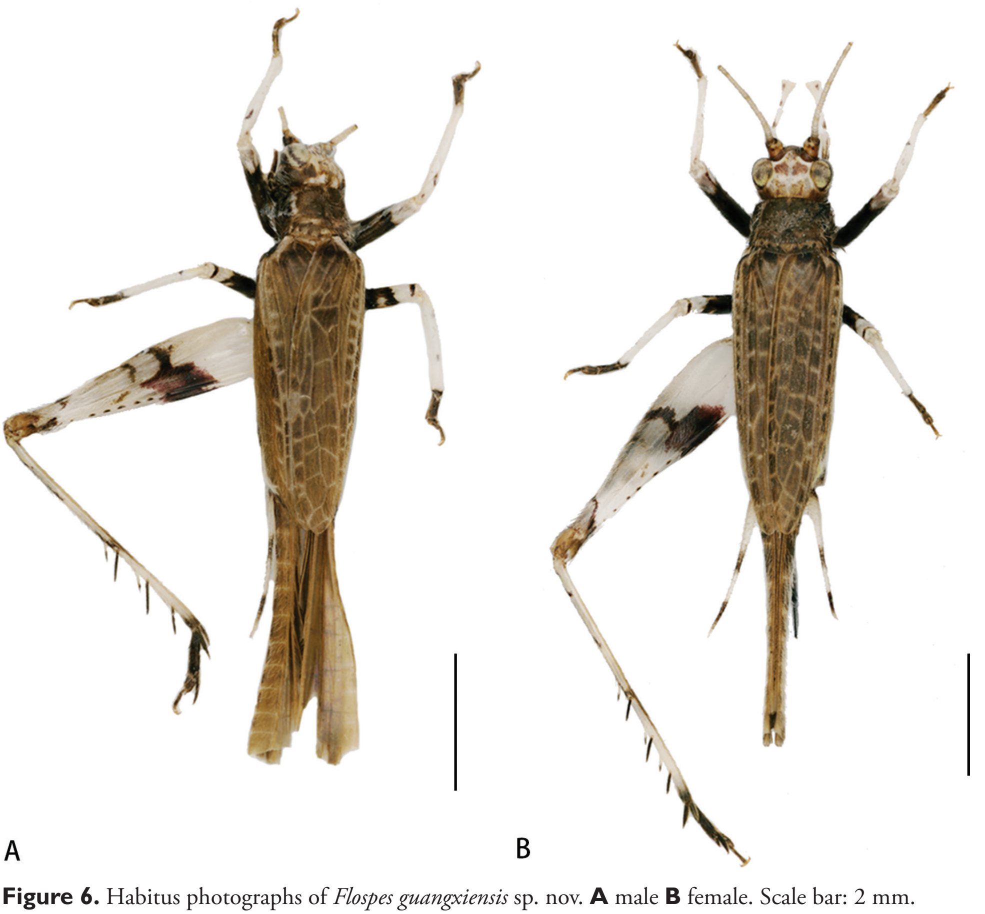

Figure 6. Habitus photographs of *Flospes guangxiensis* sp. nov. **A** male **B** female. Scale bar: 2 mm.

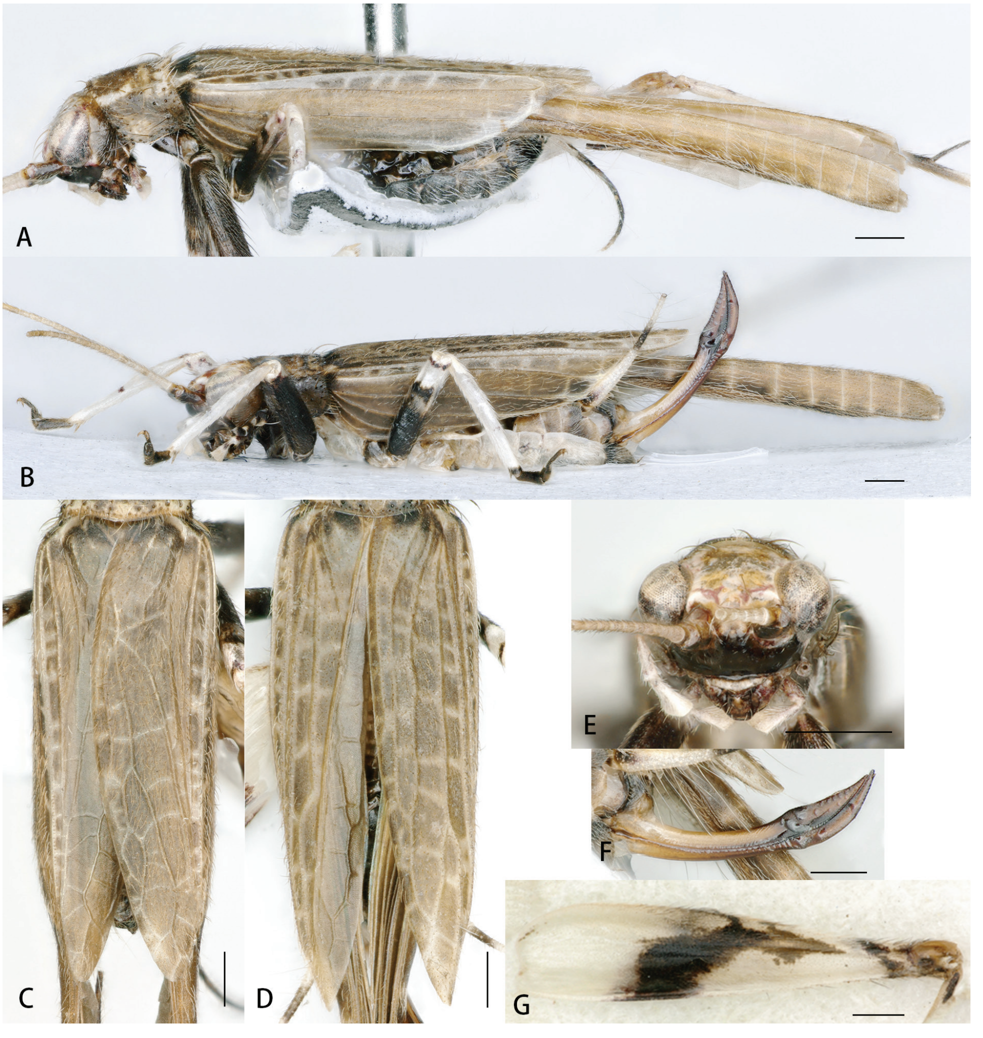

Figure 7. *Flospes guangxiensis* sp. nov. **A** lateral view of male **B** lateral view of female **C** male tegmen **D** female tegmen **E** face in anterior view **F** female ovipositor in lateral view **G** lateral view of hind femur. Scale bars: 0.5mm.

Remarks. This species is similar in appearance to *F. fujianensis* and *F. denutilatus* but differs in its squared ectoparamere (that of *F. fujianensis* is round) and blunt apex of epiphallic lateral lobe (that of *F. denutilatus* is acute). The transverse cells of female tegmen of the new are more darker than that of *F. fujianensis*.

Flospes hainanensis comb. nov.

Chinese name: 海南花蛉蟋

Amusurgus (*Paranaxipha*) *hainanensis* He et al., 2010: 60
Sectus hainanensis, Ma & Pan, 2019: 567

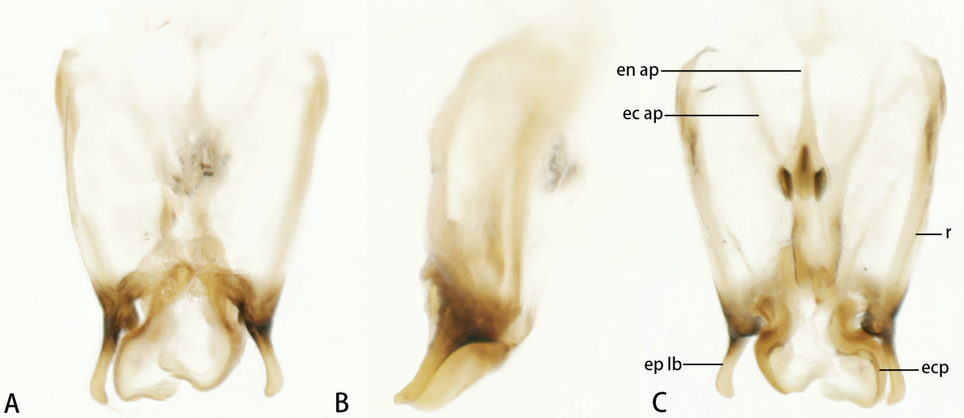

Figure 8. Male genitalia of *Flospes guangxiensis* sp. nov. **A** dorsal view **B** lateral view **C** ventral view.

Holotype information. Type locality: China. Hainan, Ledong, Jianfeng. Deposited at East China Normal University, Biology of History Museum (HSUN), Shanghai, China (not examined).

Distribution (Fig. 1). China (Hainan).

Remarks. This species has very unique male genitalia; the epiphallus is relatively short and the lateral lobe is nearly absent. These features correspond to some other genera of Trigonidiinae (e.g., *Sectus* and *Anaxiphomorpha*), and even species of Nemobiinae. This species has been assigned in the genus *Sectus* according to the genitalic form (Ma and Pan 2019). Because the type species of *Sectus* bears acoustical devices (tympana and stridulatory vein and mirror, etc.) and can sing, the placement of *F. hainanensis*, a silent cricket species, in *Sectus* is unsuitable. The similar appearance of this species with *F. fujianensis* makes it more suitable to move it to the new genus.

Flospes viridipennis He, Ma & Zhang, sp. nov.

http://zoobank.org/5B3364B1-B998-4433-8DBD-27A324D288D5
Chinese name: 青翼花蛉蟋
Figs 1, 9–12

Amusurgus (*Paranaxipha*) *fujianensis* (= *Sectus fujianensis*), He et al. 2010: 60; He et al. 2020: 126. misidentification of *F. viridipennis* sp. nov.

Type materials. ***Holotype.*** **China:** Male, Hainan, Lingshui, Diaoluoshan National Nature Reserve, bush leaves, 14.IX.2019, 18.66°N, 109.92°E, Zhixin He & Tao Zhang, sweep net, leg. ***Paratypes.*** 2 females, same data as holotype; 1 female, Hainan, Wuzhishan National Nature Reserve, bush leaves, 17.IX.2019, Zhixin He & Tao Zhang, sweep net, leg.; 1 male, 2 females, Hainan, Ledong, Jianfengling National Nature Reserve, bush leaves, 20.IX.2019, Zhixin He & Tao Zhang, sweep net, leg. (SNNU).

Figure 9. Habitus (alive) of *Flospes viridipennis* sp. nov. on leaf **A** male **B** female.

Description. Male (Figs 9A, 10A, 11A, C, E, G). Body size small. Head small, slightly broader than anterior margin of pronotum. Frons significantly narrower than antennal scape. Eyes large and protruding laterally. Three apical joints of maxillary palpi distinctly elongate, and fifth joint apically truncated. Pronotum transverse, posterior margin conspicuously broader than anterior one. Tegmina extending over abdominal apex, and six primary veins staggered with many transverse veins between them. Visible part of hindwing is half length of tegmen. Internal tympanum large and long-oval, external one shaped as a small pit. Hind tibia bearing three dorsal spurs on each side.

Genitalia (Fig. 12A–C). Lateral lobes of epiphallus stick-like and apically blunt. In dorsal view, these lobes are straight and hirsute on the inner margin. Ectoparamere bifurcated as two rectangular branches, and the upper larger than lower one. Rami arcuate, very long, and surpass ectophallic and endophallic apodemes.

Figure 10. Habitus photographs of *Flospes viridipennis* sp. nov. **A** male **B** female. Scale bars: 2 mm.

Female (Figs 9B, 10B, 11B, D, F). Resembles male. Body size slightly larger than male. Longitudinal veins of tegmen parallel and forming rectangular cells with some pale transverse veins (filled yellowish brown). Ovipositor falcate and similar to the species described above.

Coloration. Body greenish-brown. Head and pronotum brown. Most of the apical three joints of the maxillary pale and proximally darkly color. Tegmen yellowish-brown with green veins. The hind femur bearing an irregular dark pattern.

Measurements. Male: BL 5.95–6.26, PL 0.76–0.86, TL 4.74–4.96, HFL 4.26. Female: BL 5.64–6.15, PL 0.78–0.88, TL 4.74–5.20, HFL 4.45–4.88, OL 1.94–2.19.

Etymology. The name refers to the green veins of the species.

Distribution (Fig. 1). China (Hainan, Zhejiang, Yunnan).

Remarks. Specimens of this species were identified as *A. fujianensis* (= *S. fujianensis*) by He et al. (2010), but this is incorrect. The true *A. fujianensis* bears brown veins and a

Figure 11. *Flospes viridipennis* sp. nov. **A** lateral view of male **B** lateral view of female **C** male tegmen **D** female tegmen **E** face in anterior view **F** female ovipositor in lateral view **G** lateral view of hind femur Scale bars: 0.5mm.

rounded ectoparamere apex, whereas those assumed to be *A. fujianensis* bear green veins and a squared ectoparamere apex. This species is similar with *Amusurgus* (*Amusurgus*) *xanthoneurus* (Chopard, 1940) in having green veins and the pattern of legs and cerci, but differs in the color of the apex of hind femur (black-brown in *A. xanthoneurus* vs yellow-white in *F. viridipennis*) and in the distance between Cu1 and Cu2 of the tegmen in females (extremely narrow in *A. xanthoneurus* vs relatively wide in *F. viridipennis*).

Figure 12. Male genitalia of *Flospes viridipennis* sp. nov. **A** dorsal view **B** lateral view **C** ventral view.

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RESEARCH ARTICLE

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A new *Gammarus* species from Xinjiang Uygur Autonomous Region (China) with a key to Xinjiang freshwater gammarids (Crustacea, Amphipoda, Gammaridae)

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Abstract
A new species of the genus *Gammarus* Fabricius, 1775 is described and illustrated from Xinjiang Uygur Autonomous Region, China. *Gammarus zhouqiongi* **sp. nov.** is characterized by pereopods III–IV with long straight setae on posterior margins; inner ramus of uropod III more than twice as long as peduncle, reaching 0.7 times the length of outer ramus; inner ramus with plumose setae, and outer ramus with both plumose setae and long simple setae. Detailed morphological comparisons with related species are discussed. The K2P distances for each marker (CO1, 16S, 28S, and EF1α) of the new species differ from those of other *Gammarus* species in Xinjiang. Both phylogenetic trees based on separate (CO1, 16S, 28S, and EF1α) and combined (CO1+16S+28S+EF1α) markers show that the new species is an independent branch. A key to identify *Gammarus* species in Xinjiang is provided.

Keywords
Amphipoda diversity, mitochondrial DNA, morphology, new species, nuclear DNA, taxonomy, Xinjiang

Introduction

The genus *Gammarus* Fabricius, 1775 is distributed in Eurasia and North America, and is one of the genera with the highest species richness in freshwater amphipods (Zhao et al. 2017). Previous studies suggest that *Gammarus* originated in the Tethys Ocean, and the regression of Paratethys played an important role in its dispersal to Eurasia (Hou et al. 2011). The Xinjiang Uygur Autonomous Region (Xinjiang afterwards) is located between the Lake Baikal and the Ponto-Caspian Basin, and is one of the most major zones of endemic amphipod species diversity (Väinölä et al. 2008), acting as a crossroad among the various regions of the Palaearctic Realm. However, only eight *Gammarus* species are described in Xinjiang. Particularly, seven of them are endemic species, including *Gammarus tastiensis* Hou, *G. decorosus* Meng, Hou & Li, *G. brevipodus* Hou & Li, *G. takesensis* Hou & Li, *G. tianshan* Zhao, Meng & Hou, *G. simplex* Zhao, Meng & Hou, *G. liuruiyui* Zheng, Hou & Li (Hou 2002; Meng et al. 2003; Hou et al. 2004; Zhao et al. 2017; Zheng et al. 2020) and one is a widespread species (*G. lacustris* Sars, 1863) in alpine lakes. The amphipod diversity of Xinjiang still remains incompletely understood.

During our field surveys in Xinjiang between 2012–2020, a new species was discovered based on morphological and molecular analyses. To further identify and understand the evolutionary origins of the new species, phylogenetic analyses of *Gammarus* in Xinjiang were performed. The distributions of endemic species of the genus *Gammarus* in Xinjiang are presented in Fig. 1.

Materials and methods

Sampling

Specimens were collected from the streams and adjacent puddles with fine-meshed hand nets (500 μm). Samples were stored in 95% ethanol in the field, and then deposited at -80 °C for long-term preservation. Type specimens are lodged in the College of Fisheries, Huazhong Agricultural University, Wuhan (China).

Morphometrics

All dissected appendages were examined and drawn using a Leica DM2500 compound microscope equipped with a drawing tube. The body length was measured from the base of the first antenna to the end of the telson while the specimens were kept straight. Terminology and taxonomic description referred to Zhao et al. (2017). Nomenclature of the setae of mandibular palps followed Cole (1980).

DNA sequencing and phylogenetic analyses

We did not obtain samples of *G. simplex* during field surveys, and no relevant record was accessible in GenBank. Genomic DNA was extracted using the Animal Genomic DNA

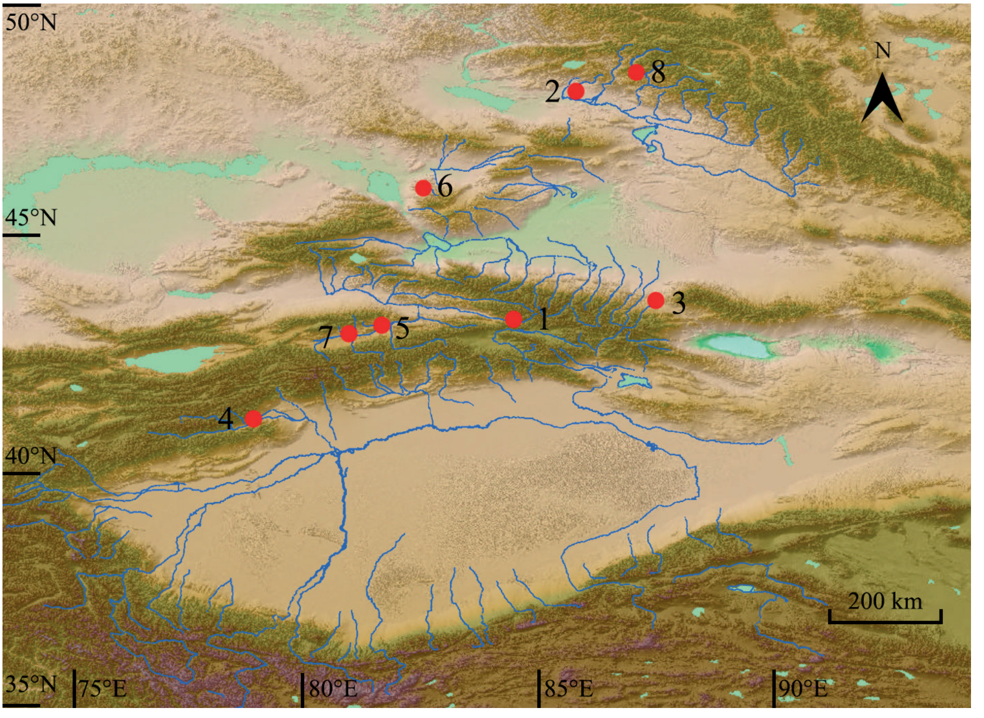

Figure 1. Distribution map of *Gammarus* species from Xinjiang (China). Type localities are shown for the species **1–8**. **1** *Gammarus brevipodus* Hou & Li, 2004 **2** *G. zhouqiongi* sp. nov. **3** *G. decorosus* Meng, Hou & Li, 2003 **4** *G. liuruiyui* Zheng, Hou & Li, 2020 **5** *G. takesensis* Hou & Li, 2004 **6** *G. tastiensis* Hou, 2002 **7** *G. tianshan* Zhao, Meng & Hou, 2017 **8** *G. simplex* Zhao, Meng & Hou, 2017 (map data from GEBCO Compilation Group [2020]).

Kit (Tsingke Biotech, Beijing). K2P distances based on each marker were calculated in MEGA 6 (Tamura et al. 2013). We utilized two mitochondrial and two nuclear markers, previously used for *Gammarus* phylogeny (Hou et al. 2007, 2011, Copilas-Ciocianu et al. 2019), based on both separate and combined markers to understand the phylogenetic relationships between *G. zhouqiongi* sp. nov. and other *Gammarus* species in Xinjiang. The mitochondrial markers included the fragments for cytochrome c oxidase 1 (CO1) and 16S ribosomal RNA (16S), whereas the nuclear markers included the fragments for 28S ribosomal RNA (28S) and elongation factor 1-alpha (EF1α). The primers are presented in Table 1. Raw sequences were aligned with muscle (Edgar 2004) and translated to amino acids to check for potential pseudogenes in MEGA 6. We selected *Jesogammarus debilis* Hou & Li, 2005, *Jesogammarus hebeiensis* Hou & Li, 2004 and *Rhipidogammarus rhipidiophorus* Catta, 1878 for EF1α as the outgroup. The details of newly obtained sequences in this study and the sequences downloaded from GenBank are shown in Table 2.

We selected the best-fit models by Akaike information criterion (AICc) in PartitionFinder (Lanfear et al. 2012). For phylogenetic analysis, we utilized the IQ-Tree 1.4.2 (Nguyen et al. 2015) to construct a phylogenetic tree based on the maximum likelihood (ML) method. 1000 bootstrap replicates were performed to assess nodal support.

Table 1. Primer sequences of PCR products for target genes.

Gene	Primer	Sequence (5'–3')	Reference
CO1	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO2198	TAAACTTCAGGGTGACCAAAAAAT	Folmer et al. (1994)
	LCO3	TCNACHAAYCATAAAGAYATTGGTAC	Krebes et al. (2010)
16S	16STf	GGTAWHYTRACYGTGCTAAG	MacDonald et al. (2005)
	16Sbr	CCGGTTTGAACTCAGATCATGT	Palumbi et al. (1991)
28S	28F	TTAGTAGGGGCGACCGAACAGGGAT	Hou et al. (2007)
	28R	GTCTTTCGCCCCTATGCCCAACTGA	Hou et al. (2007)
EF1α	EF1αF	CACTACTGGTCATCTCATCTAC	Hou et al. (2011)
	EF1αR	ACTTCCAGGAGAGTCTCAAAC	Hou et al. (2011)

Table 2. Taxon information and Genbank numbers for the complete dataset.

Taxon	Coordinates	CO1	16S	28S	EF1α	Reference
Gammarus brevipodus	43.28N, 84.28E	MW723045	MW729654	MW729697	MW749858	This study
*G. zhouqiongi*1	46.76N, 84.42E	MW723044	MW729651	MW729694	MW749855	This study
*G. zhouqiongi*2	48.08N, 86.35E		MW729649	MW729692	MW749853	This study
G. decorosus	43.80N, 87.60E	JF965875		JF965684	JF966031	Hou et al. 2011
G. lacustris	47.24N, 88.47E	MW717900	MW729628	MW729674	MW749832	This study
G. liuruiyui	40.88N, 78.19E	MK455899		MK455898		Zheng et al. 2020
G. takesensis	43.63N ,81.80E	MW723041	MW729638	MW729681	MW749842	This study
G. tastiensis	45.95N, 82.57E	MW723046	MW729655	MW729698	MW749859	This study
G. tianshan	43.1N, 81.1E	EF570327	EF582873	EF582971		Hou et al. 2007
Jesogammarus debilis	39.5N, 115.8E	EF570351	EF582846	EF582997		Hou et al. 2007
*J. hebeiens*is	40.4N, 115.9E	EF570352	EF582847	EF582998		Hou et al. 2007
Rhipidogammarus rhipidiophorus	40.28N, 9.63E				JF966114	Hou et al. 2011

Results

Molecular analyses

The values of K2P distances between *Gammarus zhouqiongi* sp. nov. and other *Gammarus* species in Xinjiang (*G. simplex* excluded) ranged between 16.6%–32.4% for CO1, 11.0%–39.3% for 16S, 1.2%–6.3% for 28S and 1.3%–9.6% for EF1α (Table 3), respectively. In contrast, many studies relevant to *Gammarus* reported similar or lower levels of divergence. Hou et al. (2014) showed 11.2–20.3% for CO1 and 1.1–3.7% for 28S (uncorrected p-distance), respectively, among *Gammarus* species in Luliang Mts and Taihang Mts. Copila-Ciocianu et al. (2019) found 13.3% for CO1, 4.3% for 16S, 0.4% for 28S and 1.8% for EF1α, respectively, between *G. hamaticornis* and *G. kischineffensis*. The genetic clusters of *Gammarus zhouqiongi* sp. nov. were clearly distinguished from other species (Figs 2, 3), suggesting one new species to science.

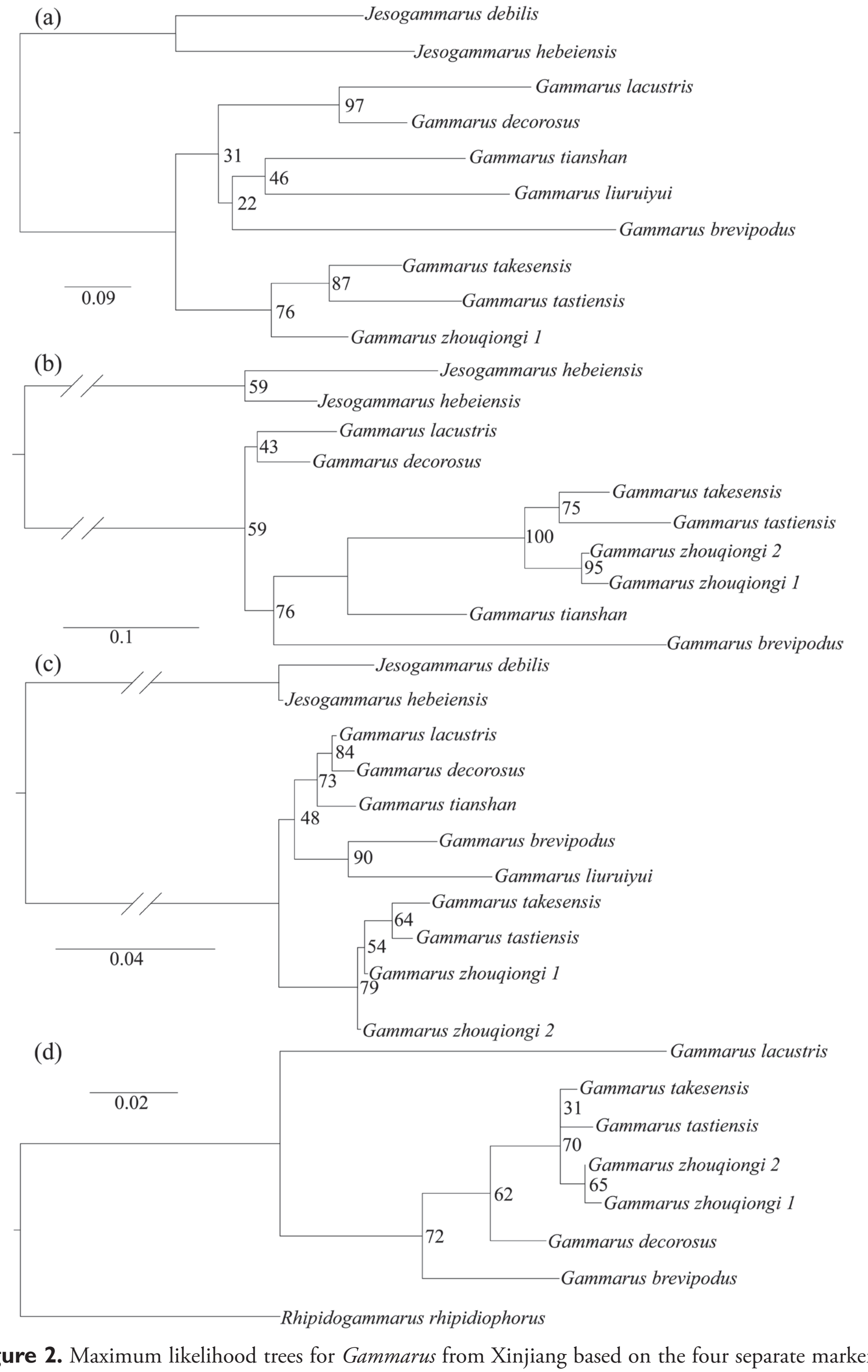

Figure 2. Maximum likelihood trees for *Gammarus* from Xinjiang based on the four separate markers: **a** CO1 **b** 16S **c** 28S **d** EF1α. Numbers near the nodes are bootstrap values.

Table 3. Kimura 2-parameter pairwise genetic distances of *Gammarus* in Xinjiang.

		Species	1	2	3	4	5	6	7	8
CO1 (below diagonal)/16S (above diagonal)	1	*Gammarus brevipodus*		0.393	0.281	0.321		0.336	0.329	0.343
	2	*G. zhouqiongi*1	0.324		0.248	0.239		0.110	0.144	0.210
	3	*G. decorosus*	0.349	0.262		0.085		0.232	0.258	0.170
	4	*G. lacustris*	0.389	0.297	0.215			0.231	0.282	0.196
	5	*G. liuruiyui*	0.316	0.308	0.265	0.329				
	6	*G. takesensis*	0.347	0.166	0.267	0.324	0.326		0.104	0.193
	7	*G. tastiensis*	0.322	0.190	0.264	0.352	0.355	0.177		0.229
	8	*G. tianshan*	0.359	0.288	0.301	0.327	0.316	0.313	0.282	
28S (below diagonal)/EF1α (above diagonal)	1	*G. brevipodus*		0.067	0.053	0.132		0.065	0.069	0.061
	2	*G. zhouqiongi*1	0.053		0.029	0.096		0.013	0.017	0.044
	3	*G. decorosus*	0.044	0.037		0.098		0.031	0.031	0.022
	4	*G. lacustris*	0.040	0.033	0.007			0.112	0.118	0.120
	5	*G. liuruiyui*	0.053	0.063	0.052	0.051				
	6	*G. takesensis*	0.058	0.017	0.042	0.038	0.071		0.011	0.039
	7	*G. tastiensis*	0.049	0.012	0.039	0.033	0.066	0.014		0.042
	8	*G. tianshan*	0.044	0.039	0.017	0.014	0.054	0.045	0.037	

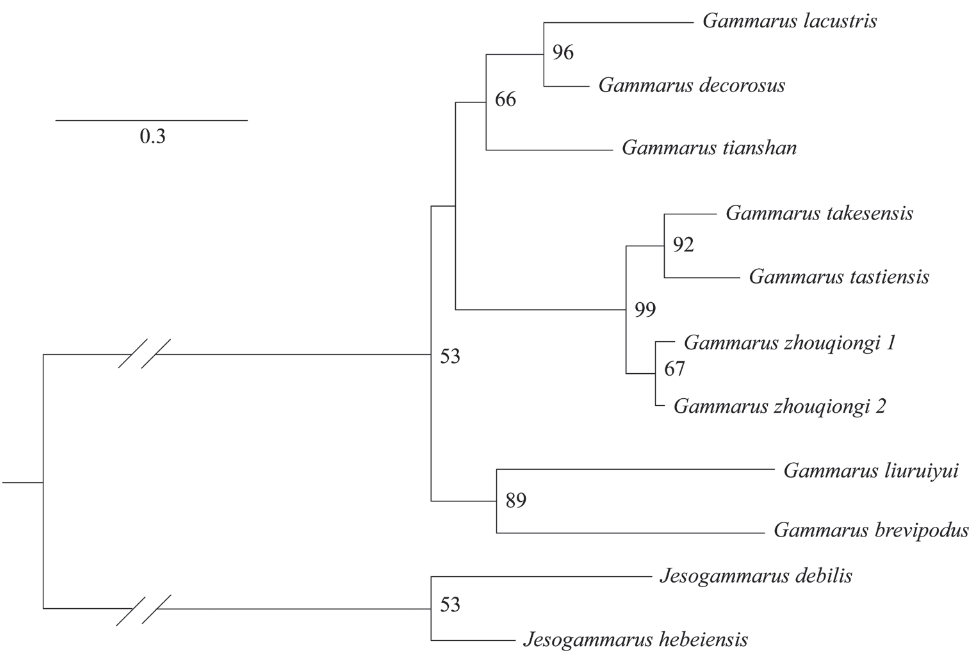

Figure 3. Maximum likelihood tree for *Gammarus* from Xinjiang based on combined markers (CO1+16S+28S+EF1α). Numbers near the nodes are bootstrap values.

Taxonomy

Family Gammaridae Leach, 1814

Genus *Gammarus* Fabricius, 1775

Type species. *Gammarus pulex* (Linnaeus, 1758).

***Gammarus zhouqiongi* sp. nov.**
http://zoobank.org/0120F1C0-D50B-45C7-A9C0-B32650AAD6F2
Figs 4–10

Material examined. ***Holotype*:** male (GAHBH-001), 14.9 mm, Habahe County (48.08°N, 86.35°E), altitude 528 m, Xinjiang Uygur Autonomous Region, China, October 16, 2020, collected by Kui Zhang. ***Paratypes*:** female (GAHBH-002), 12.3 mm; five males and three females (GAHBH003-010), same data as holotype. three males and two females (GAKLY001-005), Emin County (46.76°N, 84.42°E), altitude 991 m, Xinjiang Uygur Autonomous Region, China, July 12, 2015, collected by Jun Wang and Yihao Ge.

Etymology. The specific name was to thank Professor Zhou for funding this study.

Diagnosis. Peduncle articles IV–V of antenna II with clusters of short setae; merus to carpus of pereopod III with clusters of long setae that exceed the width of the underlying segment on posterior margins; epimeral plates III with subacute posterodistal corners; inner ramus of uropod III more than twice times as long as peduncle, reaching 0.7 times the length of outer ramus, both inner and outer margins of inner ramus and the inner margins of outer ramus with plumose setae, and outer margin of outer ramus with long simple setae.

Description of male holotype. (GAHBH-001), 14.9 mm.

Head. (Fig. 5A): eyes reniform, inferior antennal sinus deep.

Figure 4. *Gammarus zhouqiongi* sp. nov., holotype.

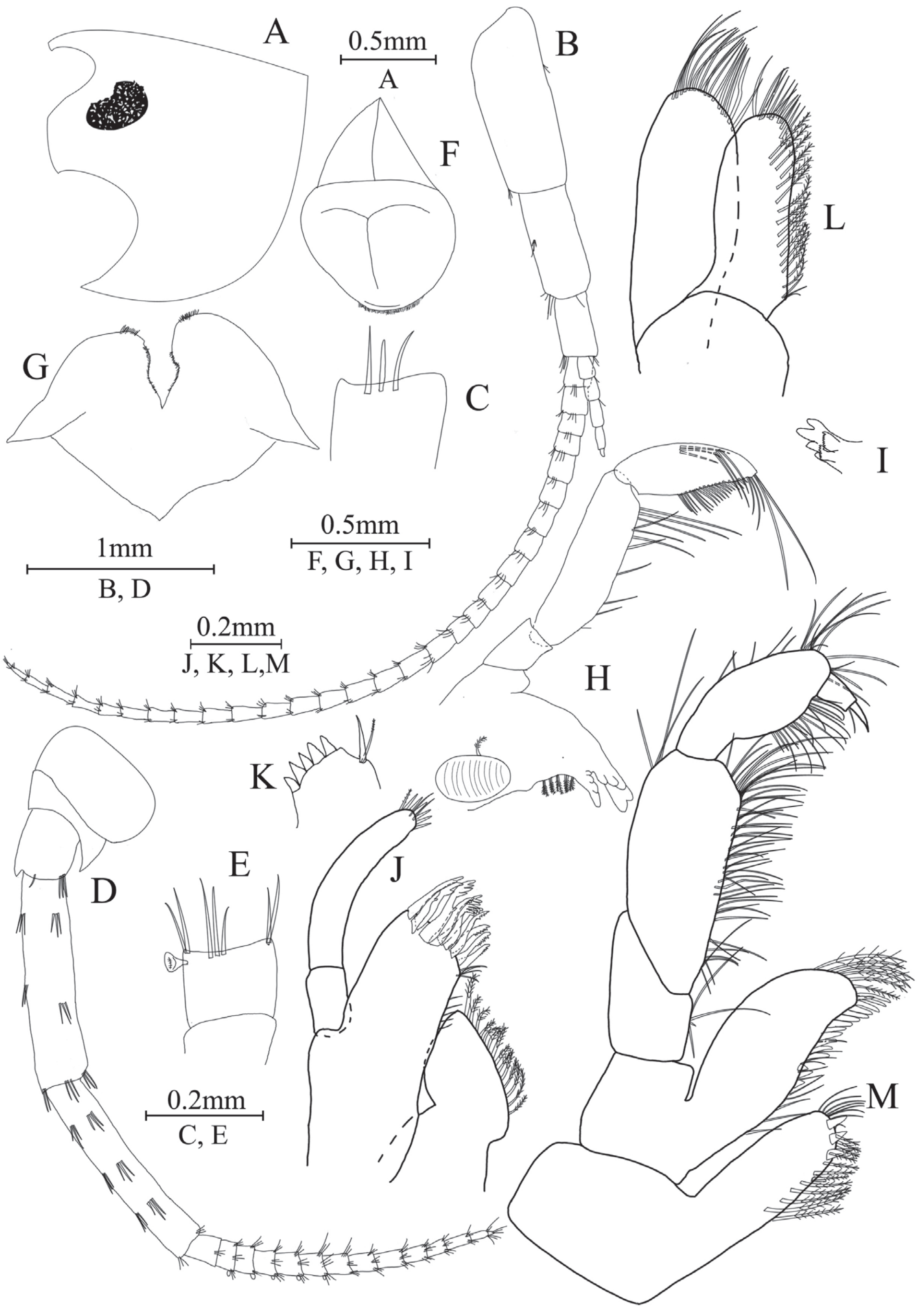

Figure 5. *Gammarus zhouqiongi* sp. nov., male holotype **A** head **B** antenna I **C** flagellar article of antenna I with aesthetasc **D** antenna II **E** calceoli of antenna II **F** upper lip **G** lower lip **H** left mandible **I** incisor and lacinia mobilis of right mandible **J** left maxilla I **K** distal part of palp article II of right maxilla I **L** maxilla II **M** maxilliped.

Antenna I (Fig. 5B, C): peduncle articles I–III in length ratio 1.0: 0.7: 0.4 bearing short setae; flagellum with 30 articles, most with aesthetascs; accessory flagellum with five articles; both primary and accessory flagella bearing small setae distally.

Antenna II (Fig. 5D, E): peduncle articles III–V in length ratio 1.0: 3.0: 2.9, peduncle article III with lateral setae, articles IV and V of peduncle with clusters of lateral and medial setae; flagellum with 14 articles, each article with setae along ventral margins; articles II–VI with calceoli.

Upper lip (Fig. 5F): ventral margin rounded, with minute setae on the distal part.

Mandible (Fig. 5H, I): left mandible incisor with five teeth; lacinia mobilis with four teeth; spine row with five pairs of plumose setae; articles I–III of palp in length radio 1.0: 2.3: 3.0, second article of palp with 11 marginal setae, article III with three A-setae, three B-setae, 19 D-setae, and five E-setae apically; incisor of right mandible with four teeth; lacinia mobilis bifurcate, with a row of small teeth at the end.

Lower lip (Fig. 5G): inner lobes lacking, outer lobes covered with thin setae.

Maxilla I (Fig. 5J, K): asymmetrical, left inner plate with 14 plumose setae on medial margin; outer plate with 11 robust serrated apical spines, each spine with small teeth; second article of left palp with six slender spines, two long setae and one spine with small setae; second article of right palp with five stout spines, one stiff seta and one slender spine.

Maxilla II (Fig. 4L): inner plate with 15 plumose facial setae in an oblique row; inner and outer plates with long setae apically.

Maxilliped (Fig. 4M): inner plate with three stout apical spines, one subapical spine, eight simple setae, and 12 plumose setae; outer plate bearing a row of blade spines and six plumose setae apically; article IV of palp hooked, with a group of setae at hinge of unguis.

Pereon. Gnathopod I (Fig. 6A, B): coxal plate bearing one seta on both anterior and posterior margins; basis with long setae on anterior and posterior margins; carpus 1.1 times as long as wide, 0.7 times as long as propodus; propodus oval, palm with one medial spine and 16 spines on posterior margin and surface; dactylus with one seta on outer margin.

Gnathopod II (Fig. 6C, D): coxal plate bearing three setae and one seta on anterior and posterior margins; basis with long setae on anterior and posterior margins; carpus 1.2 times as long as wide, 0.6 times as long as propodus; propodus subrectangular, palm margin with one medial spine and four spines on lateral posterior margin and surface; dactylus with one seta on outer margin.

Pereopod III (Fig. 7A, B): both anterior and posterior margins of coxal plate bearing one setae; basis elongate, with setae along anterior and posterior margins; merus with two spines accompanied by one seta on anterior margin and clusters of long setae on posterior margin, 1 spine accompanied by setae in anterodistal corner; carpus with five spines accompanied by setae on posterior margin, one spine with setae in anterodistal corner; propodus with five spines accompanied by setae on posterior margin and one spine on posterodistal corner; dactylus with one plumose seta on anterior margin, and one setae at hinge of unguis.

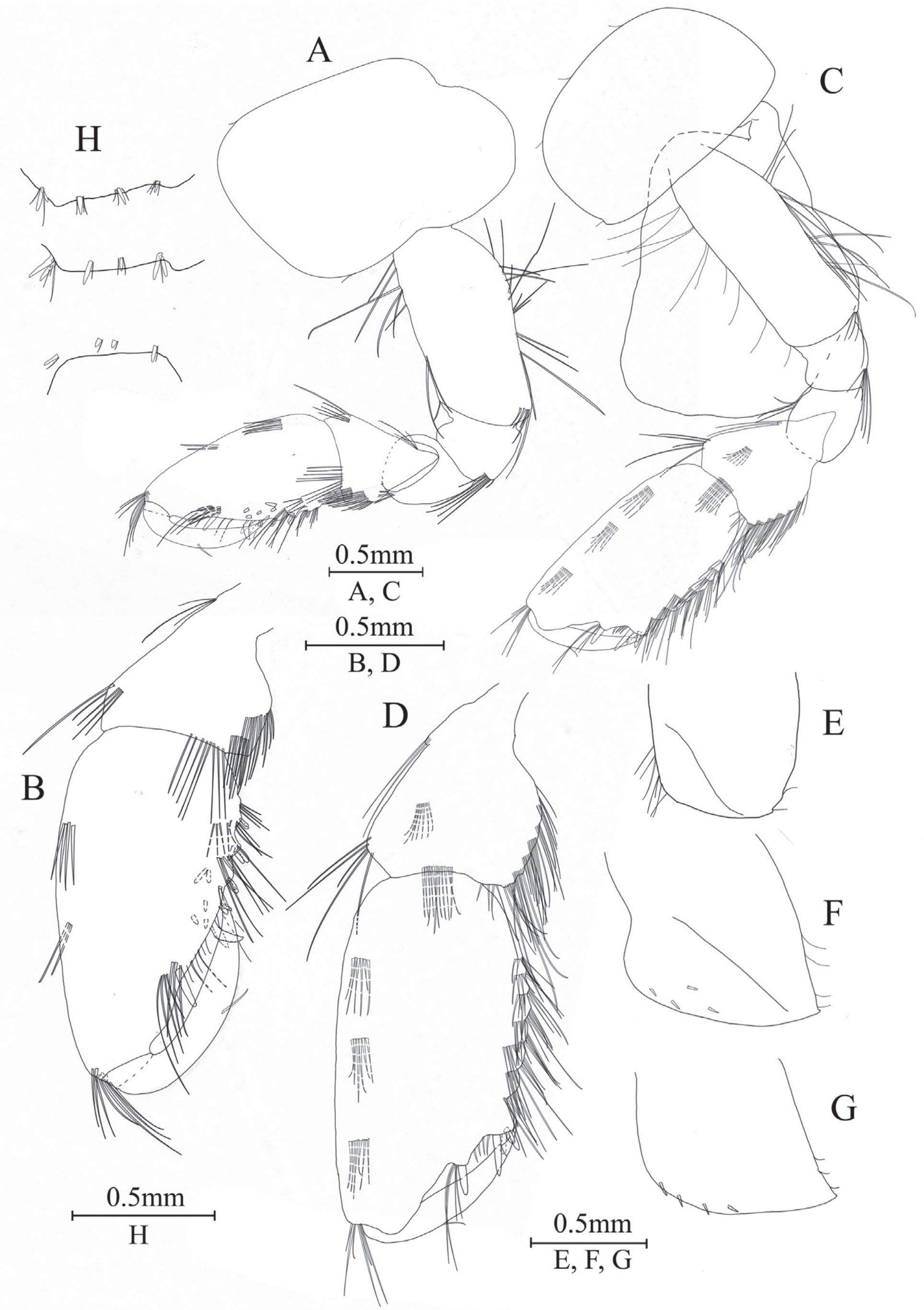

Figure 6. *Gammarus zhouqiongi* sp. nov., male holotype **A** gnathopod I **B** propodus and dactylus of gnathopod I **C** gnathopod II **D** propodus and dactylus of gnathopod II **E** epimeral plate I **F** epimeral plate II **G** epimeral plate III **H** dorsal margins of urosomites I–III.

Pereopod IV (Fig. 7C, D): coxal plate concave, bearing five setae on posterior margin; basis with clusters of setae on anterior and posterior margin; merus has several clusters of setae on posterior margin and 1 spine on anterior margin, anterodistal corner with one spine accompanied by setae; carpus with five spines on posterior margin and two spines accompanied by setae on posterodistal corner; propodus with seven spines accompanied by setae on posterior margin and two spines on posterodistal corner; dactylus with one plumose seta on anterior margin and one seta at hinge of unguis.

Pereopod V (Fig. 7E, F): coxal plate bearing two setae on posterior margin; basis expanded, with setae and six spines on anterior margin, anterodistal corner with one spine and three setae, posterior margin with seven setae; merus with three spines accompanied by setae on both anterior margin and anterodistal corner, posterior margin with one spine and posterodistal corner with three spines; carpus with three or two groups of spines on anterior margin and posterior margin, respectively; propodus with five groups of spines on anterior margin; dactylus with one plumose seta on posterior margin, and one seta at hinge of unguis.

Pereopod VI (Fig. 7G, H): coxal plate bearing two setae on posterior margin; basis expanded, with three setae and four spines on anterior margin, anterodistal corner with two spines accompanied by setae, posterior margin with nine setae; merus with three pairs of spines on anterior margin and three spines accompanied by setae on anterodistal corner, posterior margin with one pair of spines and posterodistal corner with three spines; carpus with three or two groups of spines on anterior margin and posterior margin, respectively; propodus with five groups of spines on anterior margin, posterior margin with one spine and five setae; dactylus with one plumose seta on posterior margin, and one seta at hinge of unguis.

Pereopod VII (Fig. 7I, J): coxal plate bearing three setae on posterior margin; basis expanded, with two setae and six spines on anterior margin, anterodistal corner with three spines, eleven setae on posterior margin and one spines accompanied by three setae on posterodistal corner, respectively; both mersus and carpus with three spines on anterior margin and one spine on posterior margin; propodus with five groups of spines on anterior margin and two setae on posterior margin; dactylus with one plumose seta on posterior margin and one seta at hinge of unguis.

Coxal gills (Figs 6C, 7A–E): coxal gill of gnathopod II longer than basis; gills of pereopod III–V are almost as long as their basis; gills of pereopod VI–VII are shorter than their basis.

Pleon. Epimeral plates (Fig. 6E–G): plate I ventrally rounded, bearing seven setae on anteroventral margin and two setae on posterior margin; plate II with four spines on ventral margin and four setae on posterior margin, posterodistal corner blunt; plate III with four spines on ventral margin and three setae on posterior margin, posterodistal corner subacute.

Pleopods (Fig. 7A–C): similar, peduncle with two retinacula accompanied by two or three setae; outer ramus slightly shorter than inner ramus, both inner and outer rami fringed with plumose setae.

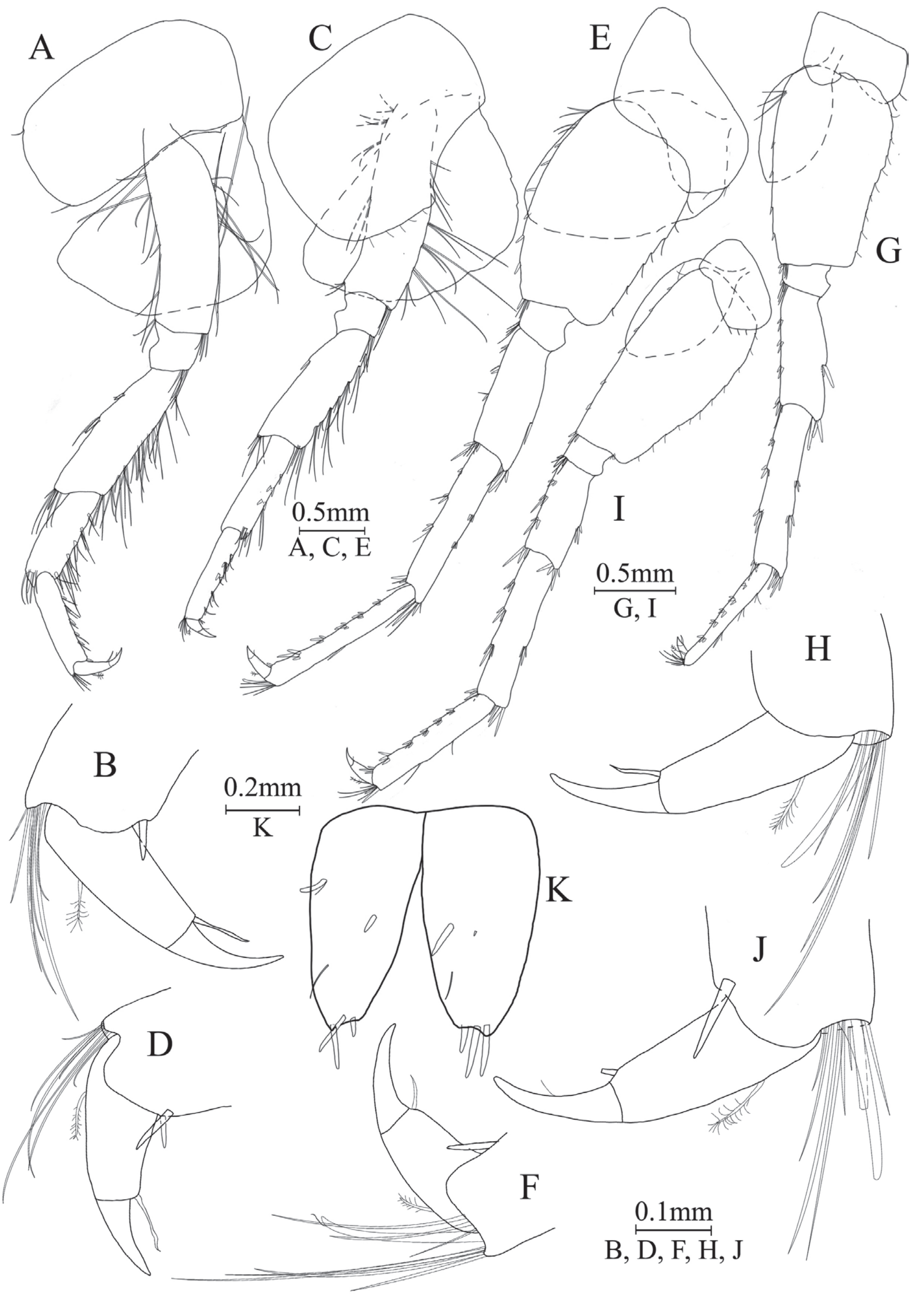

Figure 7. *Gammarus zhouqiongi* sp. nov., male holotype **A** pereopod III **B** dactylus of pereopod III **C** pereopod IV **D** dactylus of pereopod IV **E** pereopod V **F** dactylus of pereopod V **G** pereopod VI **H** dactylus of pereopod VI **I** pereopod VII **J** dactylus of pereopod VII **K** telson.

Urosome. Urosomites (Fig. 6H): urosomite I with two-one-one-two spines accompanied by setae on dorsal margin; urosomite II with two-one-one-two spines accompanied by setae on dorsal margin; urosomite III with one-one-one-one spine accompanied by one seta.

Uropods I–III (Fig. 8D–F): uropod I peduncle with one basofacial spine, one and three spines on inner and outer margins, with one and two spines on inner and outer distal corners, respectively; inner ramus with one spine on inner margin; outer ramus with one and two spines on inner and outer margins, respectively; both rami with five terminal spines. Uropod II peduncle with two spines on both inner and outer margins and one distal spine on each corner; inner ramus with three spines on inner margin, outer ramus with two spines on outer margin, both rami with five terminal spines. Uropod III peduncle with one spine accompanied by three setae and eight distal spines; inner ramus about 2.4 times as long as peduncle, reaching 0.7 times the length of outer ramus, with two spines on inner margin, both inner margin and outer margin have plumose setae; proximal article of outer ramus with five pairs of spines accompanied by several simple setae on outer margin, inner margin with both simple setae and plumose setae, and four distal spines accompanied by long simple setae; terminal article with long simple setae.

Telson (Fig. 7K): deeply cleft, approximately as long as wide; left lobe with two spines and two setae on surface; right lobe with one spine and one single seta; each lobe bearing three distal spines.

Description of paratype female. (GAHBH-002). 12.3 mm

Pereon. Gnathopod I (Fig. 9A, B): coxal plate bearing one seta on both anterior and posterior margins; basis with long setae on anterior and posterior margins; propodus oval, palm with 8 spines on posterior margin and surface; dactylus with one seta on outer margin.

Gnathopod II (Fig. 9C, D): coxal plate bearing three setae and one seta on anterior and posterior margins; basis with long setae on anterior and posterior margins; propodus subrectangular, palm margin with four spines on lateral posterior margin and surface; dactylus with one seta on outer margin.

Pereopods III–VII (Fig. 10A–E, J–N): similar to those of males.

Oostegite (Fig. 9F–I): oostegite of gnathopod II broad, oostegites of pereopods III–V elongated and oostegite of pereopod V smallest.

Urosome. Uropods I–III (Fig. 9G–F): uropod I peduncle with one or three spines on inner and outer margins respectively, with one spine on both inner and outer distal corners; both rami with two spines on inner margin and five terminal spines. Uropod II peduncle with one or two spines on inner and outer margins respectively and one distal spine on each corner; both rami with two spines on inner margin and five terminal spines. Uropod III peduncle with one spine accompanied by setae and eight distal spines; inner ramus about 2 times as long as peduncle, reaching 0.8 times the length of outer ramus, with four spines on inner margin and one distal spine accompanied by long setae, both inner and outer margins have plumose setae; proximal

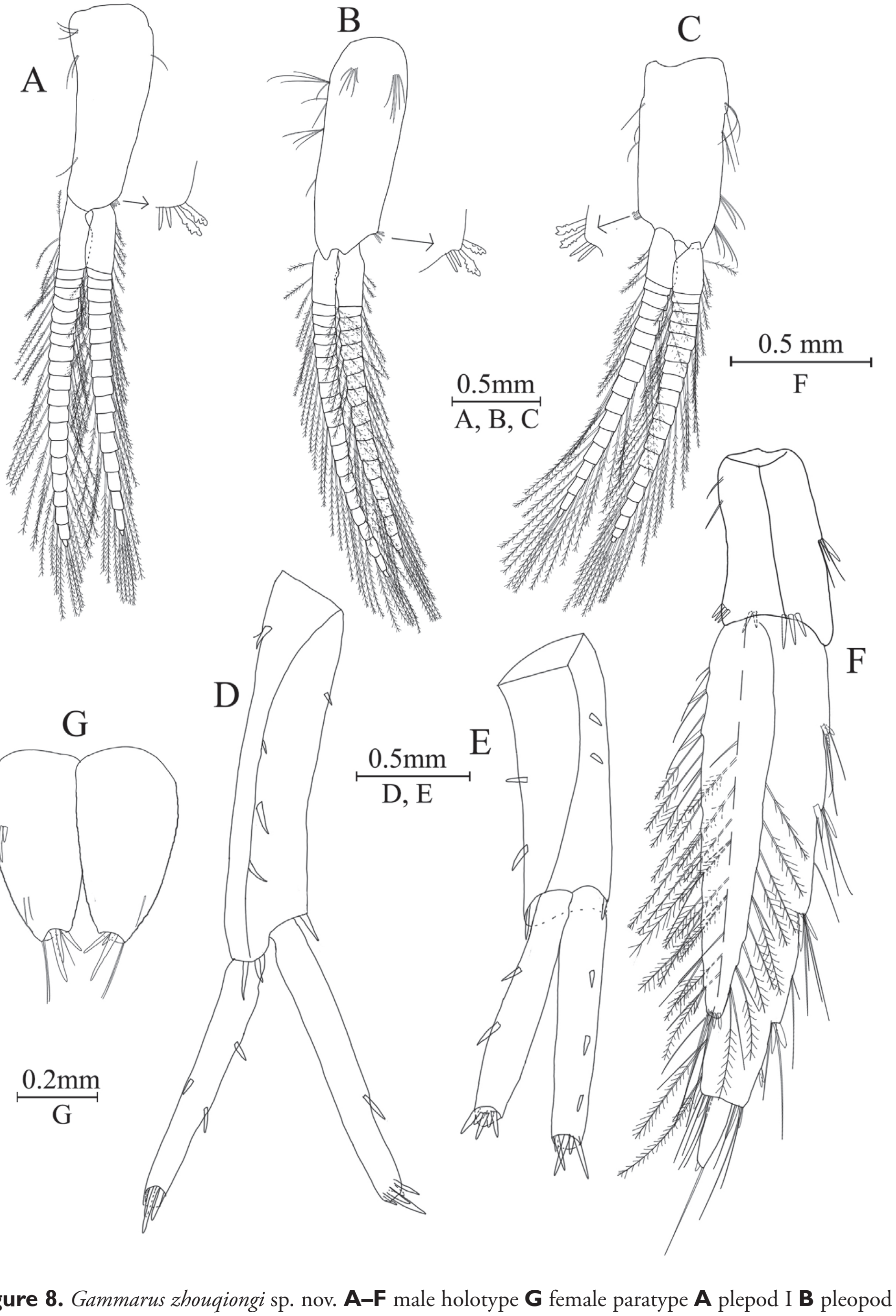

Figure 8. *Gammarus zhouqiongi* sp. nov. **A–F** male holotype **G** female paratype **A** plepod I **B** pleopod II **C** pleopod III **D** uropod I **E** uropod II **F** uropod III **G** telson.

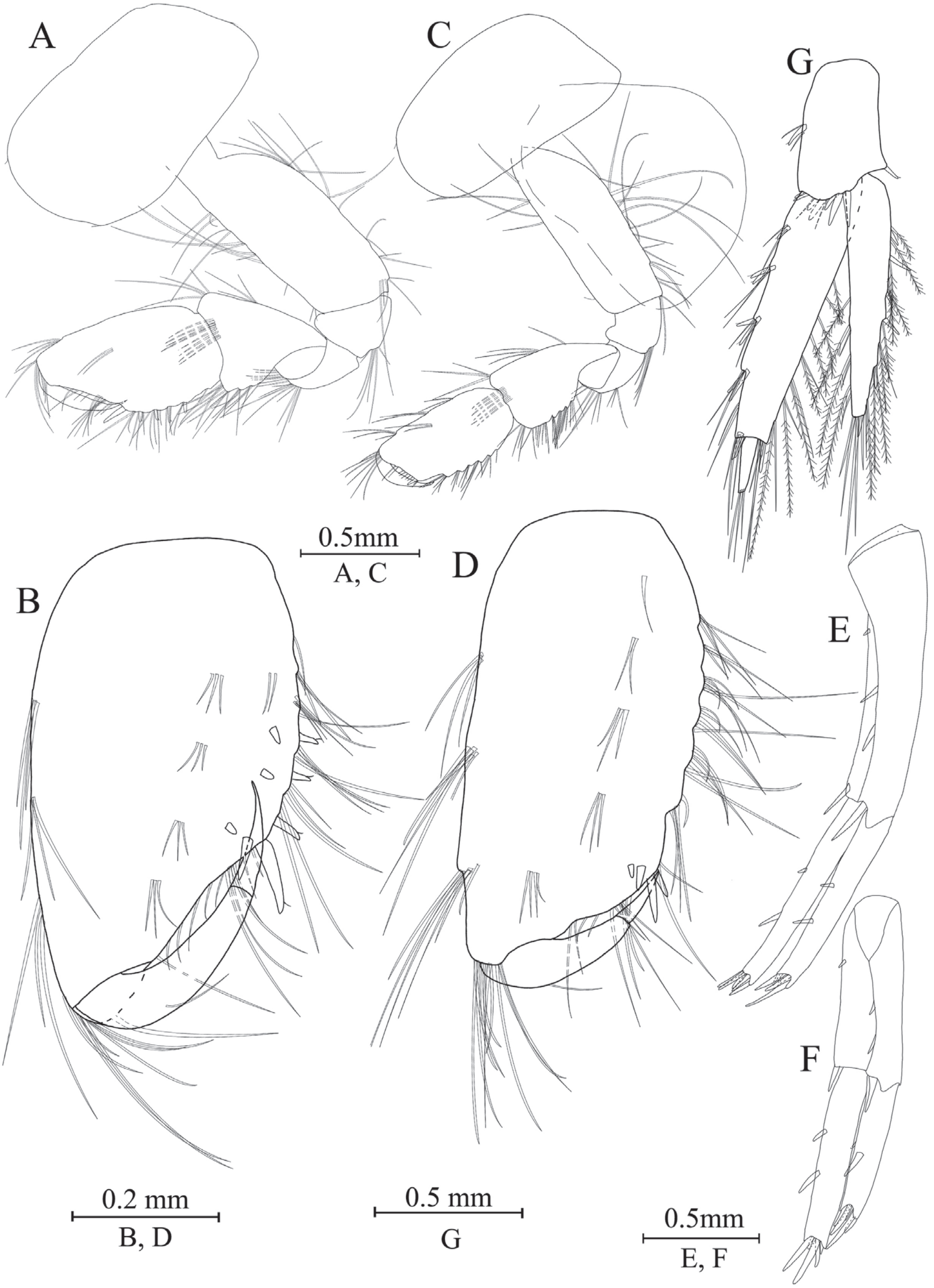

Figure 9. *Gammarus zhouqiongi* sp. nov., female paratype (GAHBH-002) **A** gnathopod I **B** propodus of gnathopod I **C** gnathopod II **D** propodus of gnathopod II **E** uropod I **F** uropod II **G** uropod III.

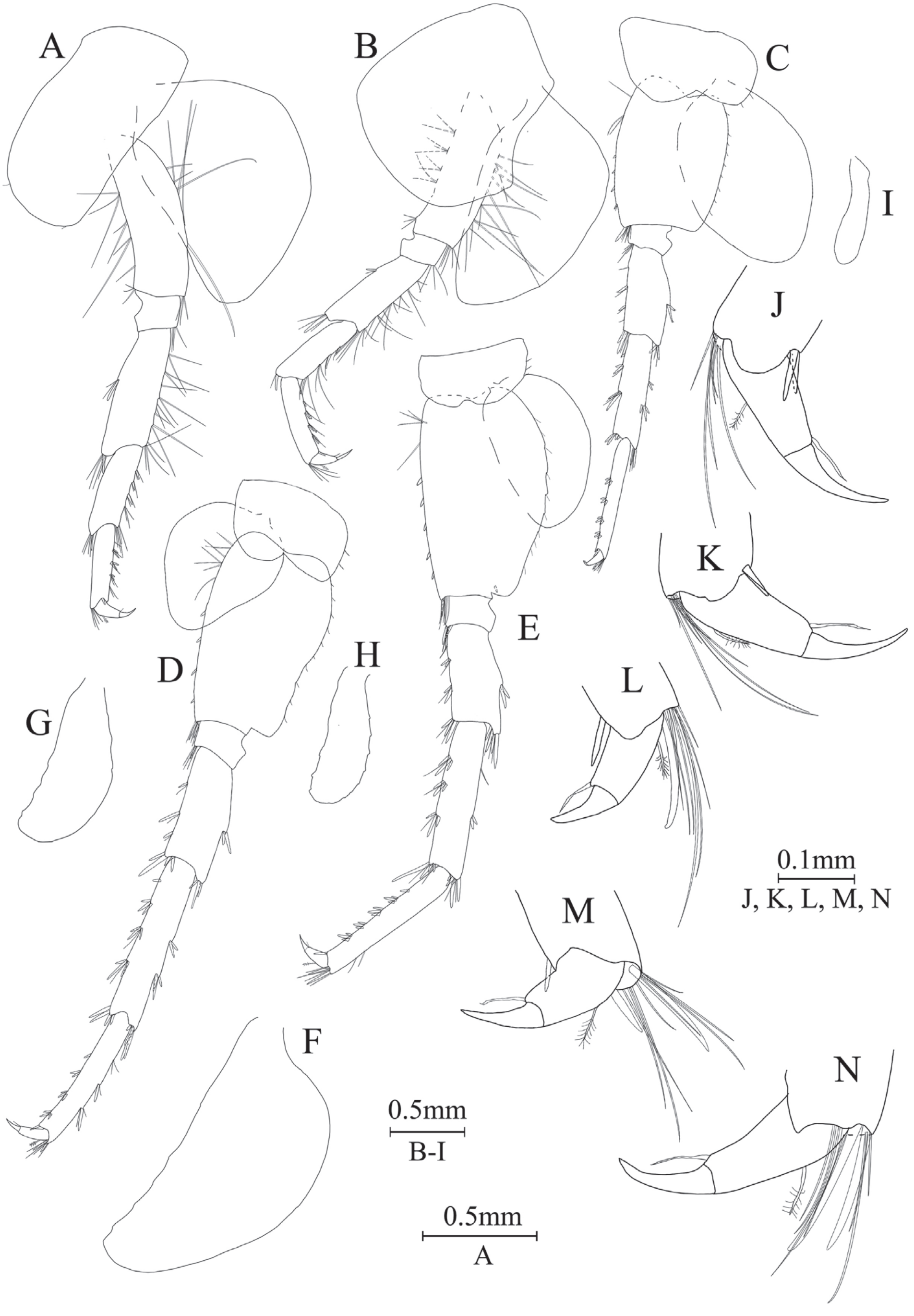

Figure 10. *Gammarus zhouqiongi* sp. nov., female paratype (GAHBH-002) **A** pereopod III **B** pereopod IV **C** pereopod V **D** pereopod VI **E** pereopod VII **F** oostegite of gnathopod II **G** oostegite of pereopod III **H** oostegite of pereopod IV **I** oostegite of pereopod V **J** dactylus of pereopod III **K** dactylus of pereopod IV **L** dactylus of pereopod V **M** dactylus of pereopod VI **N** dactylus of pereopod VII.

article of outer ramus with one spine and three pairs of spines accompanied by several simple setae on outer margin, inner margin with both simple setae and plumose setae, and four distal spines accompanied by long simple setae; terminal article with long simple setae.

Telson (Fig. 8G): deeply cleft, approximately as long as wide; left lobe with two spines and two setae on surface; right lobe with two setae; each lobe bearing three distal spines.

Habitat. This species was collected from streams and the adjacent small puddles, usually under big rocks.

Remarks. The new species *Gammarus zhouqiongi* sp. nov. is similar to *G. takesensis* in pereopods III and IV with straight setae on posterior margin; epimeral plates III with subacute posterodistal corners; and inner ramus of uropod III about 0.7 times as long as outer ramus. It differs from *G. takesensis* (*G. takesensis* in parentheses) by accessory flagellum of antenna I with five articles (four articles); inner and outer margins of inner ramus and the inner margins of outer ramus of uropod III with long plumose setae (short plumose setae); posterodistal corner of basis of pereopod VII with spines and setae (only with setae).

Gammarus zhouqiongi sp. nov. is also similar to *G. tastiensis* in peduncle articles IV–V of antenna II with short setae; pereopods III and IV with long and straight setae on posterior margin; both inner and outer margins of inner ramus and the inner margins of outer ramus of uropod III with plumose setae, and outer margin of outer ramus of uropod III with simple setae. It can be distinguished from *G. tastiensis* by the following characters (*G. tastiensis* in parentheses): inner ramus of uropod III more than 2 times as long as peduncle (inner ramus uropod III less than 2 times as long as peduncle); pereopods III–V are slender (strong).

A comparison between *Gammarus* species in Xinjiang is presented in the following key.

Key to the *Gammarus* species from Xinjiang Uygur Autonomous Region (China)

1	Eyes present	**2**
–	Eyes absent	***Gammarus liuruiyui***
2	Uropod III inner ramus less than 0.6 times the length of outer ramus	**3**
–	Uropod III inner ramus more than 0.6 times the length of outer ramus	**5**
3	Pereopod III–IV posterior margins and uropod III bearing sparse setae	***G. brevipodus***
–	Pereopod III–IV posterior margins and uropod III bearing normally distributed setae	**4**
4	Peduncle articles IV–V of antenna II with long setae and epimeral plate III with blunt posterodistal corner	***G. simplex***
–	Peduncle articles IV–V of antenna II with short setae and epimeral plate III with subacute posterodistal corner	***G. tianshan***
5	Uropod III outer ramus with plumose setae	**6**
–	Uropod III outer ramus with simple setae	**7**

6	Telson bearing short setae and epimeral plate III with acute posterodistal corner	***G. lacustris***
–	Telson bearing long setae and epimeral plate III with blunt posterodistal corner	***G. decorosus***
7	Posterodistal corner of basis of pereopod VII with setae	***G. takesensis***
–	Posterodistal corner of basis of pereopod VII with spines	**8**
8	Pereopod V–VII are slender and inner ramus uropod III more than twice as long as peduncle of uropod III	***G. zhouqiongi* sp. nov.**
–	Pereopod V–VII are strong and inner ramus uropod III less than twice as long as peduncle of uropod III	***G. tastiensis***

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Two new species of *Squamosa* Bethune-Baker, 1908 (Lepidoptera, Limacodidae) and first female record of *S. chalcites* Orhant, 2000 from southern Asia

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Abstract

Two new species of the genus *Squamosa* Bethune-Baker, 1908 (Lepidoptera: Limacodidae): *S. medogensis* **sp. nov.** and *S. undulophallus* **sp. nov.**, are described from southern Asia. These new species are illustrated with images of the adults and male genitalia, and compared with similar species. A new synonymy is established for the subspecies *S. brevisunca brevisunca* Wu & Fang, 2009 = *S. svetlanae* Solovyev & Witt, 2009, **syn. nov.** The female genitalia of *S. chalcites* Orhant, 2000 are illustrated and described for the first time. A distribution map for the new species and illustrations of Asian members of *Squamosa* are given, and a key to Asian species of the genus is also provided.

Keywords

China, India, key, Myanmar, slug caterpillar moths, synonymy, taxonomy, Tibet

Introduction

The genus *Squamosa* was erected by Bethune-Baker (1908), with *S. ferruginea* Bethune-Baker, 1908 as its type species [type locality New Guinea (Kebea)]. The second species of this genus, *S. ocellata* (Moore, 1879), was originally placed in the genus *Monema* until Hering (1931) transferred it to *Squamosa* in 1931. Thereafter, it was not until 2000 that a third species, *S. chalcites* Orhant, 2000, was described from Myanmar and Thailand by Orhant (2000). In 2009, an additional species, *S. brevisunca* Wu & Fang, 2009, was described, including two subspecies: *S. brevisunca brevisunca* Wu & Fang, 2009 (=*S. svetlanae* Solovyev & Witt, 2009, syn. nov.) from China and Vietnam and *S. brevisunca yunnanensis* Wu & Fang, 2009 from Yunnan, China (Solovyev and Witt 2009; Wu and Fang 2009). Wu and Fang (2009) also clarified that the record of *S. ocellata* in China was based on a misidentification of *S. brevisunca*, and it had also been reported in Nepal and Bhutan (Cai 1981; Yoshimoto 1994; Irungbam et al. 2017). Later, Pan and Wu (2015) described a species, *S. monosa* Wu & Pan, 2015, from Xizang, China.

The moths belonging to this genus are of medium to large size. The antennae are broadly bipectinated at least in the basal half to three quarters, then serrate in the male and filiform in the female. The labial palpus is short, not quite reaching the vertex. The forewing has veins $R_{3\text{-}5}$ stalked and R_2 separated. The diagnostic external characters of the Asian *Squamosa* species are as follows: the forewing ground colour is yellow, with a conspicuous, large, rounded medial patch on the outside of the cell, and a narrow, curved, black subterminal line running from the costal margin to the tornus. The male genitalia have an apically bifid uncus and small gnathos; the valva is wide at the base and rounded at the cucullus; the saccular process is usually absent or in a well-developed hook-shape; the juxta is usually asymmetrical and rarely symmetrical; and the phallus is slender. The tibia spurs number 0–2–4. The type species of the genus, *S. ferruginea* Bethune-Baker, 1908, is known from New Guinea (Kebea). It differs considerably in appearance from the Asian members, and its male genitalia have not been described yet. As a consequence, clarification of the generic limits requires further investigation.

To date, the genus contains five described species ranging from New Guinea, India to China, including: *S. ferruginea* Bethune-Baker, 1908; *S. ocellata* (Moore, 1879); *S. chalcites* Orhant, 2000; *S. brevisunca brevisunca* Wu & Fang, 2009; *S. brevisunca yunnanensis* Wu & Fang, 2009; and *S. monosa* Wu & Pan, 2015. Four species are described from Asia and three occur in China.

In this study, two species, *S. medogensis* sp. nov. and *S. undulophallus* sp. nov., collected from the southeast of Xizang Autonomous Region (= Tibet), China, as well as India and Myanmar, are described as new to science.

Materials and methods

The specimens were collected with a 220V/450W mercury vapour lamp and a DC black light. Standard methods for dissection and preparation of the genitalia slides were used (Kononenko and Han 2007). The specimens were photographed using a Nikon D700 camera, whereas the genitalia slides were photographed with an Olympus photo microscope aided by the Helicon Focus software and further processed in Adobe Photoshop CS6.

The terminology of morphology follows Epstein (1996), and the following abbreviations are used in the figures:

AA	apophysis anterioris;	**DB**	ductus bursae;	**Sig**	signa;
Aed	aedeagus;	**Gn**	gnathos;	**SP**	saccular process;
AP	apophysis posterioris;	**Jx**	juxta;	**Un**	uncus;
CB	corpus bursae;	**PA**	papillae anales;	**Va**	valva.

All the type materials of the new species are deposited in the collection of Northeast Forestry University (**NEFU**), Harbin, China, except for five male paratypes of *Squamosa undulophallus* sp. nov., which are deposited in the Museum Witt München / Zoologische Staatssammlung München, Munich, Germany (**MWM/ZSM**). Material from the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**IZCAS**) was also examined in this study.

Taxonomic account

Genus *Squamosa* Bethune-Baker, 1908

Squamosa Bethune-Baker, 1908, Novit. zool., 15: 183. Type species (original designation): *Squamosa ferruginea* Bethune-Baker, 1908. Type locality New Guinea: Kebea.

Squamosa medogensis sp. nov.

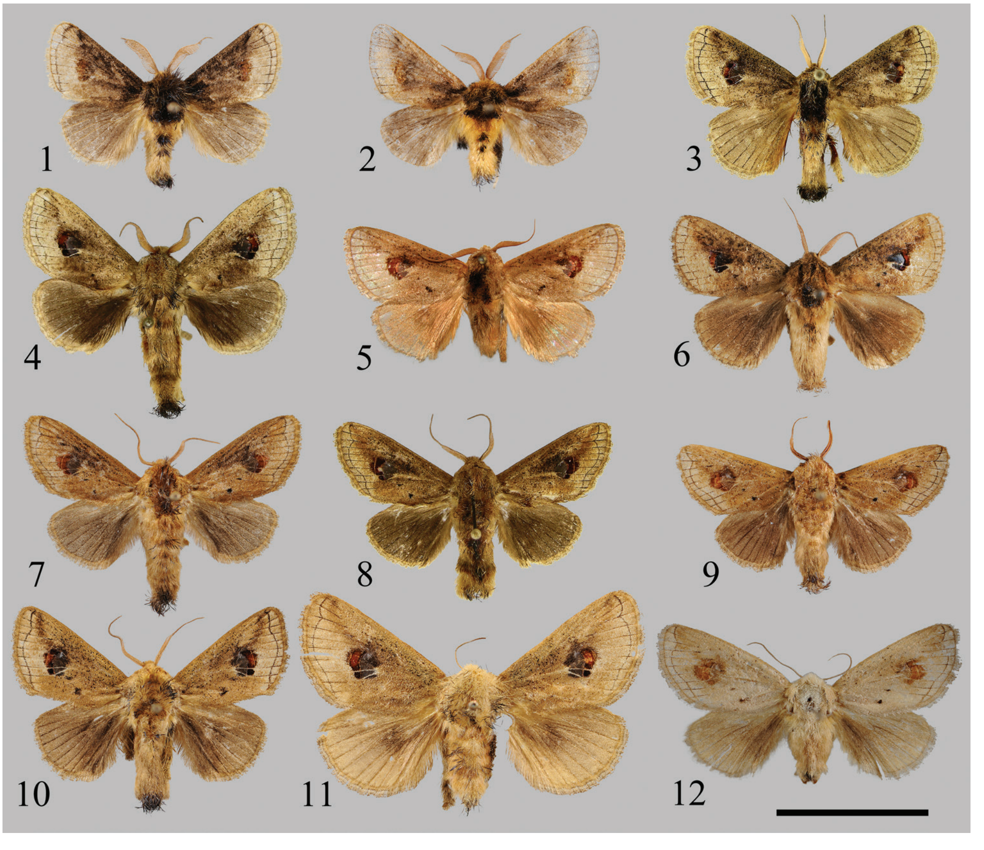
http://zoobank.org/11275919-013D-46BC-A7EB-D30BC2D59A17
Figs 1, 2, 13, 14

Material examined. ***Holotype.*** ♂, China, Xizang Autonomous Region, Linzhi (= Nyingchi) City, Motuo (= Medog) County, Gedang Countryside, 25.V.–5.VI.2021, leg. J. Wu and JJ. Fan, genit. prep. WuJ-519-1 (NEFU). ***Paratypes.*** 4♂, same data as for holotype, genit. prep. WuJ-520-1 (NEFU).

Diagnosis. The new species can be easily distinguished from the known species by its appearance: the antennae are broadly bipectinated at basal 3/4 in male; the thorax is black mixed with a little yellow; the base and costal margin area of forewing are dark brown to black; the rounded patch located on the outside of the cell is blurry; the abdomen bears two distinct black hair tufts dorsally. In the other Asian congeners (Figs 3–12) the male antennae are bipectinated only in the basal half; the ground colour of the thorax and forewing is yellow mixed with black; the medial patch of the forewing is more distinct than in *S. medogensis* sp. nov. (Figs 1, 2); the dorsal black hair tuft on the abdomen is weak.

The male genitalia are clearly different from those of the other congeners: in *S. medogensis* sp. nov. (Figs 13, 14), the valva has a well-developed saccular process and the juxta is symmetrical. However, the same structures in other Asian species (Figs 15–22) are very different: the valvae without saccular processes; the juxta are asymmetrical with a lateral process.

Description. Adult (Figs 1, 2). Wingspan 30–32 mm in male. Head yellow; labial palpus short, yellow; male antennae brown, broadly bipectinated in basal 3/4 then serrate. Thorax and tegula black mixed with a little yellow. Scales on legs black to yellow. Forewing broad, ground colour brown, wing base and costal margin area dark brown to black, outer margin area pale brown; a large, silky reddish brown, rounded medial patch located at outside of cell; subterminal line narrow, black, smoothly curved, running from costal margin near the apex to the tornus, almost parallel to outer margin, bearing a dent in the region between vines R_4 and R_5 towards base; wing venation visible in outer margin area, black; fringe yellow. Hindwing brown; fringe yellow. Abdomen yellow, with two distinct black dorsal hair tufts and long black hairs at terminal area.



Figures 1–12. Adults of *Squamosa* spp.: **1, 2** *S. medogensis* sp. nov., males, holotype (**1** in NEFU) and paratype (**2** in NEFU) **3** *S. ocellata* (Moore, 1879), male, Sikkim, India (in MWM/ZSM) **4** *S. brevisunca brevisunca* Wu & Fang, 2009 (= *S. svetlanae* Solovyev & Witt, 2009, syn. nov., male, holotype) (in MWM/ZSM) **5** *S. brevisunca brevisunca* Wu & Fang, 2009, male, holotype (in IZCAS) **6** *S. brevisunca yunnanensis* Wu & Fang, 2009, male, Yunnan, China (in NEFU) **7, 8** *S. undulophallus* sp. nov., males, holotype (**7** in NEFU) and paratype (**8** in MWM/ZSM) **9** *S. chalcites* Orhant, 2000, male, Chongqing, China (in NEFU) **10, 11** *S. monosa* Wu & Pan, 2015, male, Xizang, China (**10** in NEFU) and female, Xizang, China (**11** in NEFU) **12** *S. chalcites* Orhant, 2000, female, Chongqing, China (in NEFU). Scale bar: 2 cm.

Male genitalia (Figs 13, 14). Uncus short, weakly bifid apically. Gnathos rod-shaped, blunt apically. Tegumen broad. Valva broad at base, cucullus rounded; costa slightly concave, bearing a triangular process at c. 1/3 distance from base that is covered by dense long setae; sacculus inflated, slightly sclerotised, densely covered with setae in upper half; saccular process strongly sclerotised, curved inwardly in a hook-shaped, bifid process near middle and tapering from base to apex, pointed apically. Juxta sclerotised, symmetrical, horseshoe-shaped. Saccus not obvious. Phallus slender, smoothly curved; vesica without cornuti.

Female genitalia. Unknown.

Distribution. China (Xizang: Motuo) (Fig. 25).

Etymology. The species is named *medogensis* for its type-locality in Motuo County, Xizang Autonomous Region, China.

Bionomics. The specimens were collected from May to June at altitudes of 1840–2120 m a.s.l., close to the subtropical evergreen broad-leaved forest, with massive shrubs, ferns and patches of grassland growing in the ground cover layer of the forest (Figs 26, 27).

Remarks. According to the original descriptions, three of the diagnostic generic characters of the genus *Squamosa* are: the antennae bipectinated only at the basal half in males, the valva without saccular process, and the juxta with lateral asymmetrical processes (Solovyev and Witt 2009; Wu and Fang 2009). *Squamosa medogensis* sp. nov. does not match any of the above three characters, but since all other typical characters for this genus were observed, we therefore tentatively place this new species in *Squamosa*.

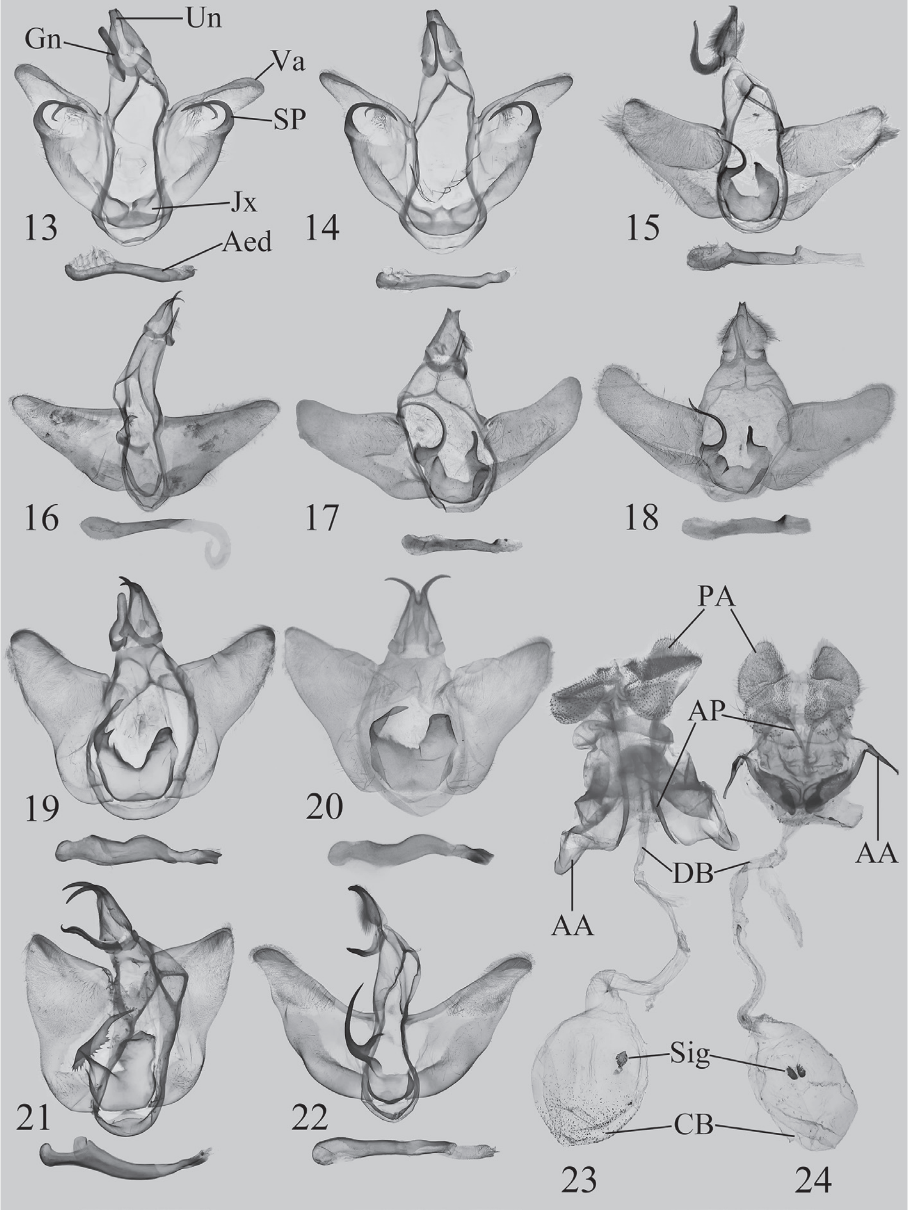
Squamosa undulophallus sp. nov.

http://zoobank.org/04666165-960B-4AFA-BE73-DFBB9F61C6C9

Figs 7, 8, 19, 20

Material examined. ***Holotype.*** ♂, China, Xizang Autonomous Region, Linzhi (= Nyingchi) City, Motuo (= Medog) County, Beibeng Countryside, Dergong Village, 850 m a.s.l., 25.V.–4.VI.2021, leg. HL. Han, genit. prep. WuJ-518-1 (NEFU). ***Paratypes.*** 1♂, India, sept. or. W. Meghalaya, Garo Hills, Nokrek Nat. Park, 25°40'N, 91°04'E, 2–13.VII.1997, 1150 m a.s.l., leg. Afonin and Siniaev, genit. prep. 16149 (MWM/ZSM); 1♂, Myanmar, Putao, 550 m a.s.l., 27. IV. 1998, leg. Murzin and Sinjaev, genit. prep. 16169 (MWM/ZSM); 1♂, Myanmar, 16 km E Putao, 500 m a.s.l., 28–30.IV.1998, leg. Murzin and Sinjaev, genit. prep. 16230 (MWM/ZSM); 1♂, Myanmar, 21 km E Putao, Nan Sa Bon Village, 550 m a.s.l., 1–5.V.1998, leg. Murzin and Sinjaev, genit. prep. 16150 (MWM/ZSM); 1♂, Myanmar, 25 km E Putao, env. Nan Sa Bon Village, 800 m a.s.l., 6–9. V. 1998, leg. Murzin and Sinjaev, genit. prep. 16231 (MWM/ZSM).

Diagnosis. The new species is very similar to *S. chalcites* (Figs 9, 12) in appearance, but it can be distinguished from the latter by the following characters: middle of costal margin area of forewing is covered by dense black scales and the medial patch of forewing is conspicuous. In *S. chalcites*, the forewing only bears small scattered black scales and the medial patch of forewing is blurry.



Figures 13–24. Genitalia of *Squamosa* spp.: **13, 14** *S. medogensis* sp. nov., males, holotype (**13** in NEFU) and paratype (**14** in NEFU) **15** *S. brevisunca yunnanensis* Wu & Fang, 2009, male, Yunnan, China, genit. prep. WuJ-090-1 (in NEFU) **16** *S. ocellata* (Moore, 1879), male, Sikkim, India (in MWM/ZSM) **17** *S. brevisunca brevisunca* Wu & Fang, 2009, male, holotype (in IZCAS) **18** *S. brevisunca brevisunca* Wu & Fang, 2009 (= *S. svetlanae* Solovyev & Witt, 2009, syn. nov., male, holotype) (in MWM/ZSM) **19, 20** *S. undulophallus* sp. nov., males, holotype (**19** in NEFU) and paratype (**20** in MWM/ZSM) **21** *S. chalcites* Orhant, 2000, male, Chongqing, China, genit. prep. WuJ-538-1 (in NEFU) **22** *S. monosa* Wu & Pan, 2015, male, Xizang, China, genit. prep. WuJ-516-1 (in NEFU) **23** *S. chalcites* Orhant, 2000, female, Chongqing, China, genit. prep. WuJ-540-2 (in NEFU) **24** *S. monosa* Wu & Pan, 2015, female, Xizang, China, genit. prep. WuJ-517-2 (in NEFU).

Description. Adult (Figs 7, 8). Wingspan 35–39 mm in male. Head brown; labial palpus short, brown; male antennae brown, bipectinated at basal half then serrate. Thorax dark brown to black dorsally, mesothorax with conspicuous tuft of long black hairs anteriorly; tegula brown. Scales on legs dark brown to pale yellow. Forewing distinct elongate, ground colour dark brown mixed with numerous black scales, especially dense in middle part of costal margin area, outer margin area pale brown; a conspicuous, large, silky, rounded medial patch located at outside of cell, inner half bluish black, outer half reddish brown with an arched bright line embedded in middle; subterminal line narrow, black, with depressions in the region of vein $R_{4,}$ and slightly concave between veins M_3 and CuP; two distinct black spots at middle of veins CuP and 1A+2A; fringe brown. Hindwing ground colour greyish brown to dark brown, anal margin area is darker; fringe pale brown. Abdomen brown to dark brown, mixed with little black hairs dorsally and long black hairs at terminal area.

Male genitalia (Figs 19, 20). Uncus short, with apex deeply bifid, strongly sclerotised. Gnathos finger-shaped or slightly widened near apex, blunt apically. Tegumen broad. Valva short and broad; sacculus swollen at base, without saccular process; costa slightly concave at middle; cucullus narrow and rounded. Juxta asymmetrical, horseshoe-shaped, central depression V-shaped; left process strongly sclerotised, long plate-shaped, bearing a distinct spur near base in some individuals; right process plate-shaped, strongly sclerotised apically. Vinculum narrow. Saccus not obvious. Phallus thick, conspicuously waved, slightly thinner near apex, strongly sclerotised and somewhat bifid terminally.

Figure 25. Distribution map of *Squamosa* spp.: triangle: *S. medogensis* sp. nov. (China: Xizang); circles: *S. undulophallus* sp. nov. (China: Xizang; India: Meghalaya; Myanmar: Kachin); squares: *S. chalcites* Orhant, 2000 (China: Hubei, Chongqing, Sichuan, Yunnan, Xizang; Thailand; Myanmar); stars: *S. brevisunca brevisunca* Wu & Fang, 2009 (China: Hainan, Guangxi, Yunnan; Vietnam).

Female genitalia. Unknown.

Distribution. China (Xizang: Motuo), India (Meghalaya), Myanmar (Kachin) (Fig. 25).

Etymology. The species is named *undulophallus* after its distinctly wavy phallus.

Bionomics. The specimens were collected from April to July at altitudes about 550–1150 m a.s.l. The collection area in China is a subtropical climate zone (Fig. 28).

Squamosa chalcites Orhant, 2000

Figs 9, 12, 21, 23

Squamosa chalcites Orhant, 2000. Lambillionea (100) 3: 471. Type locality Myanmar: Maymyo.

Specimens examined. 1♂, China, Prov. Yunnan, Pu'er City, Manxieba Village, 3.VI.2018, leg. HL. Han, J. Wu and MR. Li, genit. prep. WuJ-109-1 (NEFU); 1♂, China, Chongqing Municipality, Mt. Simian, 23.VII–6.VIII.2018, leg. GX. Wang and WJ. Li, genit. prep. WuJ-539-1 (NEFU); 2♂, China, Chongqing Municipality, Mt. Simian, 24–30.VII.2019, leg. TT. Zhao and SC. Deng, genit. prep. WuJ-538-1 (NEFU); 4♀, China, Chongqing Municipality, Mt. Simian, 29.VII.–2.VIII.2020, leg. HL. Han and J. Wu, genit. prep. WuJ-540-2 and 541-2 (NEFU).

Female genitalia (Fig. 23). Papillae anales flattened, foot-shaped, covered with dense hairs on surface. Postvaginal plate flattened, strongly sclerotised. Apophysis anterioris highly modified, short, tongue-shaped; apophysis posterioris long and slender, c. 3 × length of apophysis anterioris. Ductus bursae long, membranous, not spiral-shaped. Corpus bursae pear-shaped, twisted in its apical part, with a strongly sclerotised, nearly elliptical central signum.

Distribution. China (Hubei, Chongqing, Sichuan, Yunnan, Xizang); Thailand, Myanmar (Fig. 25).

Remarks. Although the female adult was described in Orhant (2000), the female genitalia are described herein for the first time. In contrast to another known female of the genus, *S. monosa*, two distinctive features of this species can be recognised: the apophysis anterioris is highly modified, tongue-shaped; and the corpus bursae only with a single signum. However, in the female genitalia of *S. monosa* (Fig. 24), the apophysis anterioris is slender and the corpus bursae has a pair of signa.

Squamosa brevisunca Wu & Fang, 2009

Figs 4, 5, 6, 15, 17, 18

Squamosa brevisunca Wu & Fang, 2009, Acta Zootaxonimica Sinica 34 (2): 237. Type locality China: Hainan.

Squamosa ocellata (not Moore): Cai 1981: 99, fig. 648.

***Squamosa brevisunca brevisunca* Wu & Fang, 2009**
Figs 4, 5, 17, 18

Squamosa brevisunca brevisunca Wu & Fang, 2009, Acta Zootaxonimica Sinica 34 (2): 237. Type locality China: Hainan. Holotype (by original designation): ♂ (IZCAS) [examined].

= *Squamosa svetlanae* Solovyev & Witt, 2009, syn. nov., Entomofauna, suppl. 16: 186. Type locality Nord-Vietnam: Mt. Fan-si-pan. Holotype (by original designation): ♂ (MWM/ZSM) [examined].

Specimen examined. 1♂, China, Prov. Yunnan, Lvchun County, Mt. Huanglian, 27–31.VII.2018, leg. HL. Han, J. Wu, MR. Li, genit. prep. WuJ-091-1 (NEFU).

Diagnosis. The nominate subspecies cannot be distinguished from *S. brevisunca yunnanensis* Wu & Fang, 2009 (Fig. 6) externally but the morphology of male genitalia is diagnostic. In the male genitalia, the left process of juxta is long and the right process is finger-shaped apically in *S. brevisunca brevisunca* (Figs 17, 18), whereas the left process of juxta is short and the right process is blunt apically, without the finger-shaped apex in *S. brevisunca yunnanensis* (Fig. 15).

Figures 26–28. Biotopes: China, SE Xizang, Linzhi (= Nyingchi) City, Motuo (= Medog) County **26, 27** Gedang countryside, two different collecting sites of *S. medogensis* sp. nov., photograph by J. Wu **28** Beibeng Countryside, Dergong Village, biotope of *S. undulophallus* sp. nov., photograph by HL. Han.

Distribution. China (Hainan, Guangxi, Yunnan), Vietnam (Fig. 25).

Bionomics. We collected a single specimen in July at altitude about 1945 m a.s.l., with a light trap close to a broad-leaved forest with ferns and shrubs.

Remarks. By examining the holotypes of *S. brevisunca brevisunca* (China: Hainan) and *S. svetlanae* (Vietnam: Mt. Fan-si-pan), we found that there are no significant differences in either the external appearance or the morphology of the male genitalia between them. In addition, we also collected a male specimen of the nominate subspecies from southern Yunnan, China, an area extremely close to the type locality of *S. svetlanae*, on the basis of which we establish the synonymy *S. brevisunca brevisunca* Wu & Fang, 2009 = *S. svetlanae* Solovyev & Witt, 2009 syn. nov. here.

Key to the Asian species of *Squamosa* based on male genitalia, with distributions

1 Valva without saccular process, juxta asymmetrical **2**
– Valva with saccular process, juxta symmetrical .... ***S. medogensis* sp. nov.** (China: Xizang)
2 Uncus slightly bifid **3**
– Uncus deeply bifid **4**
3 Juxta with both lateral processes **5**
– Juxta with a single left lateral process .... ***S. monosa* Wu & Pan** (China: Xizang)
4 Valva short and broad; tegumen short and broad; phallus sinuous **6**
– Valva elongate; tegumen long and narrow; phallus slender .... ***S. ocellata* (Moore)** (India, Nepal, Bhutan, Myanmar)
5 Left process of juxta long; right process finger-shaped apically .... ***S. brevisunca brevisunca* Wu & Fang** (China: Hainan, Guangxi, Yunnan; Vietnam)
– Left process of juxta short; right process blunt apically, without finger-shaped apex .... ***S. brevisunca yunnanensis* Wu & Fang** (China: Yunnan)
6 Left process of juxta sawblade-shaped; phallus smoothly curved .... ***S. chalcites* Orhant** (China: Hubei, Chongqing, Sichuan, Yunnan, Xizang; Thailand, Myanmar)
– Left process of juxta long plate-shaped; phallus distinctly waved .... ***S. undulophallus* sp. nov.** (China: Xizang, India: Meghalaya, Myanmar: Kachin)

Acknowledgements

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RESEARCH ARTICLE

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Order Euryalida (Echinodermata, Ophiuroidea), new species and new records from the South China Sea and the Northwest Pacific seamounts

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Abstract

Ophiuroids were collected by the manned submersible 'Shenhaiyongshi' from the deep-sea seamounts in the South China Sea and Northwest Pacific regions at 602–1920 m depth, during 2018 to 2020. A total of nine species was identified, including two new species and seven new records from the South China Sea and one new record from the Northwest Pacific region. Two new species are described as *Asteroschema shenhaiyongshii* **sp. nov.** and *Asteroschema domogranulatum* **sp. nov**. The seven new records included five species from the genus *Asteroschema*, and one species each from the genera *Asterostegus* and *Astrodendrum*. Comprehensive descriptions of morphological features are provided, including characteristics of the arm skeleton, as well as a phylogenetic analysis based on 16S and COI sequences. Intraspecific genetic distance ranges of Euryalida species from the present study were 0.34% to 1.38%, which was relatively low compared to other orders in the class Ophiuroidea. The present study suggests a high probability that species of the order Euryalida are more widely spread around the Indo-Pacific region than previously expected.

Keywords

Asteroschema, COI, molecular phylogeny, morphology, SEM, taxonomy

Introduction

The order Euryalida Lamarck, 1816 (basket stars and snake stars) includes the families Euryalidae Gray, 1840, Asteronychidae Ljungman, 1867, and Gorgonocephalidae Ljungman, 1867, and these include the species with largest known body size in the class Ophiuroidea, the brittle stars (Stöhr et al. 2021). The majority of the Euryalida are epizoic, living attached to hosts, such as corals, gorgonians, and sponges (Baker 1980). Currently, the order Euryalida contains 193 accepted species within 48 genera (Stöhr et al. 2021). The largest families are Euryalidae and Gorgonocephalidae with 95% of all Euryalida (Stöhr et al. 2021). These two families include 44 genera (Euryalidae 11 genera, Gorgonocephalidae 33 genera).

This study presents species in the genera *Asteroschema* Örsted & Lütken in Lütken, 1856 and *Asterostegus* Mortensen, 1933 from Euryalidae, and *Astrodendrum* (Döderlein, 1902) from family Gorgonocephalidae, found in the South China Sea and on Northwest Pacific seamounts.

Asteroschema is one of the largest genera in the Euryalidae, but it is still ill-defined due to limited published information and high morphological similarity between the species. Currently, 33 species are included in *Asteroschema* and the most recently described one was *Asteroschema sampadae* Parameswaran & Abdul Jaleel, 2012 from the Indian Ocean. Most of the species are pentamerous, but two hexamerous species have been recorded from New Zealand waters (*Asteroschema wrighti* McKnight, 2000 and *Asteroschema bidwillae* McKnight, 2000). Previous studies differentiated *Asteroschema* species based on epidermal ossicle shape and arrangement on the disc and arms, size variance and shape of inner and outer arm spines, and starting point of the second arm spine on the proximal region of the arm (Okanishi and Fujita 2009; Parameswaran and Jaleel 2012). The term epidermal ossicle has been used for small superficial, often granule-like, skeletal elements on the disc and arms (Okanishi and Fujita 2009). Echinoderm skeleton generally develops in the dermis (Byrne 1994), but it is unknown if these ossicles originate in the epidermis or in the dermis, and their possible homology with granules or spines in non-euryalid groups is also unknown. Epidermal thus does not refer to the place of origin of these ossicles, but to their position in adult specimens. *Asteroschema* species have been divided into three groups according to the shape of their epidermal ossicles such as: species with only granular ossicles, with conical and granular ossicles, and domed and with plate-like granular ossicles (Okanishi and Fujita 2009).

The genus *Asterostegus* includes only three species and is morphologically related to the genus *Astroceras* Lyman, 1879, but differs in having the oral shield replaced by several small interradial plates (McKnight 2003; Okanishi and Fujita 2014). Understanding morphological variations and diversity of *Asterostegus* is limited due to a lack of material (Okanishi and Fujita 2014). In the present study, *Asterostegus maini* McKnight, 2003 from the South China Sea is recorded as the first record since the holotype, but recent studies of *Asterostegus* included detailed descriptions of all three species (Okanishi and Fujita 2014). However, this study includes the intraspecific morphological variation among *A. maini* specimens between the South China Sea and South Pacific waters, and the development of morphological characters relative to size variations. Lastly, the genus *Astrodendrum* is widely distributed from the Indo-Pacific to South Africa, and includes six species. It differs from other genera in the family Gorgonocephalidae by having external ossicles of various shapes on the disc, and by lacking calcareous plates on the lateral disc margin (Okanishi and Fujita 2018).

The present study covers deep waters around the South China Sea (Xisha and Zhongsha Islands) and in the Northwest Pacific region (southwest of Guam Island). Here, we present an account of the *Asteroschema*, *Asterostegus*, and *Astrodendrum* species collection, with descriptions of new species and new records. Our goal is to present a detailed documentation of the morphological features of these species, to complement the limited original descriptions and the lack of figures in the literature. We present the first ever comprehensive tabular key for all species in the genus *Asteroschema*. Two new species are described and seven species are redescribed, including seven new records from the South China Sea and one new record from the Northwest Pacific, all richly illustrated. DNA barcoding was used to identify ophiuroid species in the past two decades (Ward et al. 2008; Hoareau and Boissin 2010; Okanishi et al. 2011, 2018; Okanishi and Fujita 2013). Hence, we use barcoding to test our morphological identifications and to understand the interrelationships within genera. This study also provides biodiversity information of Euryalida species living on seamounts, which may be useful for further studies of euryalid diversity and biogeography.

Materials and methods

Sample collection

Ophiuroid specimens were collected by the manned submersible vehicle 'Shenhaiyongshi', from 602 to 1920 m depth (Fig. 1). Most of the specimens were frozen at -80°C without preservation fluid, then transported to the Institute of Deep-sea science and Engineering, Chinese Academy of Sciences (**CAS**), Sanya, China, for further analysis. The samples were sorted and identified by using literature (Pallas 1788; Ljungman 1871; Lyman 1869, 1872, 1875, 1878, 1879, 1882, 1883; Lütken and Mortensen 1889; Alcock 1894; Verrill 1894, 1899; Koehler 1904, 1906, 1907, 1914, 1930; Matsumoto 1911, 1915, 1917; H. L. Clark 1915, 1916b, 1917, 1939, 1941; Mortensen 1924; A. H. Clark 1916a, 1949; Döderlein 1911, 1927, 1930; Murakami 1944; Baker 1980; Guile 1981; Peterson 1985; McKnight 2000; Liao 2004; Mah et al. 2009; Pawson et al. 2009; Parameswaran and Jaleel 2012; Smirnov et al. 2014; Olbers et al. 2015) and by molecular analysis.

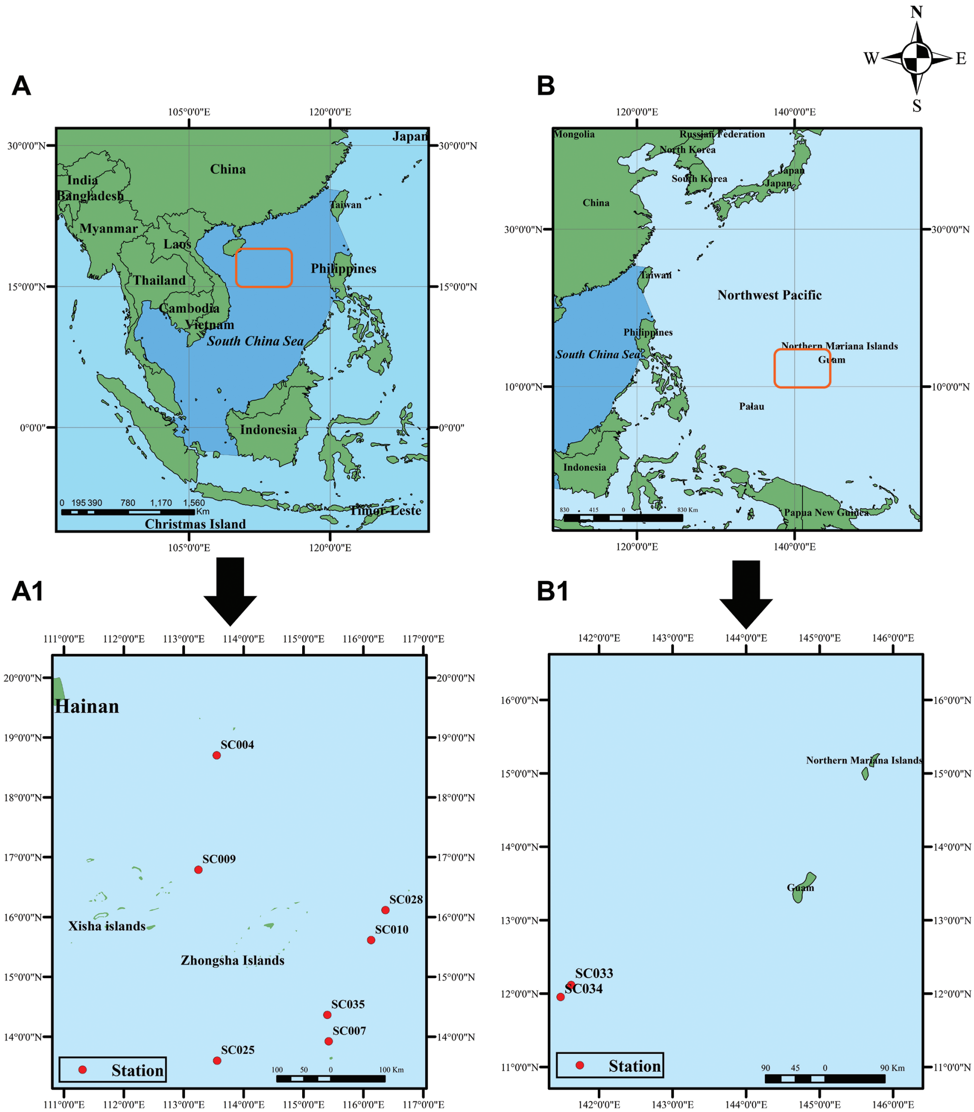

Figure 1. Collecting stations in this study **A, A1** South China Sea (Hainan, Xisha, and Zhongsha Islands) **B, B1** Northwest Pacific (southwest of Guam). Source: International Hydrographic Organization and Sieger (2012).

Morphological analysis

Specimens were photographed through a dissecting stereo microscope (OLYMPUS SZX7) or with a digital camera (Canon EOS 6DII) to identify morphological characters. Arm skeletons were examined with a scanning electron microscope (**SEM**) Phenom ProX. Skeletal elements were prepared by using undiluted NaOCl to dissolve the soft tissue of part of an arm. The excess NaOCl in skeletal elements was removed by repeated flushing with distilled water. Then, the ossicles were mounted on a stub using dissolved carbon tapes. Holotypes, paratypes and all other specimens are deposited at the Institute of Deep-sea Science and Engineering (**CAS**), Sanya, China. The terms used to describe ophiuroids follow previous authors (Martynov 2010; Stöhr 2011, 2012; Okanishi and Fujita 2014, 2018; O'Hara et al. 2017; Hendler 2018; Stöhr and O'Hara 2021). We define granules and spines as articulated ossicles on plates or scales, but tubercles as non-articulated stereom outgrowth, following Stöhr et al. (2012) and Goharimanesh et al. (2021). Following Turner et al. (2021), we utilize the term "pedicellarial bands" for what was previously known as "girdle bands" and for the "girdle hooklets" we use the term "pedicellariae".

Molecular analysis

We extracted DNA from identified specimens by using the TIANamp Marine Animals DNA kit (TianGen, Beijing) following the manufacturer's protocol. We sequenced cytochrome c oxidase I (COI) and the 16S partial gene for phylogenetic analysis by amplifying primer sets, with suitable PCR cycle (Suppl. material 1: Table S1) (Hoareau and Boissin 2010; Okanishi and Fujita 2013). Total PCR mixture was 50 μL volume, containing 25 μL Premix Taq with 1.25 U Taq, 0.4 mM of each dNTP and 4 mMMg2+ (Ex Taq version, Takara, Dalian, China), 0.5 μM each of the primers and approximately 100 ng template DNA. We performed electrophoresis using a 1.0% agarose gel and the NanoDrop 1000 (Thermo Scientific, Waltham, MA, USA) to assess PCR product quality of the specimens. PCR products were sequenced in both directions on an ABI3730 DNA Analyzer. All new sequences were deposited at NCBI GenBank (Table 1).

We constructed two maximum likelihood (**ML**) phylogenetic trees to represent the families Euryalidae and Gorgonocephalidae. Family Euryalidae: to construct the ML tree, we used 12 COI and nine 16S sequences from our collection and additionally 22 COI and 14 16S sequences from GenBank (Table 1). To construct the ML tree for the family Gorgonocephalidae, we used one species from our collection and an additional eight COI sequences from GenBank (Table 1). As outgroup we used COI and 16S sequences of *Astrogymnotes irimurai* Baker et al., 2001 and *Ophiomyxa anisacantha* H. L. Clark, 1911 for the ML trees.

All sequences were aligned using the ClustalW algorithm in MEGA X. When constructing the Euryalidae ML tree, we used the concatenated sequence alignment function in MEGA X to input both COI and 16S sequences. The best-fit substitution model of the COI and 16S gene in the ML trees was the General Time Reversible + Gamma Distributed (GTR + G) model, estimated by the "Find Best DNA/Protein Models" Option of MEGA X. Phylogenetic trees were reconstructed using the maximum likelihood bootstrap method. ML analysis was run with MEGA X, and ML trees were constructed, including 1,000 bootstrap replicates

Table 1. Localities, voucher information, and GenBank accession numbers for all specimens used in this study.

Species	Locality	Voucher number	COI	16S
Asteroschema shenhaiyongshii sp. nov.	South China Sea, near Xisha islands	IDSSE-EEB-SW0086	OK044292	OL712208
Asteroschema bidwillae	New Zealand	MVF188856	KU895077	-
Asteroschema rubrum	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0071	OK044293	OL712209
Asteroschema rubrum	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0072	OK044294	OL712210
Asteroschema rubrum	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0073	OK044295	OL712211
Asteroschema tubiferum	New Zealand	MVF188857	KU895076	-
Asteroschema tubiferum	Mariana Trench, Southeast of Guam Isl.	IDSSE-EEB-SW0078	OK044296	OL712212
Asteroschema tubiferum	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0106	OK044297	OL712213
Asteroschema tubiferum	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0077	OK044298	-
Asteroschema cf. *lissum*	Mariana Trench, Southeast of Guam Isl.	IDSSE-EEB-SW0081	OK044299	OL712207
Asteroschema cf. *lissum*	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0079	OK044300	-
Asteroschema salix	Australia	TOH_666	HM400451	-
Asteroschema salix	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0082	OK044301	OL712214
Asteroschema sp.	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0092	OK044302	OL712215
Asteroschema sp.SO2392113	Pacific Ocean: Clarion Clapperton Fracture Zone	SO2392113	MN088049	-
Asteroschema clavigerum	North Atlantic seamounts	-	HM587852	-
Asteroschema sublaeve	Canada: British Columbia	RBCM EC00271	HM400328	-
Asteroschema ajax	Australia: off Lord Howe Isl.	MVF99759	AB758762	AB605078
Asteroschema oligactes	Off Dominica	MNHN OM62	AB758766	AB758483
Asteroschema edmondsoni	Off Santa Isabel Isl., New Caledonia	MNHN OM13B	AB758831	AB758486
Asteroschema horridum	Off Reunion Isl.	MNHN OM126	AB758764	AB758487
Asteroschema migrator	Off Santa Isabel Isl., New Caledonia	MNHN OM3	AB758765	AB758485
Ophiocreas ambonesicum	Off Amami-oshima Isl., Kagoshima, Japan	NSMT E-6502	AB758813	AB605084
Ophiocreas spinulosus	Caribbean Sea, USA	NMNH OM43	AB758820	AB758490
Ophiocreas glutinosum	Off Katsuura, Chiba, Japan	NSMT E-6710	AB758815	AB605086
Ophiocreas japonicus	New Zealand	NIWA T2494	AB758816	AB758488
Ophiocreas sibogae	South Norfolk Ridge, New Zealand	MV F99763	AB758818	AB605087
Ophiocreas caudatus	Sagami Sea, Japan	NSMT E-6259	AB758814	AB605085
Ophiocreas oedipus	Off Hachijo-jima Isl., Ogasawara, Japan	NSMT E-6375	AB758817	AB758489
Asterostegus maini	South China Sea, near Xisha islands	IDSSE-EEB-SW0076	OK044303	-
Asterostegus tuberculatus	Western coast of Madagascar	SMNH-123461	AB758769	AB758515
Asterostegus sabineae	Madagascar: Off Reunion Island.	SMNH-Type-8333	AB758768	AB758511
Astrodendrum sagaminum	Japan: Sagami Sea	NSMT E-5645	AB758795	-
Astrodendrum cf. *sagaminum*	South China Sea, near Zhongsha islands	IDSSE-EEB-SW0104	OK044304	-
Gorgonocephalus pustulatum	New Zealand	MVF188859	KU895114	-
Gorgonocephalus sundanus	Australia	MVF162682	KU895115	-
Gorgonocephalus arcticus	Canada: Nunavut, Barrow Strait	HLC-30309	HM543017	-
Gorgonocephalus caputmedusae	Sweden: Skagerrak	Echin 6305V	MG935270	-
Gorgonocephalus eucnemis	Japan: Iwate, Off Miyako	NSMT E-5640	AB758809	-
Gorgonocephalus tuberosus	Antarctic Sea.	NIWA 38224	AB758811	-
Gorgonocephalus chilensis	Antarctic Sea	NIWA 38714	AB758812	-
Astrogymnotes irimurai	Seseko Beach, Okinawa, Japan	NSMT E-6716	AB758829	AB605123
Ophiomyxa anisacantha	Sagami Sea, Japan	NSMT E-6269	AB758822	AB605124

(Kimura 1980; Thompson et al. 1994; Kumar et al. 2016, 2018). The genetic distances were analyzed according to the Kimura 2-parameter model (Kimura 1980), and the standard error of each group was discovered by performing 1,000 bootstrap replications.

The following abbreviations are used in the text, tables, and figures

ap	articular pad of the base;	**lap**	lateral arm plate;
ars/ARS	arm spine;	**ML**	Maximum Likelihood;
arsb	arm spine base;	**mo**	muscle opening;
as	adoral shield;	**mp**	median plate;
asa	arm spine articulation;	**msv**	manned submersible vehicle;
ass/ASS	adoral shield spine;	**NAT**	North Atlantic;
au	auricle;	**no**	nerve opening;
AUS	Australia;	**NWP**	North-West Pacific;
CAN	Canada;	**NZ**	New Zealand;
co/CO	conical ossicle;	**oars**	outer arm spine;
COI	Cytochrome C oxide subunit I;	**ob**	oral bridge;
CS	Caribbean Sea;	**os**	oral shield;
d	dorsal;	**PAO**	Pacific Ocean;
de	depression;	**pb**	podial basin;
dist	distal;	**pd**	pedicel of the apophysis;
fo	foramina of the base;	**peb**	pedicellarial band;
fs	fossa between adjacent tubercles;	**po/PO**	plate-like ossicle;
go/GO	granular ossicle;	**prox**	proximal;
goc	granular ossicles coat;	**pt**	primary tooth of the blade;
gs/GS	genital slit;	**rs/RS**	radial shield;
hd	head of the apophysis;	**SCS**	South China Sea;
iars	inner arm spine;	**sh**	sheath of the base;
IDSSE	Institute of Deep-sea science and Engineering;	**st**	secondary tooth;
		su	sulcus of tubercle head;
irp	interradial plate;	**t**	teeth;
j	jaw;	**TEP**	terminal projection;
JAP	Japan;	**tp**	tentacle pore;
lac	lateral ambulacral canal;	**v**	ventral.
MAD	Madagascar;		

Results

Seven species of *Asteroschema* were identified, among them two new to science that are described below. One species of each of the genera *Asterostegus* and *Astrodendrum* were identified, both of them are new to the South China Sea and described below. A tabular key to all species of *Asteroschema* is provided in Table 2. ML phylogenetic trees are presented in Figs 2 and 3, and genetic distances in Suppl. material 2: Tables S2 and Suppl. material 3: Table S3 of most of the species described in the study.

Molecular phylogenetic analysis

In total, 34 COI sequences trimmed to 592 bp and 25 16S sequences trimmed to 453 bp were obtained after removing ambiguous aligned sites and successfully reconstructing an ML tree for the studied Euryalidae (Fig. 2). Two main clades were detected within the ML tree of Euryalidae (clade 01: genus *Asterostegus*; clade 02: genera *Asteroschema* and *Ophiocreas*). Overall average genetic distances of COI between two clades were 10.04±1.34% SE (*Asteroschema* and *Ophiocreas*) and 3.08±0.75% SE

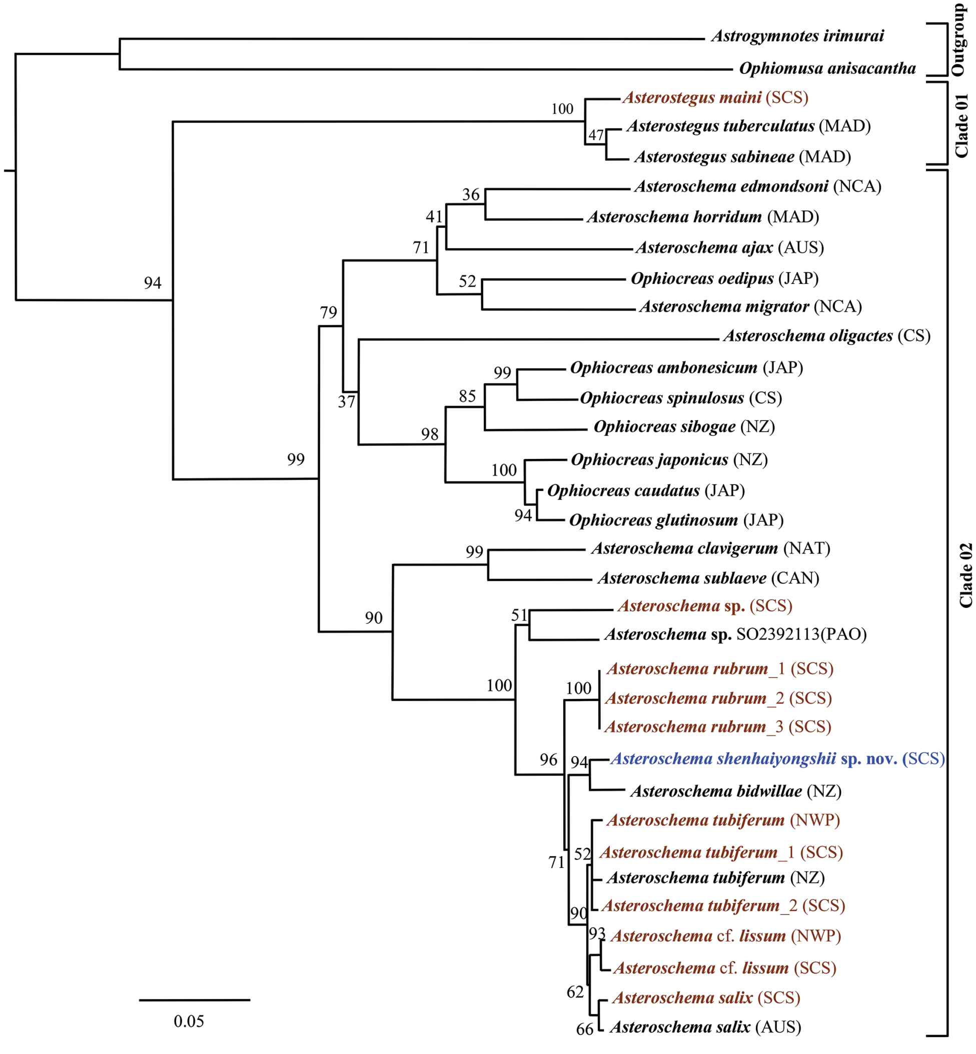

Figure 2. Family Euryalidae, maximum likelihood (ML) tree based on partial COI and 16S sequences (bootstrap support values were generated with rapid bootstrapping algorithm for 1,000 replicates; blue = new species; brown = specimens from this study).

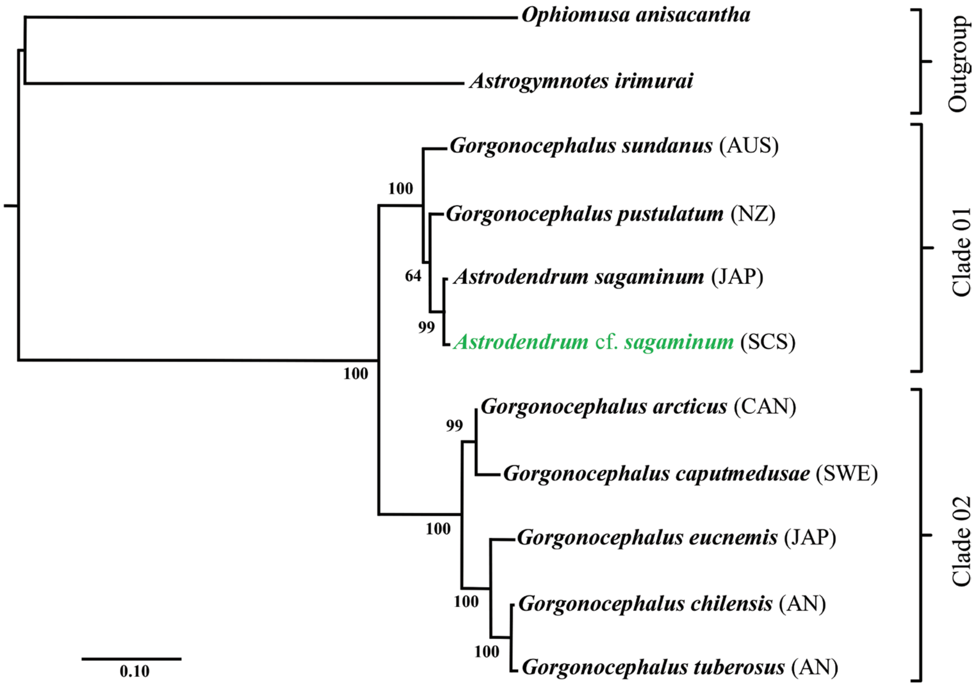

Figure 3. Family Gorgonocephalidae, maximum likelihood (ML) tree based on partial COI sequences (bootstrap support values were generated with rapid bootstrapping algorithm for 1,000 replicates; green = specimen from this study).

(*Asterostegus*). The maximum value between two clades was 24.79%. Species from the genera *Asteroschema* and *Ophiocreas* separated into two subclades within main clade 02, but *Asteroschema oligactes* (Pallas, 1788), *A. migrator* Koehler, 1904, *A. edmondsoni* A. H. Clark, 1949, *A. ajax* A. H. Clark, 1949 and *A. horridum* Lyman, 1879 clustered with *Ophiocreas* species. Genetic distance between *Asteroschema bidwillae* and *Asteroschema shenhaiyongshii* sp. nov. was 2.59±0.67% SE (Suppl. material 2: Table S2).

A total of 11 COI sequences trimmed to 730 bp were obtained after removing ambiguous aligned sites, and successfully reconstructing an ML tree for the genera *Gorgonocephalus* and *Astrodendrum* (Fig. 3). Two clades were detected between the species. Clade 1 consists of *Astrodendrum sagaminum* (Döderlein, 1902), *Gorgonocephalus pustulatum* (H. L. Clark, 1916), and *G. sundanus* (Döderlein, 1927). Clade 2 consists of *Gorgonocephalus arcticus* Leach, 1819, *G. eucnemis* (Müller & Troschel, 1842), *G. chilensis* (Philippi, 1858), and *G. tuberosus* Döderlein, 1902. Overall average genetic distances of COI between two clades were 2.88±0.58% SE (clade 01) and 5.39±0.87% SE (clade 02). The maximum value between the two clades was 15.21%. Genetic distance between *Astrodendrum sagaminum* (AB758795) and *Astrodendrum* cf. *sagaminum* (OK044304) was 0.69±0.30% SE (Suppl. material 3: Table S3).

Taxonomic account

Class Ophiuroidea Gray, 1840
Superorder Euryophiurida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Euryalida Lamarck, 1816
Family Euryalidae Gray, 1840
Genus *Asteroschema* Örsted & Lütken in Lütken, 1856

Asteroschema domogranulatum sp. nov.

http://zoobank.org/68786758-AC50-415B-8835-1CCE871304E5
Figures 4, 5

Material examined. ***Holotype*:** China • 1 specimen; South China Sea, East of Zhongsha Islands, seamount; 16°22.11'N, 113°6.01'E; depth 1742 m; 09 Aug. 2020; Collecting event: stn. SC028; 'Shenhaiyongshi' msv leg; preserved in -80 °C; IDSSE-EEB-SW0089.

***Paratypes*:** China • 2 specimens; same data as for holotype; IDSSE-EEB-SW0090, IDSSE-EEB-SW0091.

Diagnosis. Radial shields straight, parallel, close together, and raised above the disc and arms (Fig. 4A). Disc concealed by large polygonal, slightly domed granular ossicles (Fig. 4C). Jaws elongated, apex covered with few granular ossicles, but distal half naked. Ventral disc covered with large polygonal plate-like ossicles but naked around distal half of jaws (Fig. 4E). Dorsal and lateral surface of arms covered with plate-like or granular ossicles but dense only on few arms segments beyond the arm base (Fig. 4F–H). Ventral surface of the arm naked except arm base (Fig. 4I–L).

Description of holotype. Disc diameter 9 mm, length of arms 165 mm, arm base width 2.8–3.0 mm (Fig. 4).

***Disc*.** Disc star-shaped, pentagonal, raised high above the arms, incised interradially and swollen on radial shields (Fig. 4A, B). Disc concealed by dense, large, polygonal, slightly domed ossicles (three or four grains in 1 mm; Fig. 4C). Radial shields bar-like, long, parallel, straight, adjacent pairs separated by narrow interradial disc, raised above the disc, and almost extending to center (Fig. 4C). Domed ossicles on distal half of radial shields larger (two or three grains in 1 mm) than in center (four grains in 1 mm; Fig. 4C). Genital slits narrow, vertical on interradii, dorsal half covered with ossicles similar to dorsal disc, ventral half similar to ventral disc (Fig. 4D). Jaws elongated, apex covered with few granular ossicles, but distal half naked (Fig. 4E). At apex of jaw a bluntly pointed tooth, at lateral edges a few granules that resemble lateral oral papillae (Fig. 4E). Ventral disc covered with large polygonal plate-like ossicles (three or four grains in 1 mm) except distal half of jaws (Fig. 4E). Adoral shields large but completely concealed by ossicles. Oral shields not discernible, and naked adoral shield spine (Fig. 4B, E).

***Arms*.** Arms slender, arched at base, sub-cylindrical, increasingly cylindrical and narrower distalwards (Fig. 4F–H). Dorsal surface of arm base covered with large polygonal plate-like ossicles (three or four grains in 1 mm), then decreasing in size (five or six grains in 1 mm) and separated along the arm (Fig. 4F–H). Lateral plate covered with granular or plate-like ossicles, larger than on dorsal surface, and continuing to near base of arm spine (Fig. 4G, H). Distal half of arm laterally and dorsally covered with similar in size, separated granular ossicles (seven or eight grains in 1 mm; Fig. 4H). Ventral surface of arm base covered with polygonal plate-like ossicles (five or six grains

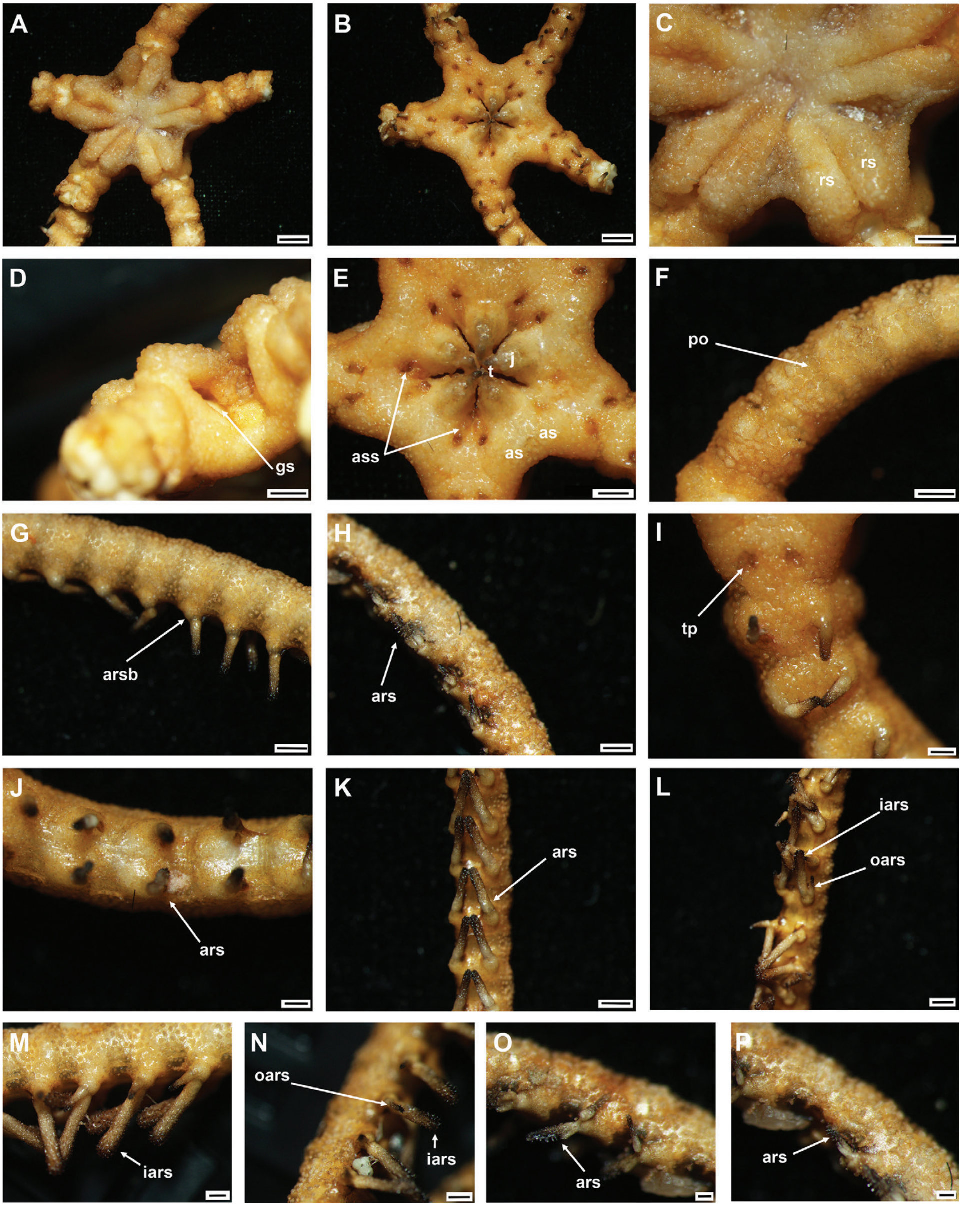

Figure 4. *Asteroschema domogranulatum* sp. nov., holotype (IDSSE-EEB-SW0089) **A** dorsal view **B** ventral view **C** dorsal disc **D** lateral disc **E** ventral disc **F** dorsal arm (proximal) **G** lateral arm (proximal) **H** lateral arm (distal) **I** ventral arm (base) **J, K** ventral arm (proximal) **L** ventral arm (middle) **M, N** arm spines (middle) **O, P** arm spines (distal). Abbreviations: **ars** arm spine, **arsb** arm spine base, **as** adoral shield, **ass** adoral shield spine, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **po** plate-like ossicle, **rs** radial shields, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A, B**); 1 mm (**C–G, K, L**); 500 μm (**H–J, M, N**); 200 μm (**O, P**).

in 1 mm), but after few arm segments from arm base completely naked (Fig. 4I–L). Tentacle pore at first arm segment without arm spine, but with small extended tube or sheath (Fig. 4I). Single arm spine from second arm segment with a second arm spine from nineteenth or twenty-second arm segment (Fig. 4I–L). Inner arm spine initially tapering to pointed thorny tip, middle half cylindrical, slightly club-shaped, one and a half arm segment in length, flattened, thorny (Fig. 4K–N). Outer arm spine half as long as inner spine in middle region, with thorny tip (Fig. 4N). Both arm spines similar in size at distal end, a compound hook with 3–6 secondary teeth (Fig. 4O, P).

Color. In live specimen, light brown color (Fig. 4).

Ossicle morphology of one paratype. IDSSE-EEB-SW090: Lateral arm plate curved around vertebrae, with strong curved rib with one arm spine articular structure, with single, completely separated large muscle and nerve openings (Fig. 5A). A depression on inner side of lateral arm plate (Fig. 5B). In proximal and middle half of arm inner arm spine slightly swollen, flat, and thorny on distal arm. Outer arm spine nearly half the size of the inner one with thorny tip (Fig. 5C). Distally, both spines changing into compound hook with secondary teeth (Fig. 5D). Arm concealed by polygonal large granular or plate-like ossicles (Fig. 5E). Vertebrae with streptospondylous articulation, with deep groove between proximal and distal end, dorsally a median longitudinal furrow, ventrally with deep median longitudinal groove containing lateral ambulacral canals, no oral bridge (Fig. 5F–J).

Paratypes variations. Disc diameter 6.5 and 8 mm, and both basically identical to holotype. However, the segment at which the second arm spine first appeared varied (14–20 free segments), but is considered intraspecific variation.

Distribution and habitat. 1742 m depth. Zhongsha Islands, the South China Sea. Attached to coral host.

Etymology. The species name is derived from the Latin words *domus*, meaning dome, and *granulatus*, meaning granulated, referring to the domed granular ossicles on the disc.

Remarks. The here examined new species was collected on a deep-sea seamount, attached to an unidentified coral species. It concurs with the group that has domed and plate-like granular ossicles, in the genus *Asteroschema*. This clade included only one species, prior to this study (*Asteroschema igloo* Baker, 1980). Large polygonal plate-like ossicles were the most significant morphological character for delimiting most of the other *Asteroschema* species from *A. domogranulatum* sp. nov. (Table 2).

Asteroschema domogranulatum sp. nov. strongly resembles *A. igloo*. They are similar in size according to McKnight's (2000) description (8 mm disc diameter). Therefore, here we include a comprehensive morphological analysis to distinguish *A. domogranulatum* sp. nov. from *A. igloo* such as (see also Table 2): in *A. domogranulatum* sp. nov. radial shields raised above the arms and disc, straight, parallel, with narrow gap, whereas in *A. igloo* distal ends of radial shields much wider apart, converging to center, in *A. domogranulatum* sp. nov. polygonal granular ossicles on dorsal disc, in center smaller than at distal edge, but in *A. igloo* concealed by polygonal or rounded domed ossicles, and in center large, domed, rounded ossicles, in *A. domogranulatum* sp. nov. teeth pointed but in *A. igloo* ventralmost one pointed and others blunt spearhead-shaped, in *A. domogranulatum* sp. nov. ventral disc covered with polygonal plate-like ossicles, and distal half of jaw naked

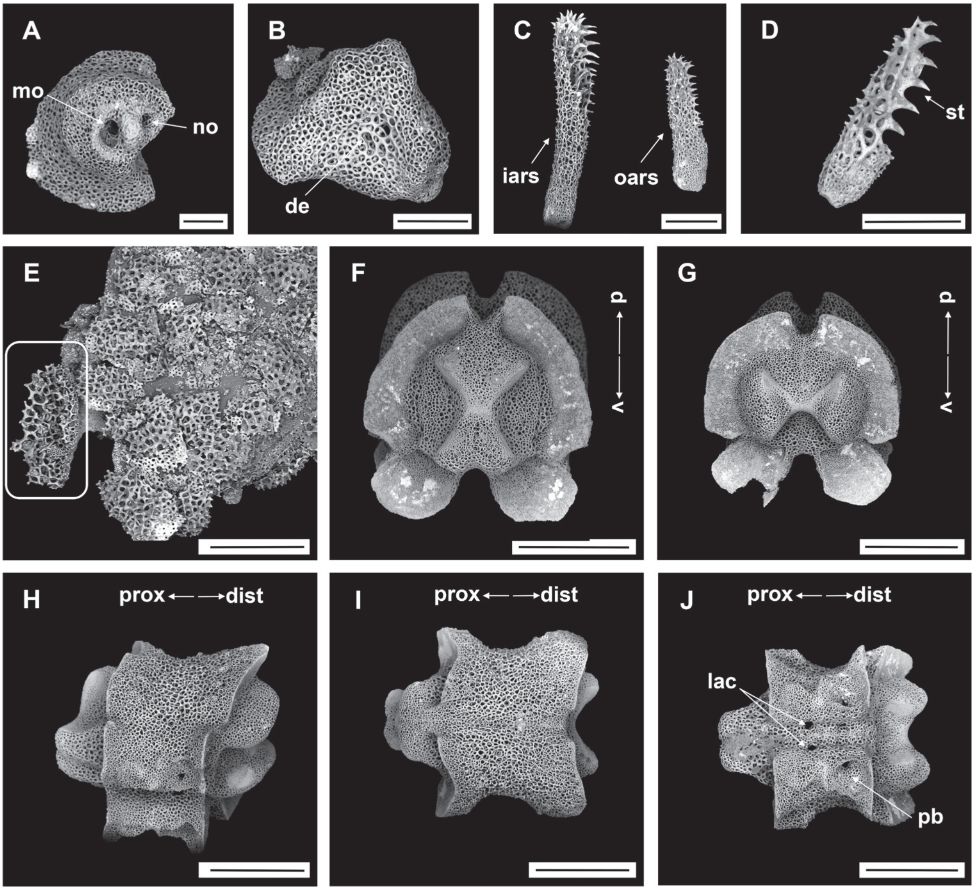

Figure 5. *Asteroschema domogranulatum* sp. nov., paratype (IDSSE-EEB-SW0090) **A, B** lateral arm plate (external, internal) **C** arm spines (middle) **D** arm spine (distal) **E** skin from dorsal arm base, insert frame shows polygonal plate-like large ossicle **F–J** vertebrae **F** proximal view **G** distal view **H** lateral view **I** dorsal view **J** ventral view. Abbreviations: **d** dorsal, **de** depression, **dist** distal, **iars** inner arm spine, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **oars** outer arm spine, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 800 μm (**F–J**); 500 μm (**C**); 300 μm (**B, D, E**); 200 μm (**A**).

but in *A. igloo* completely covered with compact polygonal or rounded domed ossicles, in *A. domogranulatum* sp. nov. only dorsal and lateral surface covered with plate-like or granular ossicles, dense only on few arm segments from arm base, and naked ventral arm except arm base but in *A. igloo* whole arm covered with dense, rounded or polygonal domed ossicles, in *A. domogranulatum* sp. nov. inner arm spine slightly swollen, blunt, flattened, and outer arm spine with thorny pointed tip but in *A. igloo* inner arm spine swollen, blunt, and outer arm spine with smooth pointed tip, in *A. domogranulatum* sp. nov. start of first arm spine at second arm segment, and second arm spine at nineteenth or twenty-second arm segment but in *A. igloo* first arm spine from third arm segment, and second arm spine starts at eighth or tenth arm segment (McKnight 2000). The most significant morphological characters of *A. domogranulatum* sp. nov. were the appearance of the radial shields, and the granulation of ventral disc and arms (Fig. 4).

Table 2. Tabular key to the species of *Asteroschema* and *Ophiocreas*. Abbreviations: ASS arm segment, ARS arm spine, GO granular ossicles, RS radial shield, CO conical ossicles, PO plate-like ossicles, TP terminal projection, GS genital slits.

Species	Disc diameter and arm length	Epidermal ossicles on the disc		Epidermal ossicles on the arm		ARS length	ARS shape	AS from segment 1st (2nd)	Reference
		Dorsal	Ventral	Dorsal	Ventral				
Asteroschema ajax A. H. Clark, 1949	13 mm and 300 mm	fine GO; RS narrow, parallel, raised above the disc not meeting at center	fine GO	well-spaced annular bands when dried, covered with GO	covered with GO as dorsal	unknown	unknown	unknown	A. H. Clark (1949)
Asteroschema arenosum Lyman, 1878	8–9 mm and arm length unknown (arm width 4 mm)	coarse GO, 5 grains in 1 mm; RS wide, not meeting at center	coarse GO but near mouth area scattered, jaw covered with GO	coarse GO but denser than on disc	as dorsal	inner ≈ 2 × outer	inner spine: cylindrical, slightly swollen, thorny dark tip	2 (4)	Lyman (1878, H. L. Clark (1941), Pawson et al. (2009)
Asteroschema bidwillae McKnight, 2000	5 mm and 50 mm (6 arms)	flat, small, very finely rugose GO, dense at center; RS and interradially (8–10 grains in 1 mm) but slightly spaced beside each RS; more or less extending to center	very small well-spaced GO, except on elongated oral plates	flat, small, very finely rugose GO, slightly spaced toward distal end, almost absent near tip, lateral surface always spaced	GO present on plates near arm base, then naked	inner > outer (inner 1 × ASE, outer 1/3 × ASE length)	inner spine: slightly flattened, denticulate over most of length, and proximal margin beset with small curved spines outer spine: small and inconspicuous distally both spines flattened and pointed, but hooks absent	2 (8–14)	McKnight (2000), Mah et al. (2009), this study
Asteroschema brachiatum Lyman, 1879	6–11 mm and 270 mm (arm base width 3 mm)	dense, uniform GO; RS elevated, extending nearly to center	similar to dorsal, inconspicuous GO, which simulate oral papillae	closely uniformly covered with GO; 6–9 grains in 1 mm	as dorsal	inner > outer (inner spine 2 mm)	inner spine: rough, slightly club-shaped	2 (4)	Lyman (1879, 1882), H. L. Clark (1941)
Asteroschema clavigerum Verrill, 1894	8–12 mm and arm length unknown (arm base width 3–3.5 mm)	small, smooth GO, 6 grains in 1 mm; RS large, extending to center, GO larger than on disc.	smooth skin lacking GO or minute, more spaced GO	small, smooth GO	only base of arm covered with minute, more spaced GO, and rest of arm naked	inner > outer	inner spine: large, long, elevated, and rough with spinules distally; somewhat swollen outer spine: small distally both spines small, slender, acute and nearly equal	3–4 (4–5)	Verrill (1894), Döderlein (1927)
Asteroschema domogranulatum sp. nov.	9 mm and 165 mm	dense, large slightly domed GO, 4 or 5 grains in 1 mm; RS wide, parallel, raised above the disc close together	large polygonal PO except distal half of jaw	large polygonal PO in proximal arm; then slightly separated, decreasing in size GO	arm base concealed by polygonal PO; remainder naked	inner ≈ 2 × outer	inner spine: pointed thorny tip to cylindrical, slightly club shaped, flattened thorny outer spine: small with thorny tip distally both compound hook with 3–6 secondary teeth	2 (19–22)	This study
Asteroschema edmondsoni A. H. Clark, 1949	13 mm and 290 mm	GO & CO; dense GO on proximal half of RS, larger CO with TP on distal half	dense rounded GO	dense PO, swollen in the middle with TP; TP absent in distal end of arm	same as on ventral disc; but smaller	unknown	unknown	unknown	A. H. Clark (1949)

Species	Disc diameter and arm length	Epidermal ossicles on the disc		Epidermal ossicles on the arm		ARS length	ARS shape	AS from segment 1st (2nd)	Reference
		Dorsal	Ventral	Dorsal	Ventral				
Asteroschema elongatum Koehler, 1914	7–11 mm and 300 mm	strongly excavated, GO rounded, unequal, slightly coarse near disc periphery; RS meeting at center, separated, GO larger and denser than on disc	minute GO, uniform, separated, slightly stronger near periphery	on first few segments GO like on RS then spaced, small, and uniform	GO much smaller and uniform, rapidly becoming fewer and finally disappearing after 30–40 mm from arm base	inner > outer	inner spine: cylindrical, strong, thinner at tip with TP outer spine: conical, pointed tip	2 (5)	Koehler (1914), Döderlein (1930)
Asteroschema fastosum Koehler, 1904	6–13 mm and 180–300 mm (arm base width 5 mm)	high, CO including RS	small CO, more rounded, close-set at disc margin	small CO, more close-set than on disc, 6 or 7 grains in 1 mm	flattened CO	inner > outer (inner spine ≤ 4 mm)	inner spine: bluntly conical at arm base, then strongly club-shaped with TP outer spine: cylindrical, thorny tip distally both spines compound hook with 2–4 secondary teeth	2 (4–5)	Koehler (1904), Döderlein (1927, 1930), Guile (1981)
Asteroschema flosculus Alcock, 1894	–	GO & CO; scattered as uniform microscopic GO	uniform microscopic GO	GO & CO; scattered as uniform microscopic GO	uniform microscopic GO	large	unknown	3 (3)	Alcock (1894)
Asteroschema glaucum Matsumoto, 1915	11 mm and 100 mm (4 mm width in arm base)	flat; coarser GO, 6 grains in 1 mm; RS mostly covered except distal end	coarser GO; near apex of jaw less GO	coarser GO, 6 grains in 1 mm, very stout at base, as high as wide	as dorsal	inner > outer	inner spine: cylindrical, club-shaped, rough end distally both spines compound hook with four curved secondary teeth	2–3 (8)	Matsumoto (1915)
Asteroschema hemigymnum Matsumoto, 1915	10 mm and 100 mm (3 mm width in arm base)	very fine, smooth, close-set GO	ventral: fine, rather sparse GO in skin, coarse, flat, smooth, pavement-like grains, corresponding to oral papillae	very fine, smooth, close-set GO; 5 grains in 1 mm; GO much finer distalwards and disappear at distal end.	entirely naked; LAP and VAP visible through skin	inner > outer (outer spine ½ × ASE length)	inner spine: cylindrical, club-shaped outer spine: small, cylindrical, enclosed in skin, more or less rough tip distally both spines compound hook with 3–6 secondary teeth	2 (5–6)	Matsumoto (1915)
Asteroschema horridum Lyman, 1879	10–12.5 mm and 160–190 mm	tumid polygonal PO; mostly tall CO with terminal projections	PO & CO higher and thinner at disc periphery	PO, larger on arm base than on disc, 4 PO in 1 mm at arm base; weakly annulated	PO & CO lower and thinner	inner ≈ 2 × outer	inner spine: cylindrical with TP, slightly swollen	1 (1–6)	Lyman (1879, 1882), Baker (1980), Mah et al. (2009), McKnight (2000)
Asteroschema igloo Baker, 1980	5.7 mm and 68.4 mm (1: 12-disc diameter to arm length)	rounded or polygonal domed GO, 4–6 grains in 1 mm length; RS short, obscured, distally visible	closely packed rounded, domed GO	dorsal & ventral: rounded or polygonal domed GO; 4–6 grains in 1 mm length	as dorsal	inner ≈ 2 × outer (inner spine 2/3 × arm width)	inner spine: long, very fine, thorny blunt tip distally both spines compound hook with 3–6 secondary teeth	3: (8–10)	Baker (1980), McKnight (2000)
Asteroschema inoratum Koehler, 1906	6–10 mm and 70+ mm	fine, contiguous GO (rounded or slightly conical); RS wider, extending to center	GO density similar to dorsal, slightly developed around GS	fine, rounded or slightly conical, contiguous GO	as dorsal	inner ≈ 1½ × ASE length	inner spine: slightly club-shaped, Swollen toward the end with conical point outer spine: smooth, much smaller distally both spines small, but not transforming into a hook	2 (5–7)	Koehler (1906), Peterson (1985), Hansson (2001), Smirnov et al. (2014)

Species	Disc diameter and arm length	Epidermal ossicles on the disc		Epidermal ossicles on the arm		ARS length	ARS shape	AS from segment 1st (2nd)	Reference
		Dorsal	Ventral	Dorsal	Ventral				
Asteroschema intectum Lyman, 1878	5–11.5 mm and 280 mm (arm width 3 mm)	fine GO, 6–7 grains in 1 mm; RS long, meeting at center, GO fine than on disc, 8–9 grains in 1 mm	fine GO except jaw	GO scattered, and smaller than on disc.	lateral and ventral side naked or fewer GO	inner > outer	inner spine: blunt, spiniform, not club-shaped	2 (3)	Lyman (1878), H. L. Clark (1941)
Asteroschema laeve (Lyman, 1872)	8.5 mm and 85 mm	flat; fine close-set GO, 7–8 grains in 1 mm; RS mostly covered with GO except distal end	minute, close, smooth GO, fewer GO near apex of jaw	fine close-set GO, 7–8 grains in 1 mm, thin skin, faint brown marking	as dorsal	inner > outer	inner spine: cylindrical, somewhat swollen, rough end distally both spines compound hook with 4 curved secondary teeth	2 (8)	Lyman (1875, 1879), H. L. Clark (1941)
Asteroschema lissum H. L. Clark, 1939	7.5 mm and 110 mm	very fine, small GO; 50–60 grains in 1 mm², but noticeably smaller at center and proximal end of RS; RS separated, narrow, straight, parallel, not meeting at center	naked with thin skin	fine GO similar on disc, laterally sparse, but continuous to base of ARS, distally sparse, and naked	naked with thin skin	inner ≈ 2–3 × outer	inner spine: long, thick, thorny tip	2 (9–11)	H. L. Clark (1939) This study
Asteroschema migrator Koehler, 1904	11 mm and 200–300 mm	sparse, domed CO with terminal projections, CO dense on RS & disc margin	few small CO	close-set, small, tumid GO	few GO or CO	inner ≈ 2 × outer	inner spine: cylindrical, swollen, TP outer spine: small, with pointed tip	3 (6–8)	Koehler (1904) Baker (1980) McKnight (2000)
Asteroschema monobactrum H. L. Clark, 1917	8 mm and 80–90 mm (base arm width 2 mm)	GO, flat, slightly raised above arm, near center 7 grains in 1 mm (50 mm²), but disc periphery 5–6 grains 1 mm (30 mm²)); RS completely covered but rounded ridges appeared when dried	similar GO density as dorsal	GO on arm base similar to disc, then separated, very minute, distally almost naked	GO, from middle slightly naked	inner ≈ 2 × outer	unknown	2 (11–16)	H. L. Clark (1917)
Asteroschema nuttingii Verrill, 1899	7 mm and 50 mm	minute rough GO/CO; close-set on RS	few GO near GS; minute rough GO/CO	minute GO/CO, distinct distally	minute rough GO/CO	inner > outer	inner spine: slender, tapering at arm base, then cylindrical, blunt, swollen distally, with TP	1 (1–2)	Verrill (1899)
Asteroschema oligactes (Pallas, 1788)	4–10 mm and 250 mm (length ≈ 17 × disc diameter)	CO	CO	CO; 4–5 CO in 1 mm on ventral arm base	as dorsal	inner > outer	unknown	unknown	Pallas (1788), H. L. Clark (1941)
Asteroschema rubrum Lyman, 1879	12 mm and 160 mm	fine, close-set GO, 6–7 grains in 1 mm; RS faintly indicated as flat ridges	fine, close-set GO	fine, close-set GO, 6–7 grains in 1 mm	as dorsal	inner spine maximum length 1.4 mm	inner spine: small spiniform at arm base, then cylindrical, swollen with TP distally both spines compound hook with secondary teeth	2 (5–6)	Lyman (1879, 1882), This study
Asteroschema salix Lyman, 1879	5–8.5 mm and 55–85 mm	flat, fine, close-set GO, 7–8 grains in 1 mm; RS mostly covered with GO except distal end	fine, minute, close-set GO, less GO near apex of jaw	fine, close-set GO, 7–8 grains in 1 mm, thin skin	as dorsal	inner > outer	inner spine: cylindrical, somewhat swollen, rough end distally both spines compound hook with 4 curved secondary teeth	2–3 (11–12)	Lyman (1879), Baker (1980), McKnight (2000), Olbers et al. (2015), This study

Species	Disc diameter and arm length	Epidermal ossicles on the disc		Epidermal ossicles on the arm		ARS length	ARS shape	AS from segment 1st (2nd)	Reference
		Dorsal	Ventral	Dorsal	Ventral				
Asteroschema sampadae Parameswaran & Jaleel, 2012	18 mm and 380–450 mm	spaced CO with terminal projections; RS covered with CO, extending to center	minute, spaced GO	spaced CO with terminal projections, denser at arm base	minute, spaced GO	inner ≈ 2 × outer, inner spine ≤ 2 × ASE (5 mm)	inner spine: bluntly conical at arm base; then cylindrical, with TP at inner edge	2 (4)	Parameswaran and Jaleel (2012)
Asteroschema shenhaiyongshii sp. nov.	10 mm and 220 mm (arm base width 3.4 mm)	small, finely rugose, rounded GO, similar in size, 8–9 grains in 1 mm; RS wide, parallel, close together, not meeting at center, distal end of RS raised above disc, swollen at center	GO similar on dorsal, spearhead-shaped teeth. GS narrow concealed with GO	dorsal: dense GO similar to disc; 8–9 grains in 1 mm; distally GO less rounded but dense	less rounded and more polygonal GO, concealing only proximal half of arm, in middle to distal ventral arm surface concealed with widely separated GO decreasing in size to completely naked	inner > outer (inner spine 2.2 mm long)	inner spine: cylindrical, thorny tip to less club-shaped with small sharp thorns on more than half its length outer spine: small in size with thorny tip similar to inner spine distally both spines similar in size, compound hook with 4 or 5 secondary teeth	2 (9–11)	This study
Asteroschema subfastostum Döderlein, 1930	8 mm and 9 × disc diameter	pointed CO, blunt at disc margin, 4–5 grains in 1 mm	smooth hemispherical GO	pointed CO	smooth hemispherical GO	inner > outer	unknown	unknown	Döderlein (1930)
Asteroschema sublaeve Lütken & Mortensen, 1889	12 mm and 300 mm (arm base width 5 mm)	round, rugose GO variable size; RS covered with larger GO than on the disc	smooth, small GO, few GO lateral at jaw	round, rugose GO variable size, smaller at lateral side, larger on dorsal surface	naked	inner ≈ 2 × outer; in middle (inner ≈ 4 × outer)	inner spine: elongated, club shaped, enclosed with thick skin	2–3 (3–4)	Lütken and Mortensen (1889)
Asteroschema sulcatum Ljungman, 1872	5 mm and arm length unknown	dense, small GO (9–15 grains in 1 mm); RS narrow, not meeting at center	dense, small GO, teeth rounded or distally lobed	dense, small GO	as dorsal	inner > outer	inner spine: strongly thorny tip, swollen, bent club shaped	(3–12)	Ljungman (1872), Lyman (1875)
Asteroschema tenue Lyman, 1875	6 mm and 200 mm (arm base width 1.5 mm)	closely, smooth GO (8–9 grains in 1 mm); RS narrow, meeting at center and GO little coarser	coarser GO; large GO in jaw	slender arms; similar to dorsal disc, distally GO much finer and more scattered	as dorsal	inner > outer, inner spine 1 mm long in middle half	inner spine: spiniform at arm base, then large, fine thorny, club-shaped	1 (3)	Lyman (1875), H. L. Clark (1915)
Asteroschema tubiferum Matsumoto, 1911	14–16 mm and 230–300 mm	closely and evenly, small rounded or polygonal GO; RS narrow, not meeting at center but convergent	entirely covered with dense GO, slightly large, rounded GO corresponding to oral papillae	GO similar to disc, 4–5 grains in 1 mm	distally GO smaller, widely spaced on ventral side	inner > outer	inner spine: cylindrical, initially tapering to a blunt, thorny tip, middle club-shaped with small sharp thorns, first 10–12 covered by sheath outer spine: small, pointed tip distally both spines compound hook with secondary teeth	2 (7)	Matsumoto (1911, 1915), Baker (1980), McKnight (2000), This study
Asteroschema tumidum Lyman, 1879	8–13 mm and 120–180 mm	dense, rounded GO proximally, CO at disc margin regularly spaced pointed; RS covered with CO, extending to center	similar to dorsal but lower	regularly spaced pointed, CO; 4 grains in 1 mm, rarely touching each other	as dorsal	inner > outer, inner spine ≤2 mm long	inner spine: rough, slightly club-shaped	2 (3)	Lyman (1879, 1882) Koehler (1904)
Asteroschema vicinum Koehler, 1907	7 mm and 93 mm	fine GO	fine GO, more than 9 grains in 1 mm, GO much larger around jaw	fine GO	as dorsal	½ × ASE length	both sub-equal, fairly short, same morphology along the arm	- (2)	Koehler (1907)

Species	Disc diameter and arm length	Epidermal ossicles on the disc		Epidermal ossicles on the arm		ARS length	ARS shape	AS from segment 1st (2nd)	Reference
		Dorsal	Ventral	Dorsal	Ventral				
Asteroschema wrighti McKnight, 2000	6.5 mm and at least 6 × disc diameter	fine and uniform GO, 8–10 grains in 1 mm; RS elongated, meeting at center	thin smooth skin, occasional small GO; relatively large irregular PO in GS	fine and uniform GO; 8–0 grains in 1 mm; extending to lateral surface	occasional small GO, thin and smooth skin	inner > outer, inner arm spine up to 2 × ASE length	inner spine: long, finely thorny, slightly club-shaped outer spine: relatively small and smooth distally both spines compound hook with secondary teeth	2(5–6)	McKnight (2000)
Asteroschema yaeyamense Murakami, 1944	7 mm and 150 mm	dense, coarse CO	rounded GO	regularly spaced CO, distally swollen GO	as dorsal	inner > outer	inner spine: long, cylindrical with TP	2 (3–6)	Murakami (1944), Liao (2004)
Ophiocreas ambonesicum Döderlein, 1927	27–30 mm and 350–390 mm	coarse, thick, naked skin (when dry widely separated GO visible); RS narrow, not meeting at center	as dorsal	naked skin, when dry widely separated GO visible), annular band	naked skin, when dry widely separated GO visible)	inner ≈ 3 × outer; in middle 2 × ASS length	inner spine: elongated, thick, enclosed with thick skin, cylindrical, club-shaped outer spine: cylindrical, pointed tip distally both spines compound hook with 2–3 secondary teeth	2 (8–12)	Döderlein (1927)
Ophiocreas carnosus Lyman, 1879	15 mm and 200 mm (arm base width 7 mm)	thick, soft wrinkled skin; RS rounded distal end, narrow, meeting at disc center	as dorsal	smooth, soft wrinkled skin	as dorsal	inner ≈ outer, inner ≈ 3 mm long	inner spine: short, enclosed by thick skin, cylindrical, thorny tip outer spine: cylindrical, thorny tip	2 (6)	Lyman (1879)
Ophiocreas caudatus Lyman, 1879	22–25 mm and 300–420 mm (arm base width 5.5–7.5 mm)	covered with thick skin, when dry micro-GO visible; RS narrow, raised above the disc, meeting at center	as dorsal	covered by thick skin, when dry micro-GO visible at arm base, annular band.	as dorsal	inner 3 mm longer in middle	inner spine: elongated, enclosed by skin, stout, thorny tip outer spine: short, peg-like	2 (10–13)	Lyman (1879, 1882), Matsumoto (1917), Döderlein (1911), H. L. Clark (1949)
Ophiocreas oedipus Lyman, 1879	5–12 mm and 70–250 mm (arm base width 3.5 mm)	thin skin with small, fine GO; RS narrow, closer together, extending to disc center	small, closely set, rounded GO or naked, GS wide	thin skin with fine GO, first 5–8 ASS swollen	as dorsal	inner 1 × ASS length, outer ½ × ASS length	inner spine: slender, elongated, enclosed by skin, blunt, thorny tip outer spine: short, cylindrical, pointed distally both spines compound hook with 6 secondary teeth	2 (6–9)	Koehler (1904, 1909), Lyman (1879, 1882), H. L. Clark (1915), Baker (1980), Peterson (1985), McKnight (2000)
Ophiocreas gilolense (Döderlein, 1927)	22 mm and 290 mm (arm base width 9 mm)	naked skin; RS meeting at center	as dorsal	naked skin, annular band	as dorsal	inner ≈ 2 × outer; in middle 2 × ASS length	inner spine: elongated, slender, cylindrical outer spine: cylindrical, pointed tip	2 (3–4)	Döderlein (1927)
Ophiocreas glutinosum (Döderlein, 1911)	17 mm and unknown (arm base height 9 mm)	dense small GO (10 grains in 1 mm); RS large (nearly covering whole disc), long, close to each other, meeting at center	as dorsal	thick arms, thick skin covers arm plates completely, proximally dense small GO (10 grains in 1 mm), distally separated,	as dorsal	inner 1½ × ASS length, outer ≈ 1/3 × inner	inner spine: slender, elongated, swollen thorny tip outer spine: small distally both spines compound hook with 2–3 secondary teeth	2 (6–7)	Döderlein (1911)

Species	Disc diameter and arm length	Epidermal ossicles on the disc		Epidermal ossicles on the arm		ARS length	ARS shape	AS from segment 1st (2nd)	Reference
		Dorsal	Ventral	Dorsal	Ventral				
Ophiocreas japonicus Koehler, 1907	4–33 and 210–655 mm (arm base width 7 mm)	smooth, thin, small specimen with dense GO coverage (4 mm disc diameter); RS thick, raised above the disc, meeting at disc center	as dorsal	smooth, thin, naked skin, annular, (small specimen with dense GO coverage (4 mm disc diameter)	somewhat fewer scattered GO	inner ≤6 mm, 3 × ASS length; outer 1 × ASS length	inner spine: elongated, thick base, cylindrical, thorny tip outer spine: cylindrical, pointed tip distally both spines compound hook with 2–3 secondary teeth	2 (3–12)	Koehler (1907), Döderlein (1911), Matsumoto (1917), McKnight (2000)
Ophiocreas lumbricus Lyman, 1869	4.5–17 mm and 50–240 mm (arm base width 2.5 mm)	covered by separated micro-thorny GO; RS meeting at center	as dorsal	covered by separated micro-thorny GO annular band	as dorsal	inner ≤ 1½–2 × ASS length outer 1 × ASS length	inner spine: cylindrical, enclosed by skin, blunt, rough surface, thorny tip outer spine: cylindrical, enclosed with skin, blunt, rough surface, thorny tip	2 (4)	Lyman (1869)
Ophiocreas mindorense (Döderlein, 1927)	12–23 mm and 160–480 mm (arm base width 3–5.5 mm)	smooth, dense GO (8 grains in 1 mm); RS narrow, closer together, extending to disc center	as dorsal	similar to disc, smooth, dense GO (8 grains in 1 mm); GO absent on ventral side of younger specimens	as dorsal	inner 3–5.5 mm, in middle 2½ –3 × ASS length; outer 1 × ASS length	inner spine: slender, elongated, swollen thorny tip outer spine: thick arm base with pointed tip	2 (8–11)	Döderlein (1927)
Ophiocreas mortenseni Koehler, 1930	7.5–25 mm and 110–400+ mm (arm base height 6 mm)	covered by thick, wrinkled, or folded skin; RS narrow, extending to disc center	covered by plate-like ossicles	skin thicker than dorsal, mostly thickened near arm spines, arched	as dorsal	inner 1 × ASS length; outer 2/3 × inner	inner spine: slightly flattened, rough in upper half, thorny tip outer spine: short, cylindrical, thorny pointed distally both spines compound hook with 3 or 4 secondary teeth	2 (4–7)	Koehler (1930), McKnight (2000)
Ophiocreas sibogae Koehler, 1904	14–28 mm and 300–350 mm (disc diameter × 30) (arm base width 5 mm)	naked skin; RS narrow, parallel, not meeting at center	as dorsal	naked skin, annular band	as dorsal	inner ≈ 2 × outer, in middle 2 × ASS length	inner spine: elongated, slender, cylindrical, club-shaped, finely rugose outer spine: cylindrical, pointed tip distally both spines compound hook with 2–4 secondary teeth	2 (3–11)	Koehler 1904, H.L. Clark 1916b, Mortensen 1924, Döderlein 1927, Baker 1980, McKnight (2000)
Ophiocreas spinulosus Lyman, 1883	8–17 mm and 60–550 mm (arm base width 3 mm)	naked skin; RS strongly marked ridges with short, stout blunt spines, meeting at center	as dorsal	higher than wide, naked skin, annular band blunt spine at each pair of ASS	as dorsal	inner ≈ 2 mm, equal in size in proximal arms	inner spine: short, blunt, rough surface, cylindrical outer spine: cylindrical, pointed tip, distally slender distally both spines compound hook with 2 secondary teeth	2 (3–4)	Lyman (1883), H. L. Clark (1915, 1941)
Ophiocreas willsi McKnight, 2000	16 mm and 380 mm	covered by thick, wrinkled, or folded skin; RS narrow, extending to disc center, dense small GO cover in the center	covered by well separated small GO.	granulation similar to the disc, extending to the lateral arm, GO coverage dense proximally, but scattered distally	first 3–5 ASS with few GO, then naked	inner 1½ × ASS, outer shorter than ASS	inner spine: slightly flattened, enclosed by skin, rough, blunt tip outer spine: short, cylindrical, thorny pointed distally both spines compound hook with 3 or 4 secondary teeth	2 (2–3)	McKnight (2000)

Asteroschema shenhaiyongshii sp. nov.

http://zoobank.org/A5459AA8-D154-47F1-833F-710652EF9636

Figures 6, 7

Material examined. ***Holotype*:** China • 1 specimen; South China Sea, Northeast of Xisha Islands archipelago; 18°41.95'N, 113°33.08'E; depth 1070 m; 29 Mar. 2018; Collecting event: stn. SC004; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044292, OL712208; IDSSE-EEB-SW0086.

***Paratype*:** China • 1 specimen; South China Sea, Southeast of Zhongsha Islands; 13°55.30'N, 115°25.44'E; depth 1111 m; 04 Aug. 2020; Collecting event: stn. SC007; 'Shenhaiyongshi' msv leg; preserved in -80 °C; IDSSE-EEB-SW0087.

Diagnosis. Disc raised high above the arm, concealed by highly dense, small, rounded, finely rugose granular ossicles (Fig. 6A–C). Jaws narrow, elongated, concealed by slightly larger, less rounded granular ossicles (Fig. 6E). Arm surface concealed by granular ossicles similar to disc, but ventral surface of arm concealed by less rounded, more polygonal granular ossicles (Fig. 6F–H). Inner arm spine cylindrical, slightly club-shaped, with small sharp thorns on more than half its length (Fig. 6L–N).

Description of holotype. Disc diameter 10 mm, length of arms 220 mm, arm base width 3.3–3.5 mm (Fig. 6).

***Disc*.** Disc more or less pentagonal, raised high above arm, and swollen in center (Fig. 6A). Entire disc concealed by highly dense, small, rounded, finely rugose granular ossicles (eight or nine grains in 1 mm; Fig. 6A–C). Granular ossicles similar in size and shape from center to periphery of disc (Fig. 6C). Radial shields wide, straight, close together, but not meeting in center, and completely concealed by dense granulation (Fig. 6C). Genital slits narrow, vertical at interradii and densely covered with less rounded granular ossicles (Fig. 6D). Jaws narrow, elongated, concealed by slightly larger less rounded granular ossicles (Fig. 6E). At apex of jaw a blunt, spearhead-shaped tooth, and granular ossicles all over oral plates (Fig. 6E). Ventral disc densely covered with granular ossicles similar to dorsal disc (seven or nine grains in 1 mm) but less rounded around distal end of jaw and adoral shields (Fig. 6E). Adoral shields large, with curved edge, and connected to first arm segment. Oral shields not discernible and adoral shield spine covered by granular ossicles (Fig. 6E).

***Arms*.** Arm width comparatively large in relation to body size, not arched, subcylindrical, width unchanged from base to middle half of arm (Fig. 6A, F). From middle to distal end, arm tapering slightly and more cylindrical (Fig. 6F–H). Dorsal and lateral arm surface concealed by dense, finely rugose, rounded granular ossicles similar to disc (eight or nine grains in 1 mm), continuing to distal end of arm (Fig. 6F–H). Distal half of dorsal and lateral arm concealed by less rounded, dense granular ossicles (eight or nine grains in 1 mm; Fig. 6H). Lateral arm plates on proximal to middle half of arm concealed by granular ossicles, including on base of arm spine, but on distal end only lateral arm plates concealed (Fig. 6G–K). Ventral surface of arm concealed by dense granular ossicles, similar to ventral disc, less rounded and more polygonal, but only covering proximal half of arm (seven or nine grains in 1 mm; Fig. 6I). Middle to distal end of ventral arm surface concealed by widely separated, in size decreasing granular ossicles (three or four grains in 1 mm) to completely naked (Fig. 6J, K). First free tentacle pore without arm spine (Fig. 6I). First arm spine appears at second arm segment, with short blunt tentacle scale. Second arm spine appears at nineth or eleventh segment (Fig. 6I, J). Inner arm spine initially tapered to pointed thorny tip, one arm segment in length, middle half cylindrical, less club-shaped, with small sharp thorns on more than half of spine length (Fig. 6L–N). Outer spine smaller, with thorny tip (Fig. 6M, N). Both arm spines similar in size at distal end of arm, and turning into compound hook with 4–5 secondary teeth (Fig. 6O, P).

Color. In live specimen, reddish brown (Fig. 6).

Ossicle morphology of paratype. Lateral arm plate curved around the vertebrae, with two arm spine articular structures, with completely separate large muscle and nerve openings (Fig. 7A). A depression on inner side of lateral arm plate (Fig. 5B, C). Inner arm spine becoming cylindrical from proximal to middle half of arm, with terminal projection, and thorny surface on upper part of spine (Fig. 7D). Outer arm spine nearly half as long as inner one with less thorny tip (Fig. 7E). Distally both spines compound hook with 3–5 secondary teeth (Fig. 7F, G). Arm and disc concealed by rounded granular ossicles (Fig. 7H). Vertebrae with streptospondylous articulation, with deep slope between proximal and distal end, dorsally a median longitudinal furrow, ventrally with median deep longitudinal groove with lateral ambulacral canals, no oral bridge, podial basins moderate in size (Fig. 7I–M).

Paratype variations. Paratype disc diameter 12 mm, similar to holotype. Second arm spine from segments 10–12 and disc slightly flatter than those of holotype; considered intraspecific variation.

Distribution and habitat. 1070–1111 m depth. Near Xisha and Zhongsha islands in the South China Sea. Attached to sponge host.

Etymology. The specific name is dedicated to the manned submersible vessel 'Shenhaiyongshi' meaning deep sea warrior in Chinese, which collected the specimen.

Remarks. *Asteroschema shenhaiyongshii* sp. nov. concurs with the group of *Asteroschema* that has only granular ossicles. This group includes nearly 20 species. Furthermore, they are divided by naked, widely separated granular ossicles on ventral disc and base of arm. Fifteen *Asteroschema* species have dense granular ossicles on the ventral disc. *Asteroschema shenhaiyongshii* sp. nov. is distinguished clearly by its unique dense, rounded, fine granular ossicles on both disc and arms, a thick sub-cylindrical proximal to middle half of the arms without annular bands, and cylindrical outer arm spine with visible thorns at middle arm segments (Fig. 7).

Asteroschema ajax and *A. laeve* (Lyman, 1872) are similar to *A. shenhaiyongshii* sp. nov. by having granular ossicles on both dorsal and ventral disc, but are easily differentiated by well-spaced annulated granular bands on the arms, and club-shaped inner arm spine (A. H. Clark 1949; Lyman 1875; FWRI 2010).

Asteroschema arenosum Lyman, 1878 is similar to *A. shenhaiyongshii* sp. nov. by having granular ossicles on both dorsal and ventral disc, but differs in having a swollen arm spine, sparser granular coverage (five grains in 1 mm), and a second arm spine from the fourth arm segment. *Asteroschema vicinum* Koehler, 1907 differs in its sub-equal arm spines and *A. sulcatum* Ljungman, 1872 in its highly dense granular ossicle coverage (9–15 grains in 1 mm). *Asteroschema igloo* and *A. domogranulatum* sp. nov. differ from *A. shenhaiyongshii* sp. nov. by large polygonal to domed granular ossicles (four or five grains in 1 mm; Table 2) (Ljungman 1872; Lyman 1878; Koehler 1907; Pawson et al. 2009).

Asteroschema glaucum Matsumoto, 1915, and *A. hemigymnum* Matsumoto, 1915 are similar to *A. shenhaiyongshii* sp. nov. by having granular ossicles on both dorsal and ventral disc, but differ by sparser granular ossicle coverage (five or six grains in 1 mm), club-shaped inner arm spine at the middle arm segments and in *A. hemigymnum* the ventral disc is covered with pavement-like ossicles. *Asteroschema inoratum* Koehler, 1906 is similar to *A. shenhaiyongshii* sp. nov. by having a similar density of the granular coverage on both dorsal and ventral disc, but differs in having granular ossicles on the ventral surface along the arm, a slightly club-shaped inner arm spine at middle arm segments, and both spines not transforming into a compound hook (Table 2) (Koehler 1906; Matsumoto 1915).

Asteroschema monobactrum H. L. Clark, 1917 is similar to *A. shenhaiyongshii* sp. nov. in having granular ossicles on both dorsal and ventral surface and in start of the second arm spine, but differs by having separate, sparser granular ossicles (seven grains in 1 mm at disc center, five or six grains in 1 mm at periphery of disc and on arm), and by the granular ossicles on both sides distalwards along the arm becoming widely separated to almost naked (H. L. Clark 1917). *Asteroschema brachiatum* Lyman, 1879 is similar to *A. shenhaiyongshii* sp. nov. in having similar density granular ossicle coverage on both dorsal and ventral disc and arms, but differs by the entire arm being covered by granular ossicles, start of the second arm spine at the fourth arm segment, and a slightly club-shaped inner spine at middle arm segments (Lyman 1879). *Asteroschema salix* Lyman, 1879, *A. tubiferum* Matsumoto, 1911, and *A. rubrum* Lyman, 1879 differ from *A. shenhaiyongshii* sp. nov. by having separated, sparser granular ossicle coverage, a club-shaped inner spine at middle arm segments, and widely spaced ossicles on the ventral arm surface (Lyman 1879; Matsumoto 1911).

Granular ossicle density of *Asteroschema wrighti* McKnight, 2000, *A. bidwillae* McKnight, 2000, and *A. tenue* (eight or ten grains in 1 mm) is similar to *A. shenhaiyongshii* sp. nov. However, *Asteroschema tenue* differs from *A. shenhaiyongshii* sp. nov. by having a club-shaped inner spine at middle arm segments, and slender long arms, and *A. wrighti* differs by having a club-shaped inner spine at middle arm segments, widely spaced granular ossicles on the ventral arm, irregular plate-like ossicles on the ventral disc, and smooth outer spines, and by being hexamerous (Table 2) (Lyman 1875; McKnight 2000).

Most *Ophiocreas* species differ from *Asteroschema shenhaiyongshii* sp. nov. by having naked or micro-granular ossicles in the skin in both disc and arms. (Table 2). In our phylogenetic tree of the family Euryalidae, all *Ophiocreas* species cluster with some *Asteroschema* species, but the average genetic distance between *Ophiocreas* species and *Asteroschema shenhaiyongshii* sp. nov. was 13.61% (Fig. 2, Suppl. material 2: Table S2).

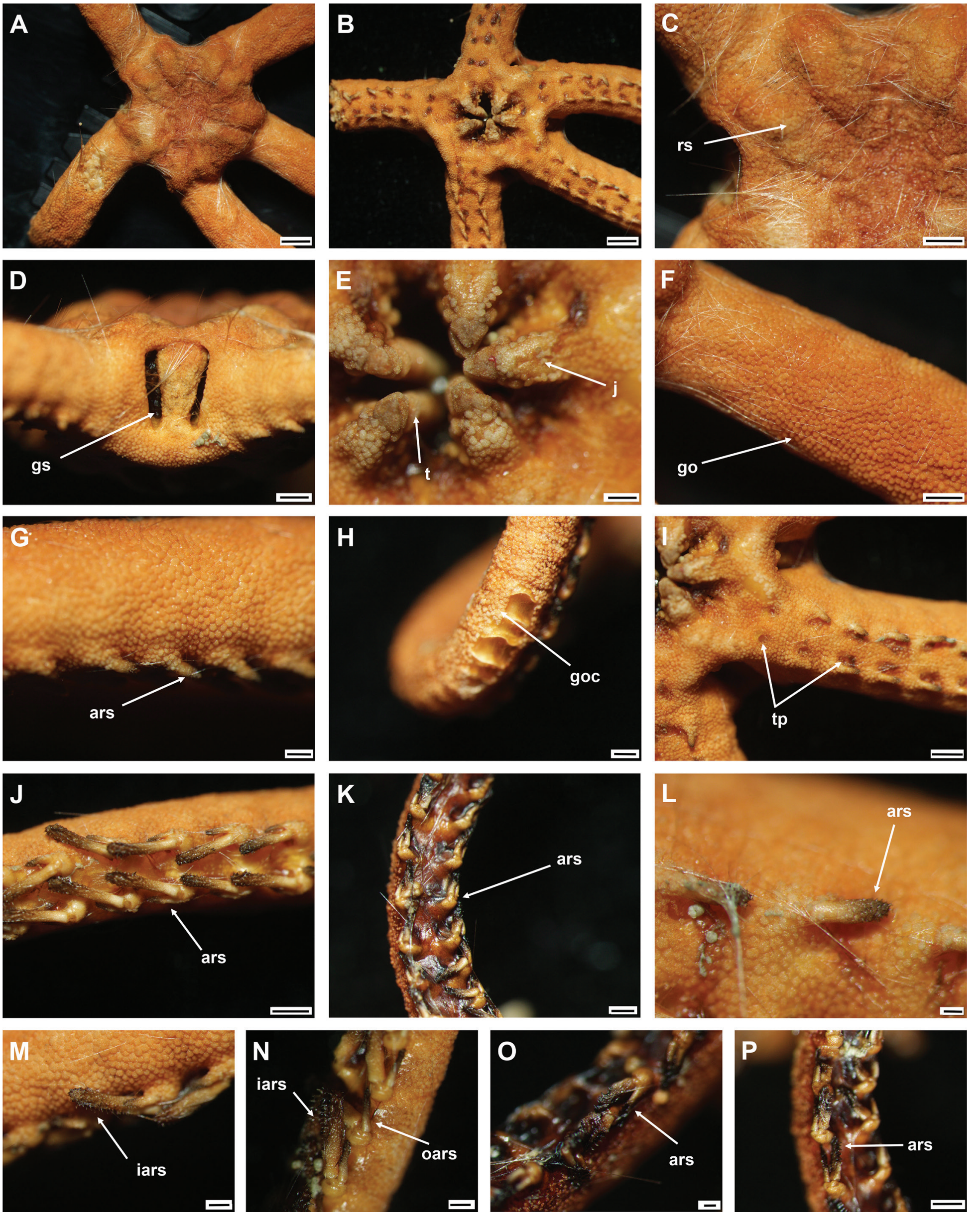

Figure 6. *Asteroschema shenhaiyongshii* sp. nov., holotype (IDSSE-EEB-SW0086) **A** dorsal view **B** ventral view **C** dorsal disc **D** lateral disc **E** oral frame **F** dorsal arm (base) **G** lateral arm (proximal) **H** dorsal arm (distal) **I** ventral arm (base) **J** ventral arm (middle) **K** ventral arm (distal) **L** arm spine (arm base) **M, N** arm spines (middle) **O, P** arm spines (distal). Abbreviations: **ars** arm spine, **go** granular ossicle, **goc** granular ossicles coat, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A, B**); 1 mm (**C, D, F, I, J**); 500 µm (**E, G, H, K, M, N, P**); 200 µm (**L, O**).

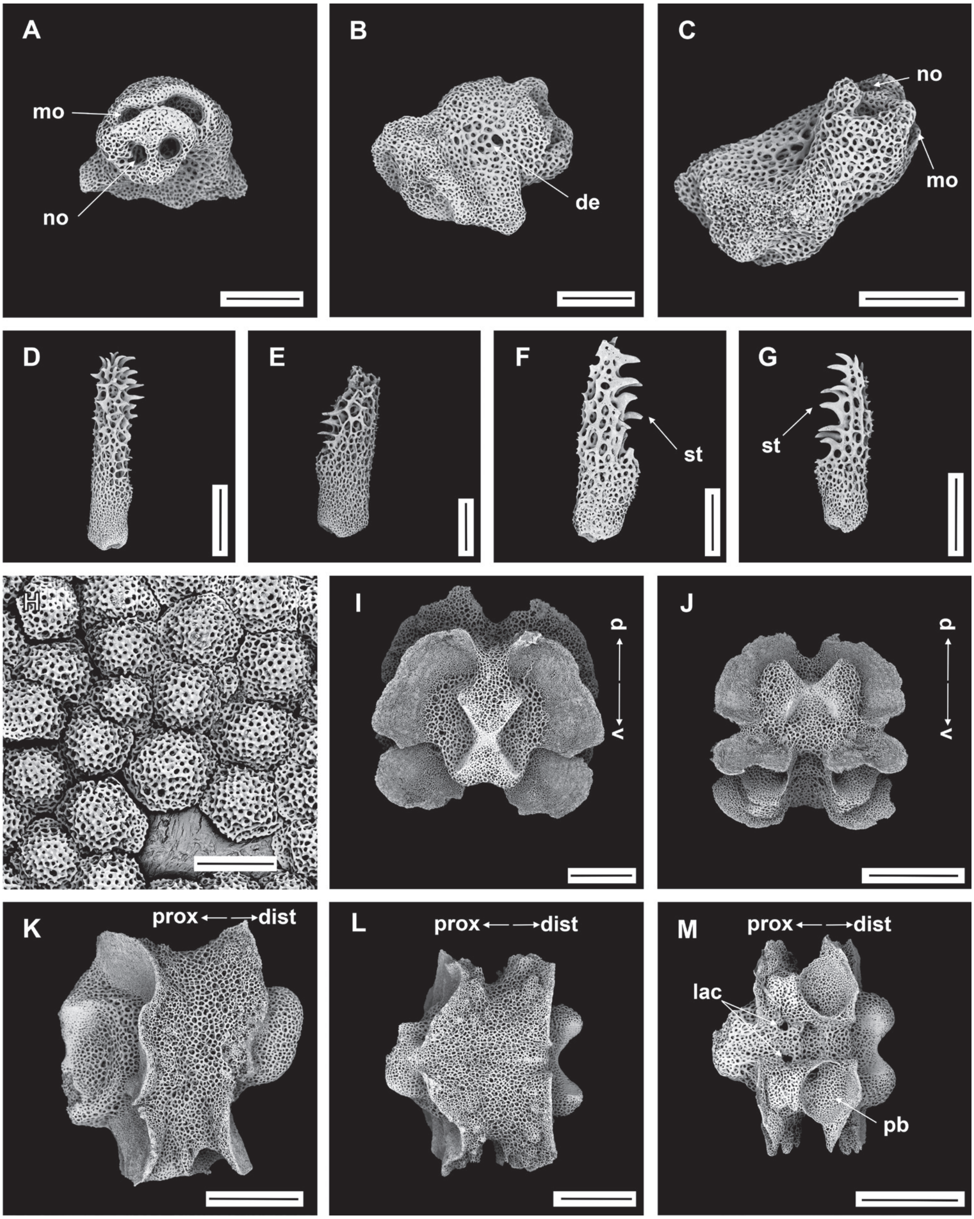

Figure 7. *Asteroschema shenhaiyongshii* sp. nov., paratype (IDSSE-EEB-SW0087) **A–C** lateral arm plate (external, internal) **D, E** arm spines (middle) **F, G** arm spine (distal) **H** skin from dorsal arm base (rounded granular ossicles) **I–M** vertebrae **I** proximal view **J** distal view **K** lateral view **L** dorsal view **M** ventral view. Abbreviations: **d** dorsal, **de** depression, **dist** distal, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 500 µm (**D, I–M**); 300 µm (**A–C, E, G**); 200 µm (**F, H**).

Asteroschema shenhaiyongshii sp. nov. clusters among *Asteroschema rubrum*, *A. salix*, *A. tubiferum*, *A.* cf. *lissum*, and *A. bidwillae*. All these *Asteroschema* species have granular ossicles on the dorsal disc and dorsal surface of the arms. *Asteroschema bidwillae* showed a close relationship with *A. shenhaiyongshii* sp. nov., and was identified as a sibling species due to similar morphological characters of granular ossicles on the dorsal disc and dorsal surface of the arms, and the shape of the inner arm spines at middle arm segments, but differs by having well-spaced granular ossicles on the ventral disc, a naked proximal ventral arm surface, and by being hexamerous and fissiparous (Table 2, Suppl. material 2: Table S2).

***Asteroschema* cf. *bidwillae* McKnight, 2000**

Figures 8, 9

Asteroschema bidwillae McKnight, 2000: 24–27, fig. 8.

Material examined. China • 1 specimen; South China Sea, Zhongsha Islands, seamount; 13°36.20'N, 113°33.74'E; depth 1515 m; 30 Mar. 2020; Collecting event: stn. SC025; 'Shenhaiyongshi' msv leg; preserved in -80 °C; IDSSE-EEB-SW0105.

Description. Disc diameter 13 mm, length of arms 195 mm, arm base width 4.5–5 mm (Fig. 8).

Disc. Disc circular, hexamerous, raised above arms, deeply swollen in center (Fig. 8A, B). Disc covered with dense, small, finely rugose granular epidermal ossicles (Fig. 8A–C). Granular ossicles dense and small in size in disc center, but slightly larger at distal edge (six or seven grains in 1 mm; Fig. 8C, D). Radial shields extending to center but proximal ends concealed by skin with granular ossicles, and distal ends raised above the disc (Fig. 8C). Granular ossicles around distal edge and periphery of disc larger and more irregular (Fig. 8C). Genital slits narrow, without ossicles and vertical on ventral interradii (Fig. 8E). Jaws elongated, mostly naked without granular ossicles (Fig. 8F). At apex of jaw flattened, pointed, and finely rugose teeth, and two to four granular tubercles that resemble lateral oral papillae (Fig. 8F). Ventral disc covered with widely separated small granular ossicles (four or six grains in 1 mm; Fig. 8B, F). Adoral shields connected to first ventral arm segment and concealed by widely separated small granular ossicles, but outline of shields clearly visible (Fig. 8F). Oral shields not discernible and adoral shield spine covered by ossicles (Fig. 8F).

Arms. Arms six, at base wide, not arched, dorsally flattened, and swollen in first few free arm segment (Fig. 8G). Arms distalwards from middle part narrowing and increasingly cylindrical (Fig. 8H). Swollen dorsal arm base covered with dense, large, irregular granular ossicles (four or seven grains in 1 mm), distalwards decreasing in size and becoming rounded (six or seven grains in 1 mm), and distally widely separated (Fig. 8G, H). Lateral arm plates covered with slightly separated granular ossicles.

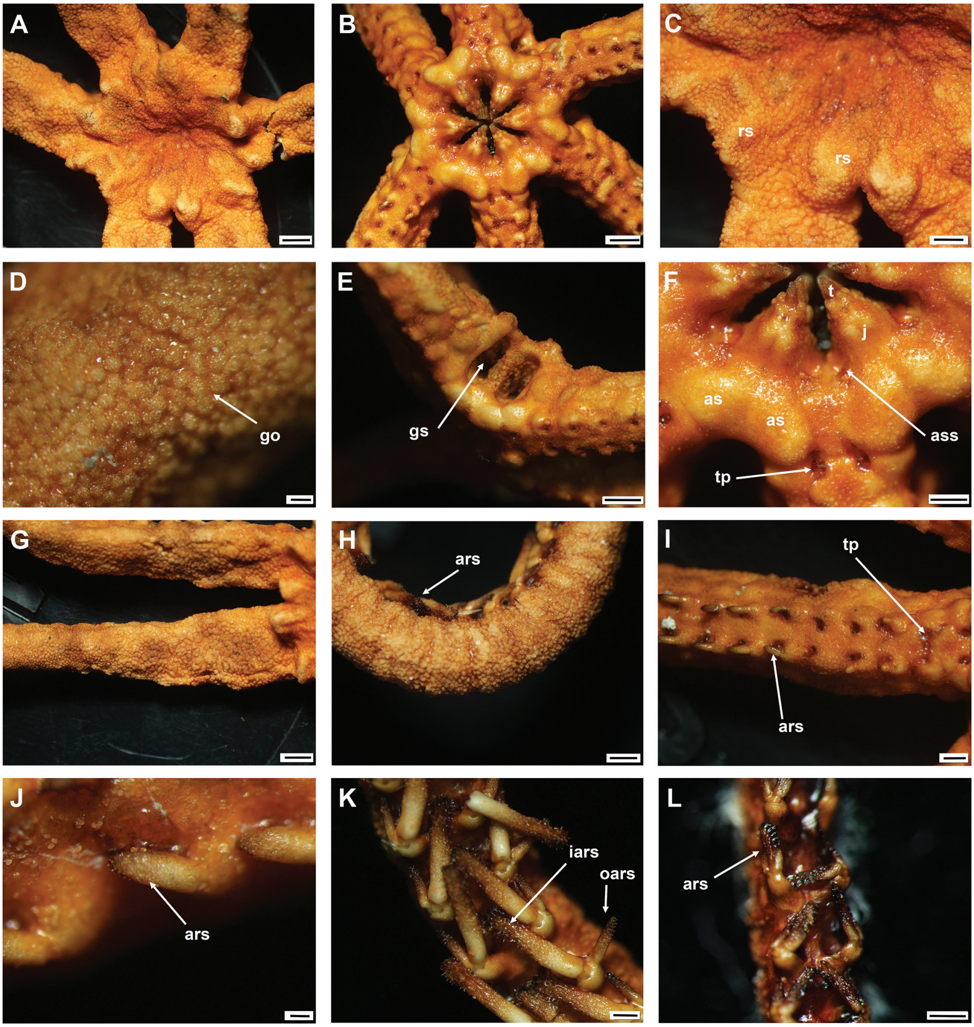

Figure 8. *Asteroschema* cf. *bidwillae* McKnight, 2000 (IDSSE-EEB-SW0105) **A** dorsal side of the specimen **B** ventral side of the specimen **C** dorsal disc **D** skin on the disc **E** lateral disc **F** oral frame **G** dorsal arms (proximal) **H** dorsal arm (middle) **I** ventral arm (arm base) **J** outer arm spine (proximal) **K** arm spines (middle) **L** arm spines (distal). Abbreviations: **ars** arm spine, **as** adoral shield, **ass** adoral shield spine, **go** granular ossicle, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A–C, E, G**); 1 mm (**F, H, I**); 500 μm (**K, L**); 200 μm (**D, G, J**).

Ventral arm near base covered with granular ossicles similar to ventral disc (five or six grains in 1 mm), but becoming widely separated to completely naked along the arm (Fig. 8I, J). First two or three arm segments without arm spine (Fig. 8I). First arm spine appeared at third or fourth arm segment, and second arm spine at eighteenth or twenty-first segment (Fig. 8I–K). Inner arm spine cylindrical, with blunt thorny tip, one and a half arm segment in length (Fig. 8J, K). Outer spine half as long as inner

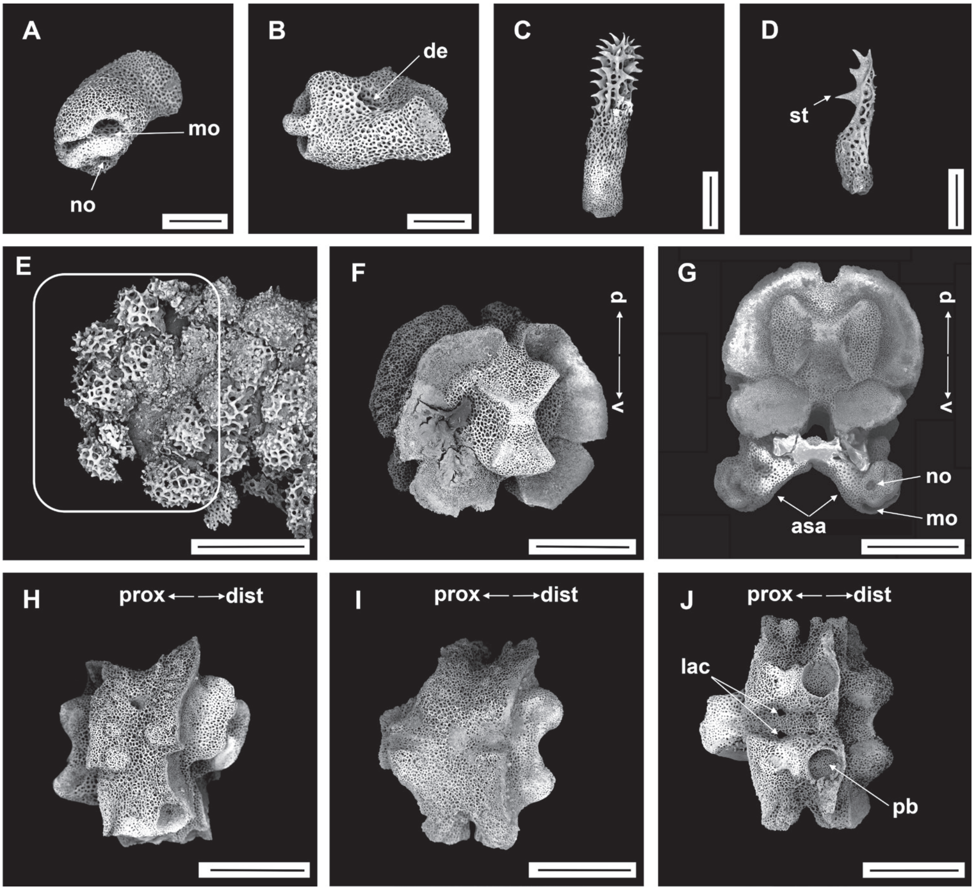

Figure 9. *Asteroschema* cf. *bidwillae* McKnight, 2000 (IDSSE-EEB-SW0105) **A, B** lateral arm plate (external, internal) **C** outer arm spine (middle) **D** arm spine (distal) **E** skin from dorsal arm base (rounded to irregular-shaped granular ossicles) **F–J** vertebrae **F** proximal view **G** distal view **H** lateral view **I** dorsal view **J** ventral view. Abbreviations: **asa** arm spine articulation, **d** dorsal, **de** depression, **dist** distal, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 800 µm (**F–J**); 500 µm (**C**); 300 µm (**A, B, E**); 200 µm (**D**).

spine in middle region, with thorny, pointed tip (Fig. 8K). Both arm spines equal in length at distal end of arm, and compound hook with 3–6 secondary teeth (Fig. 8L).

Color. In live specimen, reddish brown (Fig. 8).

Ossicle morphology. Lateral arm plate with two arm spine articular structures, with slightly separated large muscle and relatively small nerve opening (Fig. 9A). A depression on inner side of lateral arm plate (Fig. 9B). Inner arm spine from proximal and middle half of arm with cylindrical, terminal projection, and upper part of spine covered with thorns (Fig. 9C). Distally, arm spine turns into compound hook with secondary teeth (Fig. 9D). Arm and disc concealed by rounded to slightly irregular granular ossicles (Fig. 9E). Vertebrae with streptospondylous articulation, dorsally a median large longitudinal furrow, ventrally with median deep groove with lateral ambulacral canals, podial basins small (Fig. 9F–J).

Distribution. 400–2000 m depth. New Zealand, Tasman Sea, Solomon Islands, South China Sea (OBIS 2021).

Remarks. *Asteroschema bidwillae* was first described by McKnight (2000), with type locality New Zealand waters in the South Pacific Ocean. This is the first redescription since the original description. The specimens from our collection concur with McKnight's description, but we noticed some differences such as: granular arrangement on radial shields, irregular ossicles on arm base, ossicles on ventral arm recorded nearly to middle region, and start of second arm spine. However, some of these variations may be related to size and maturity of the specimen (the holotype had a disc diameter of 5 mm). We hesitate to fully associate our specimen with *Asteroschema bidwillae* due to uncertainty with the morphological variation in *A. bidwillae*. The genus *Asteroschema* contains only two hexamerous species as far as known. Therefore, the closest one is *Asteroschema wrighti* McKnight, 2000, but it differs in characters of the radial shields, granulation on disc and arm, innermost arm spine, and start of second arm spine (Table 2). This is the first record of *A. bidwillae* from the North Pacific Ocean, if it is indeed this species.

Asteroschema rubrum **Lyman, 1879**

Figures 10, 11

Asteroschema rubrum Lyman, 1879: 68–69, fig. 17, figs 454–457.

Material examined. China • 3 specimens; South China Sea, near Zhongsha Islands, seamount; 13°55.44'N, 115°25.37'E; depth 958 m; 09 Mar. 2020; Collecting event: stn. SC007; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044293, OL712209, OK044294, OL712210, OK044295, OL712211; IDSSE-EEB-SW0071, IDSSE-EEB-SW0072, IDSSE-EEB-SW0073 • 1 specimen; South China Sea, near Zhongsha Islands, seamount; 14°21.93'N, 115°23.89'E; depth 922 m; 17 Mar. 2020; Collecting event: stn. SC035; 'Shenhaiyongshi' msv leg; preserved in -80 °C; IDSSE-EEB-SW0088.

Description. IDSSE-EEB-SW0072: disc diameter 12 mm, length of arms from 165–175 mm (Fig. 10).

Disc. Disc flat, slightly raised above arms, swollen in center, and small in relation to total body size of specimen (Fig. 10A, B). Disc covered with smooth, dense, evenly distributed, small rounded or irregular granular ossicles, similar in size (seven or eight granular ossicles in 1 mm; Fig. 10C, D). Radial shields closely together, parallel, raised above distal disc edge, but mostly concealed by skin with granular ossicles (Fig. 10C). Radial shields do not meet in center. Genital slits wide and vertical on ventral interradii (Fig. 10E). Jaw large, long and covered with dense irregular ossicles (Fig. 10F). Spearhead-shaped teeth and granular ossicles that resemble lateral oral papillae at apex of jaw (Fig. 10F). Adoral shields large, connected to first ventral arm segment, and concealed by granular ossicles (Fig. 10F). Oral shields not discernible and adoral shield

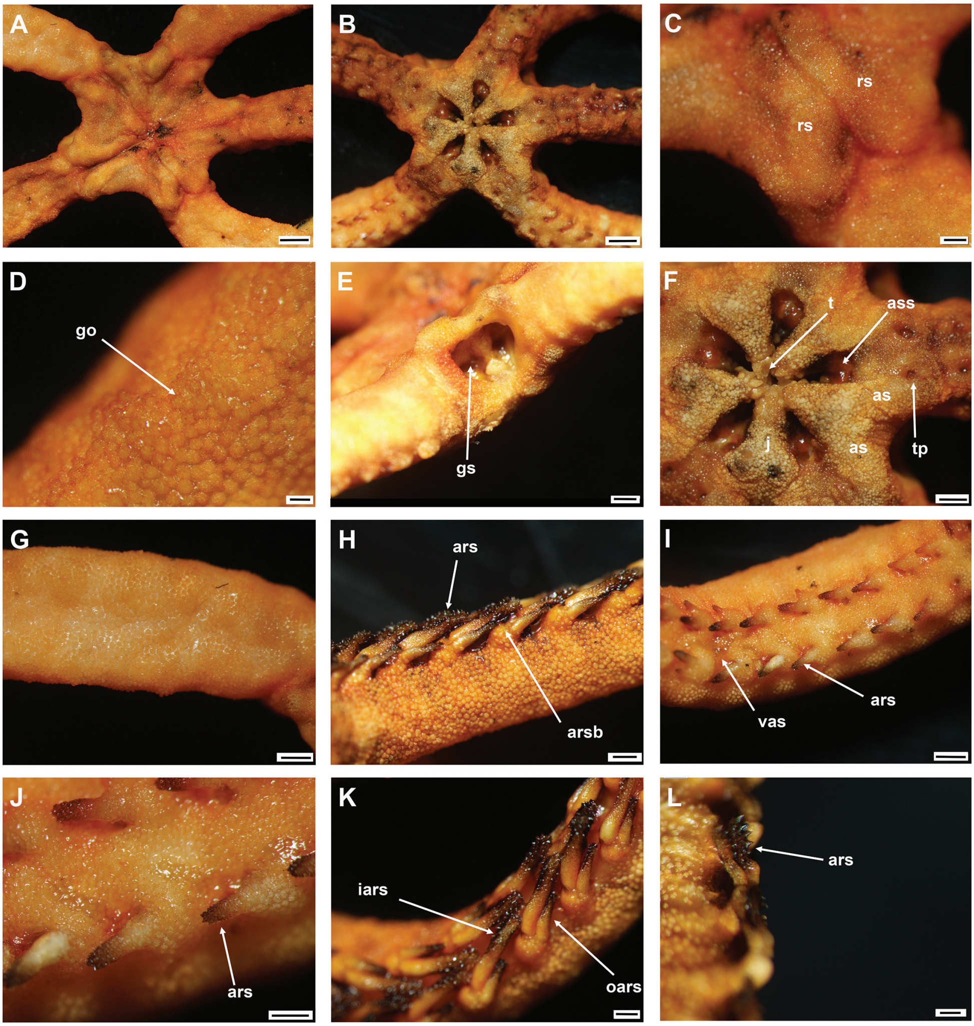

Figure 10. *Asteroschema rubrum* Lyman, 1879 (IDSSE-EEB-SW0072) **A** dorsal view **B** ventral view **C** dorsal disc **D** skin on the disc **E** lateral disc **F** ventral disc **G** dorsal arm (proximal) **H** lateral arm (middle) **I** ventral arm (proximal) **J** outer arm spine (proximal) **K** arm spines (middle) **L** arm spines (distal). Abbreviations: **as** adoral shield, **ass** adoral shield spine, **ars** arm spine, **go** granular ossicle, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **ass** adoral shield spine, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A, B**); 1 mm (**E–G, I**); 500 µm (**C, H, J, K**); 200 µm (**D, L**).

spine naked. Whole oral region swollen nearly to genital slit. Ventral disc covered with dense granular ossicles (seven or eight grains in 1 mm; Fig. 10F).

Arms. Arms at base wide, not arched, dorsally flattened, and slightly swollen in first few free segments (Fig. 10A, G). Arms distalwards from middle part narrowing and more cylindrical (Fig. 10H). Dorsal arm base covered with smooth rounded granular ossicles (six or seven grains in 1 mm), middle segments with dense granular ossicles all the way to the arm spine base (seven or eight grains in 1 mm), and distally

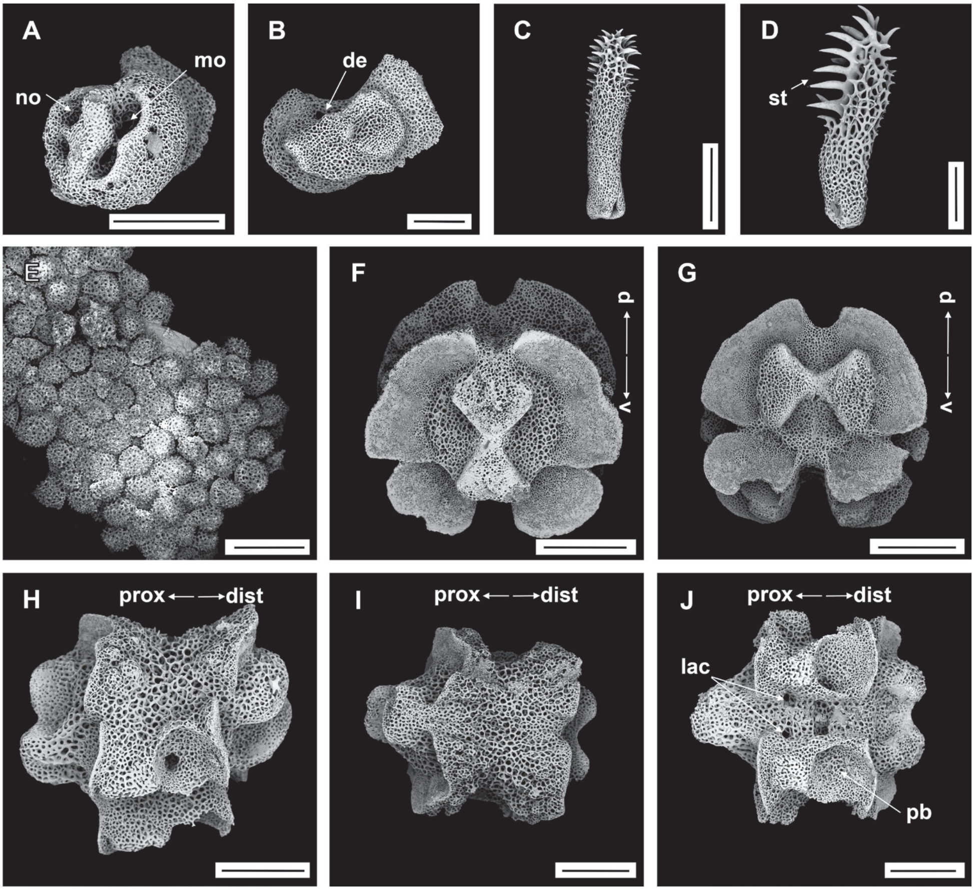

Figure 11. *Asteroschema rubrum* Lyman, 1879 (IDSSE-EEB-SW0072) **A, B** lateral arm plate (external, internal), **C** outer arm spine (middle), **D** arm spine (distal), **E** skin from dorsal arm base (rounded to somewhat cone shaped granular ossicles), **F–J** vertebrae; **F** proximal view, **G** distal view, **H** lateral view, **I** dorsal view, **J** ventral view. Abbreviations: **d** dorsal, **de** depression, **dist** distal, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 800 µm (**C**); 500 µm (**A, F, G**); 300 µm (**B, E, H–J**); 200 µm (**D**).

decreasing in size and separated (seven or eight grains in 1 mm) (Fig. 10G–L). Ventral arm base covered with dense granular ossicles similar to the ventral disc (eight or nine grains in 1 mm), distally decreasing in size and separated to naked (Fig. 10H–K). First one to two tentacle pores without arm spine (Fig. 10F). First arm spine appears at second or third arm segment, and second arm spine at ninth or eleventh segment (Fig. 10I). Outer arm spine half as long as inner spine in middle region, thorny pointed tip, distally compound hook (Fig. 10K, L). Inner arm spine cylindrical, one to one and a half arm segment in length, initially tapering to a pointed thorny tip, in middle blunt, slightly swollen with thorny surface on more than half its length, distally compound hook with three or four secondary teeth (Fig. 10I–L).

Color. In live specimen, reddish brown (Fig. 10).

Ossicle morphology. Lateral arm plate with two arm spine articular structures, with slightly separate large muscle and nerve openings (Fig. 11A). A depression on inner side of lateral arm plate (Fig. 11B). Inner arm spine from proximal and middle half of arm cylindrical, slightly swollen, with thorny tip (Fig. 11C). Distally arm spine turns into compound hook with secondary teeth (Fig. 11D). Arm and disc concealed by granular ossicles, slightly wider than high, round to short stumps with convex tip (Fig. 11E). Vertebrae with streptospondylous articulation, with deep slope between proximal and distal end, dorsally a median longitudinal groove, ventrally with median deep longitudinal groove with lateral ambulacral canals, podial basins moderate in size (Fig. 11F–J).

Distribution. 730–958 m depth. Near Brandella, Chile and in the South China Sea.

Remarks. *Asteroschema rubrum* was first described by Lyman (1879), with type locality in the Southwest Pacific Ocean near South America. This is the first rediscovery after the original description. The specimens from our collection concur well with Lyman's holotype description, the only difference was the starting point of the second arm spines. However, this morphological character is highly variable among individuals. According to the holotype description, *A. rubrum* belongs in the clade with granular ossicles only in the genus *Asteroschema*, but Okanishi and Fujita (2009) considered *A. rubrum* in the clade with conical and granular ossicles. Although, the SEM images of granular ossicles in the skin appear as granular to somewhat small stumps with convex tip (Fig. 11E). However, the description of the holotype is identical with our specimen, and it was described as granular ossicles. The characters of the swollen oral region, smooth granulation on the disc, and innermost spine can be used to distinguish *A. rubrum* from other species of *Asteroschema* (Table 2). The dorsal disc of *A. rubrum* seems naked in wet condition due to its smooth granulation which can lead to misidentification as *Ophiocreas* species (Fig. 10A). This is the first record from the South China Sea.

***Asteroschema tubiferum* Matsumoto, 1911**

Figures 12, 13

Asteroschema tubiferum Matsumoto, 1911: 52; 1917: 44; Baker 1980: 22, fig. 4; McKnight 2000: 24, fig. 7.

Material examined. China • 1 specimen; South China Sea, Zhongsha Islands, seamount; 13°36.20'N, 113°33.74'E; depth 1515 m; 30 Mar. 2020; Collecting event: stn. SC025; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044298; IDSSE-EEB-SW0077 • 1 specimen; South China Sea, East of Zhongsha Islands, seamount; 16°22.11'N, 116°06.60'E; depth 1619 m; 09 Aug. 2020; Collecting event: stn. SC028; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044297, OL712213; IDSSE-EEB-SW0106. Northwest Pacific • 1 specimen; near Mariana Trench, Southeast of Guam Island, deepsea seamount, 11°57.20'N, 141°28.67'E; depth 1377 m; 03 Sep. 2019; Collecting event: stn. SC034; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044296, OL712212; IDSSE-EEB-SW0078.

Description. IDSSE-EEB-SW0078: disc diameter 10 mm, length of arms 200 mm (Fig. 12).

Disc. Disc flat, slightly raised above arms, swollen in center (Fig. 12A, B). Disc covered with smooth, small, closely spaced, and evenly rounded or polygonal granular ossicles, dense in disc center (seven or eight grains in 1 mm), but larger and polygonal at distal edge (six or seven grains in 1 mm) (Fig. 12C, D). Radial shields not meeting in center, but converging (Fig. 12C). Distal end of radial shields raised above disc and wider than proximal end (Fig. 12C). Genital slits narrow, vertical on ventral interradii (Fig. 12E). Jaws elongated, covered densely with granular ossicles (Fig. 12F). Flattened, pointed, and spearhead-shaped teeth and granular ossicles that resemble lateral oral papillae at apex of jaw (Fig. 12F). Ventral disc densely covered with granular and polygonal ossicles (seven or eight grains in 1 mm; Fig. 12F). Adoral shields connected to first ventral arm segment and concealed by granular ossicles but outline of shields visible. Oral shields not discernible and adoral shield spine densely covered by ossicles (Fig. 12F).

Arms. Arms at base wide, dorsally flattened, and swollen in first few free segments (Fig. 12G). Arms distalwards from middle part narrowing and more cylindrical (Fig. 10H). Swollen dorsal arm base and proximal end of arm covered with dense granular or polygonal ossicles similar to disc (five or seven grains in 1 mm), on middle segments with slightly separated granular ossicles (six or seven grains in 1 mm), and distally decreasing in size and separated (seven or eight grains in 1 mm) (Fig. 12G, H). Granular ossicles on lateral arm plates slightly separated, but continuing along arm. Ventral arm near arm base covered with granular ossicles similar to ventral disc (seven or eight grains in 1 mm), but less dense on middle half (five or six grains in 1 mm), and distally widely separated or naked (six or seven grains in 1 mm) (Fig. 12I, J). On first few arm segments, tentacle pore with extended tube (Fig. 12J). First tentacle pore without arm spine (Fig. 12F). First arm spine appears at second arm segment, and second arm spine at eighth segment. Inner arm spine cylindrical, one arm segment in length, with blunt thorny tip, and slightly club-shaped (Fig. 12K). Outer arm spine smaller in size, with smooth to thorny tip (Fig. 12K). Both arm spines equal in length at distal end of arm, and compound hook with three or four secondary teeth (Fig. 12L).

Color. In live specimen, reddish brown on dorsal disc and arm, light brown on ventral disc and arm (Fig. 12).

Ossicle morphology. Lateral arm plate with two arm spine articular structures, with large, separated muscle and nerve openings (Fig. 13A). Inner arm spine distalwards from proximal part of arm cylindrical, with terminal projection, and thorny surface (Fig. 13B). Outer arm spine cylindrical, with pointed tip with few thorns (Fig. 13C). Distally arm spine turns into compound hook with four secondary teeth (Fig. 13D). Arm and disc concealed by less dense, wider, and shorter granular ossicles (Fig. 13E). Vertebrae with streptospondylous articulation, dorsally a large longitudinal furrow, ventrally with deep median longitudinal groove with lateral ambulacral canals, no oral bridge, podial basins relatively small (Fig. 13F–J).

Distribution. 325–1800 m depth. New Zealand, Tasman Sea, Kermadec Islands, Bay of Plenty, Hawaii, Sagami Sea, the South China Sea, and Northwest Pacific seamount.

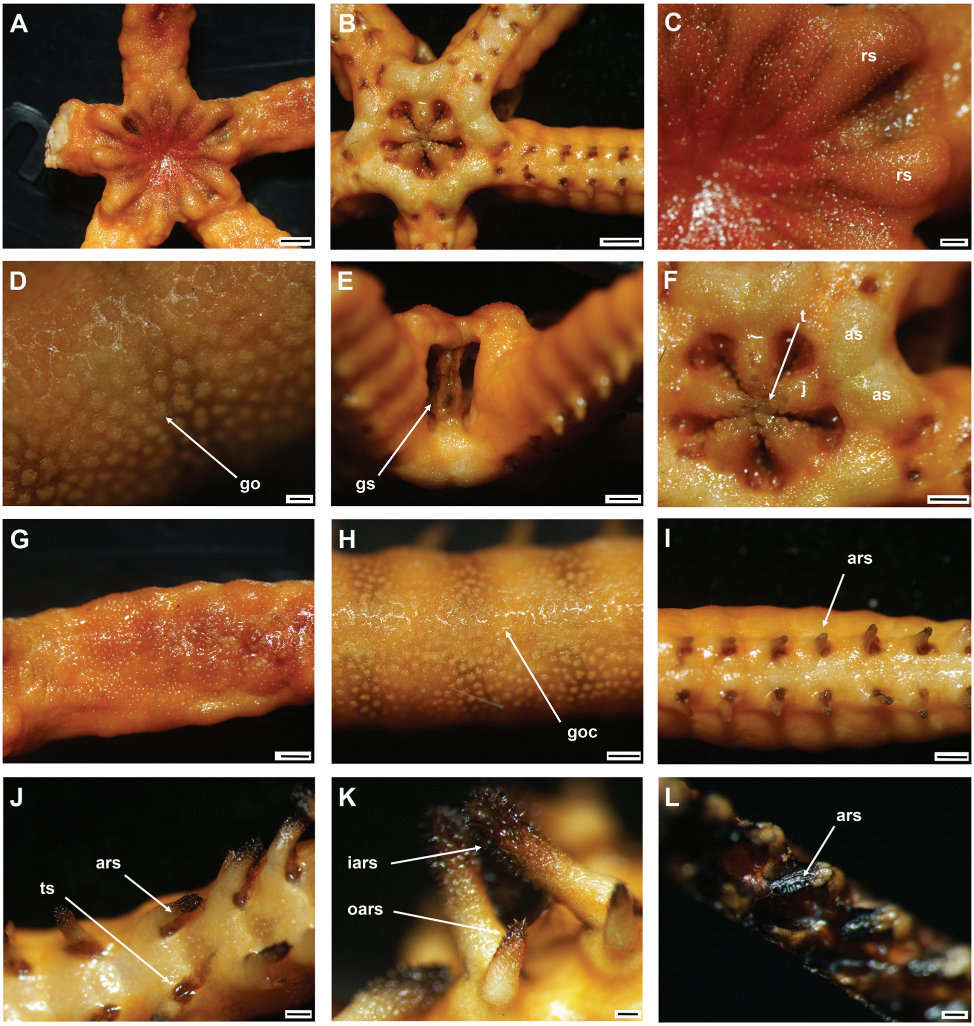

Figure 12. *Asteroschema tubiferum* Matsumoto, 1911 (IDSSE-EEB-SW0078) **A** dorsal view **B** ventral view **C** dorsal disc **D** skin on the arm **E** lateral disc **F** ventral disc **G** dorsal arm (proximal) **H** dorsal arm (middle) **I** ventral arm (proximal) **J** outer arm spine (proximal) **K** arm spines (middle) **L** arm spines (distal). Abbreviations: **as** adoral shield, **ars** arm spine, **go** granular ossicle, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A, B**); 1 mm (**E–G, I**); 500 µm (**C, H, J, K**); 200 µm (**D, L**).

Remarks. *Asteroschema tubiferum* was first described by Matsumoto (1911), then redescribed by Matsumoto (1917), Baker (1980), and McKnight (2000). These redescriptions are helpful to identify individual morphological character variation. Matsumoto (1911, 1917) mentioned that in *Asteroschema tubiferum* the first ten arm segments have an extended tube in the tentacle pore (a sheath around the tentacle) that is closely attached to the arm spine and this character is present in our

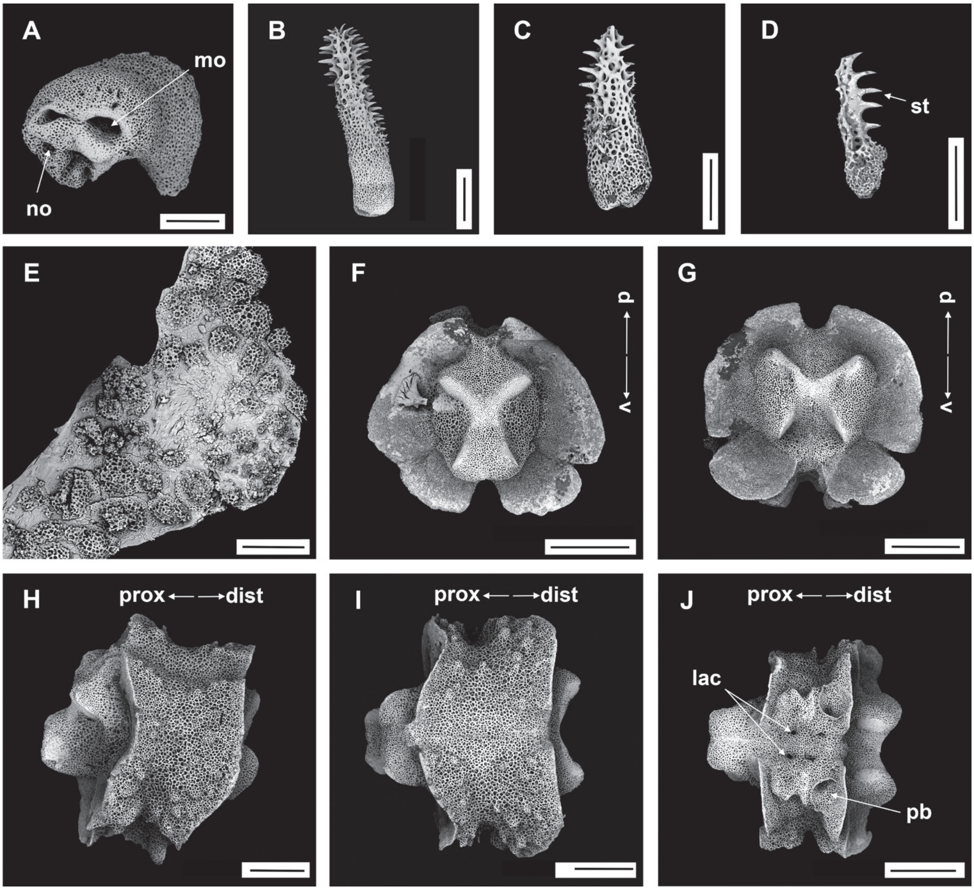

Figure 13. *Asteroschema tubiferum* Matsumoto, 1911 (IDSSE-EEB-SW0078) **A** lateral arm plate **B** outer arm spine (middle) **C** inner arm spine (middle) **D** arm spine (distal) **E** skin from dorsal arm base (granular ossicles) **F–J** vertebrae **F** proximal view **G** distal view **H** lateral view **I** dorsal view **J** ventral view. Abbreviations: **d** dorsal, **dist** distal, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 800 μm (**F, G, J**): 500 μm (**B, H, I**); 300 μm (**A, C–E**).

specimens. Previously, *A. tubiferum* had been recorded from both North and South Pacific Oceans at a wide distribution range. However, this is the first record from the South China Sea. The specimens from our collection concur with previous re-descriptions, but we noticed a few variations such as less densely packed ossicles on ventral and lateral arm. The *A. tubiferum* specimen from the South China Sea collection showed less dense granular ossicles on the ventral disc and arm. *Asteroschema tubiferum* strongly resembles *A. rubrum*, *A. laeve*, and *A. inoratum*, but the characters of the granulation pattern, tentacle scale on first few arm segments, shape of the arm and inner arm spine characters can be used to distinguish it from these species (Table 2).

Asteroschema salix Lyman, 1879

Figures 14, 15

Asteroschema salix Lyman, 1879: 66–67, fig. 17, figs 466–469; 1882: 277, fig. 22, figs 13–15; Baker 1980: 22; McKnight 2000: 21–22, fig. 6; Olbers et al. 2015: 85, fig. 1A, B; 2019: 51–52, fig. 24–25.

Material examined. China • 1 specimen; South China Sea, Zhongsha Islands, seamount; 15°36.64'N, 116°7.73'E; depth 1775 m; 19 Sep. 2020; Collecting event: stn. SC010; 'Shenhaiyongshi' msv leg; preserved in 95% ethanol; GenBank: OK044301, OL712214; IDSSE-EEB-SW0082.

Description. Disc diameter 10 mm, length of arms 145 mm (Fig. 12).

Disc. Disc flat, strongly raised above arms (Fig. 14A, B). Disc covered by thin skin with fine, small, rounded granular ossicles, dense in center (seven or eight grains in 1 mm), but separated at distal edge (six or seven grains in 1 mm) (Fig. 14C, D). Radial shields long, narrow, widely separated distally, convergent proximally, meeting in disc center (Fig. 14C). Genital slits narrow, and vertical on ventral interradii (Fig. 14E). Jaws elongated, covered with granular ossicles but near apex fewer granular ossicles (Fig. 14E). Flattened, spearhead-shaped teeth and granular ossicles that resemble lateral oral papillae at apex of jaw (Fig. 14E). Ventral disc covered with granular ossicles similar to dorsal disc (six or seven grains in 1 mm), slightly separated (Fig. 14E). Adoral shields large, connected to first ventral arm segment, concealed by thin skin with granular ossicles, but plate outline visible (Fig. 14E). Oral shields not discernible and adoral shield spine covered with ossicles (Fig. 14E).

Arms. Arms sub-cylindrical, not swollen, narrower and more cylindrical in distal half of arm (Fig. 14F, G). Dorsal and lateral arm base covered with granular ossicles similar to disc (six or seven grains in 1 mm), on middle segments granular coverage similar to arm base (six or seven grains in 1 mm), and distally decreasing in size and widely separated (grains six or eight in 1 mm) (Fig. 14F, G). On lateral arm plate, granular ossicles continue toward base of arm spine (Fig. 14G, J). Ventral surface of arm base covered with granular ossicles similar to ventral disc but less dense (six or seven grains in 1 mm), widely separated and decreasing in size to naked at middle to distal end of arm (Fig. 14H, I). First tentacle pore without arm spine (Fig. 14E). First arm spine appears at second arm segment, second arm spine at fifteenth or nineteenth segment. Inner arm spine cylindrical, one arm segment in length, flattened, with blunt, thorny tip, slightly club-shaped (Fig. 14J, K). Outer arm spine half as long as inner, with thorny tip (Fig. 14K). Both arm spines equal in length at distal end of arm, and turning into compound hook with 3–5 secondary teeth (Fig. 14L).

Color. In ethanol, pink but when dried, dull brown to whitish (Fig. 14).

Ossicle morphology. Lateral arm plate with two arm spine articular structures, with two large muscle and nerve openings (Fig. 15A). Inner arm spine at proximal and middle half of arm cylindrical, with thorny tip (Fig. 15B). Outer arm spine cylindrical with pointed tip (Fig. 15C). Distally arm spine turns into compound hook with

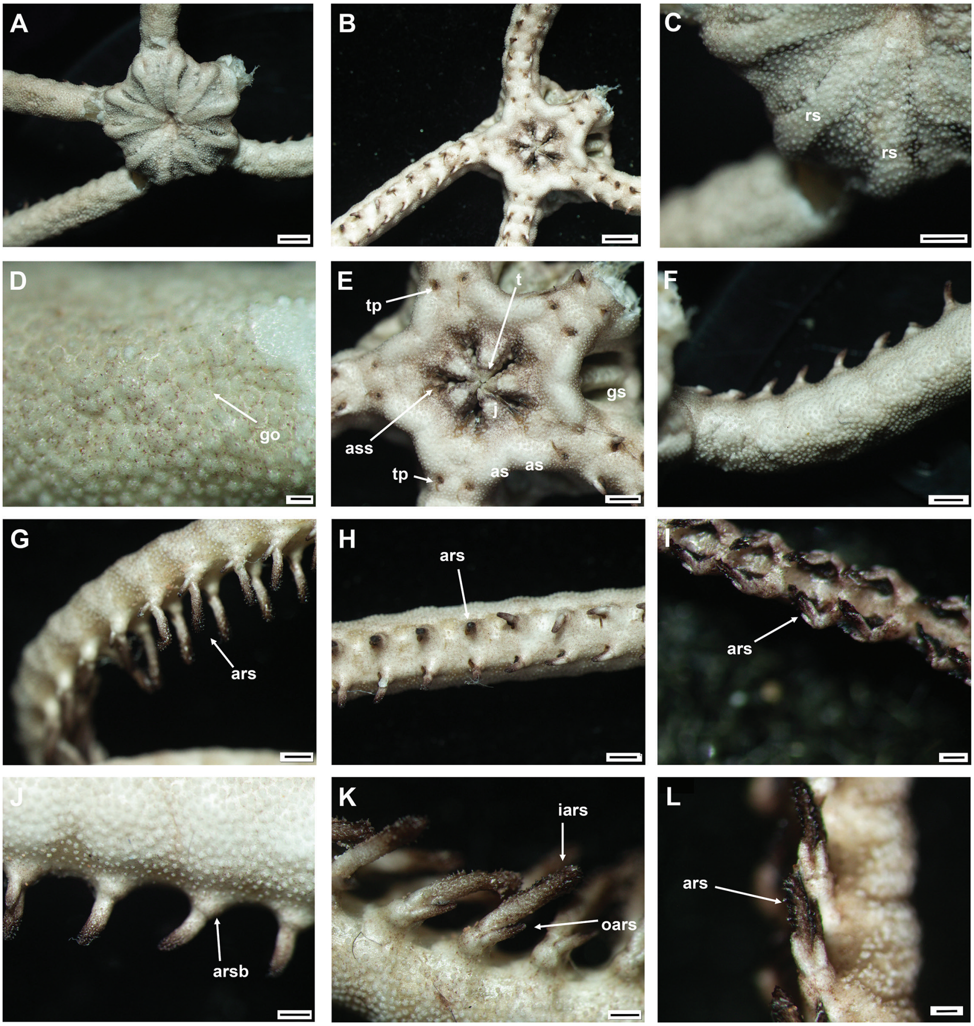

Figure 14. *Asteroschema salix* Lyman, 1879 (IDSSE-EEB-SW0082) **A** dorsal view **B** ventral view **C** dorsal disc **D** skin on the arm **E** ventral disc **F** dorsal arm (proximal) **G** lateral arm (middle) **H** ventral arm (proximal) **I** ventral arm (distal) **J** outer arm spine (proximal) **K** arm spines (middle) **L** arm spines (distal). Abbreviations: **as** adoral shield, **ass** adoral shield spine, **ars** arm spine, **go** granular ossicle, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **ots** oral tentacle scale, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A, B**); 1 mm (**C, E–H**); 500 μm (**J, K**); 200 μm (**D, I, L**).

secondary teeth (Fig. 15D). Arm and disc concealed by wider polygonal to rounded granular ossicles (Fig. 15E). Vertebrae with streptospondylous articulation, dorsally a median longitudinal furrow, ventrally with deep median longitudinal groove with lateral ambulacral canals, no oral bridge, podial basins relatively small (Fig. 15F–J).

Distribution. 341–1800 m depth. New Zealand, Tasman Sea, Kermadec Islands, Bay of Plenty, Solomon Island, Coral Sea, Timor Sea, South Africa (off Glenmore), the South China Sea.

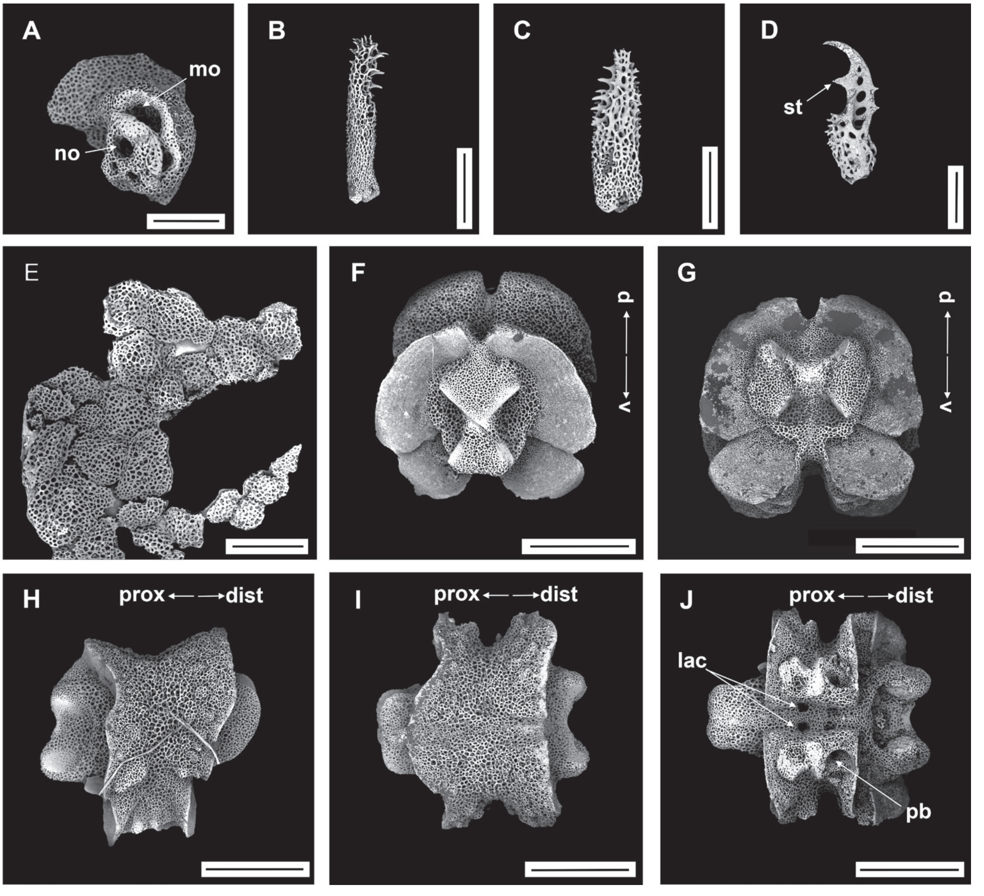

Figure 15. *Asteroschema salix* Lyman, 1879 (IDSSE-EEB-SW0082) **A** lateral arm plate **B** outer arm spine (middle) **C** inner arm spine (middle) **D** arm spine (distal) **E** skin from dorsal arm base (granular ossicles) **F–J** vertebrae **F** proximal view **G** distal view **H** lateral view **I** dorsal view **J** ventral view. Abbreviations: **d** dorsal, **dist** distal, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 800 µm (**B, F–J**); 300 µm (**A, C, E**); 100 µm (**D**).

Remarks. *Asteroschema salix* was first described by Lyman (1879), then redescribed by Lyman (1882), Baker (1980), McKnight (2000), and Olbers et al. (2015). These redescriptions are useful to understand individual morphological character variation of *A. salix*. Specimens from our collection concur with previous redescriptions, but we noticed some variation such as: slightly separated granular ossicles on the disc, fewer granular ossicles on the ventral arm surface, and slightly longer arms. However, most of these morphological variations vary within individual specimens according to previous descriptions (Baker 1980; McKnight 2000). *Asteroschema salix* strongly resembles *A. tubiferum*, *A. rubrum*, *A. laeve*, *A. inoratum*, *A. arenosum*, and *A. glaucum* but the characters of granulations and ossicle shape on the disc and arm, radial shield, and inner arm spine can be used to delimit *A. salix* from these species (Table 2). Previously, *A. salix* had been recorded from the South Pacific Ocean, and

South African waters at a wide distribution range. This is the first record from the South China Sea.

Asteroschema cf. *lissum* H. L. Clark, 1939

Figures 16, 17

Asteroschema lissum H. L. Clark, 1939: 37–39, figs 1–3.

Material examined. China • 2 specimens; South China Sea, Zhongsha Islands, seamount; 13°36.20'N, 113°33.74'E; depth 1515 m; 30 Mar. 2020; Collecting event: stn. SC025; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044300; IDSSE-EEB-SW0079, IDSSE-EEB-SW080. Northwest Pacific • 1 specimen; near Mariana Trench, Southeast of Guam Island, seamount, 12°6.67'N, 141°37.27'E; depth 1160 m; 03 Sep. 2019; Collecting event: stn. SC033; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044299, OL712207; IDSSE-EEB-SW0081.

Description. IDSSE-EEB-SW0079: disc diameter 11.5 mm, length of arms 165 mm, arm base width 3–3.5 mm (Fig. 16).

Disc. Disc flat, slightly raised above arms, swollen in center (Fig. 16A, B). Disc covered with smooth, small granular ossicles (Fig. 16C, D). Granular ossicles dense and small in disc center (six or eight grains in 1 mm), but slightly larger and separated at distal end of radial shield (five or six grains in 1 mm) (Fig. 16C). Radial shields wide, similar in size, curved, slightly raised above disc but not meeting in center (Fig. 16A, C). Radial shields clearly recognizable under thin skin embedded with ossicles (Fig. 16A, C). Genital slits narrow, concealed by polygonal granular ossicles, and vertical on ventral interradii (Fig. 16E). Jaws elongated, mostly naked without granular ossicles (Fig. 16F). Flattened, spearhead-shaped teeth, and six to seven granular ossicles that resemble lateral oral papillae at apex of jaw (Fig. 16F). Ventral disc covered with widely separated small granular ossicles (six or seven grains in 1 mm), but mostly covered by translucent thin skin (Fig. 16F). Adoral shields large, distal edge convex, concealed by thin skin with scattered small, smooth granular ossicles (Fig. 16F). Oral shields not discernible and oral tentacle pore naked without ossicles (Fig. 16F).

Arms. Arms slightly arched, circular, from middle to distal half narrower and more cylindrical (Fig. 16G). Dorsal arm base covered with granular ossicles similar to dorsal disc (six or eight grains in 1 mm), increasingly separated and decreasing in size along the middle segments of the arm (seven or eight grains in 1 mm), distally widely separated (five or six grains in 1 mm) (Fig. 16G, H). On lateral arm plates, granular ossicles widely separated but continuing to base of arm (Fig. 16H, K). Only one or three ventral arm segments near arm base covered with few granular ossicles similar to ventral disc (six or seven grains in 1 mm), then completely naked along the arm (Fig. 16I, J). First arm spine appears at second arm segment, second arm spine at ninth or thirteenth segment (Fig. 16I–K). Inner arm spine initially short, thick with thorny pointed tip, at middle arm cylindrical, taller, one and a half arm segment in length, with flattened thorny tip (Fig. 16J, K). Outer arm spine half as long as inner spine in middle region,

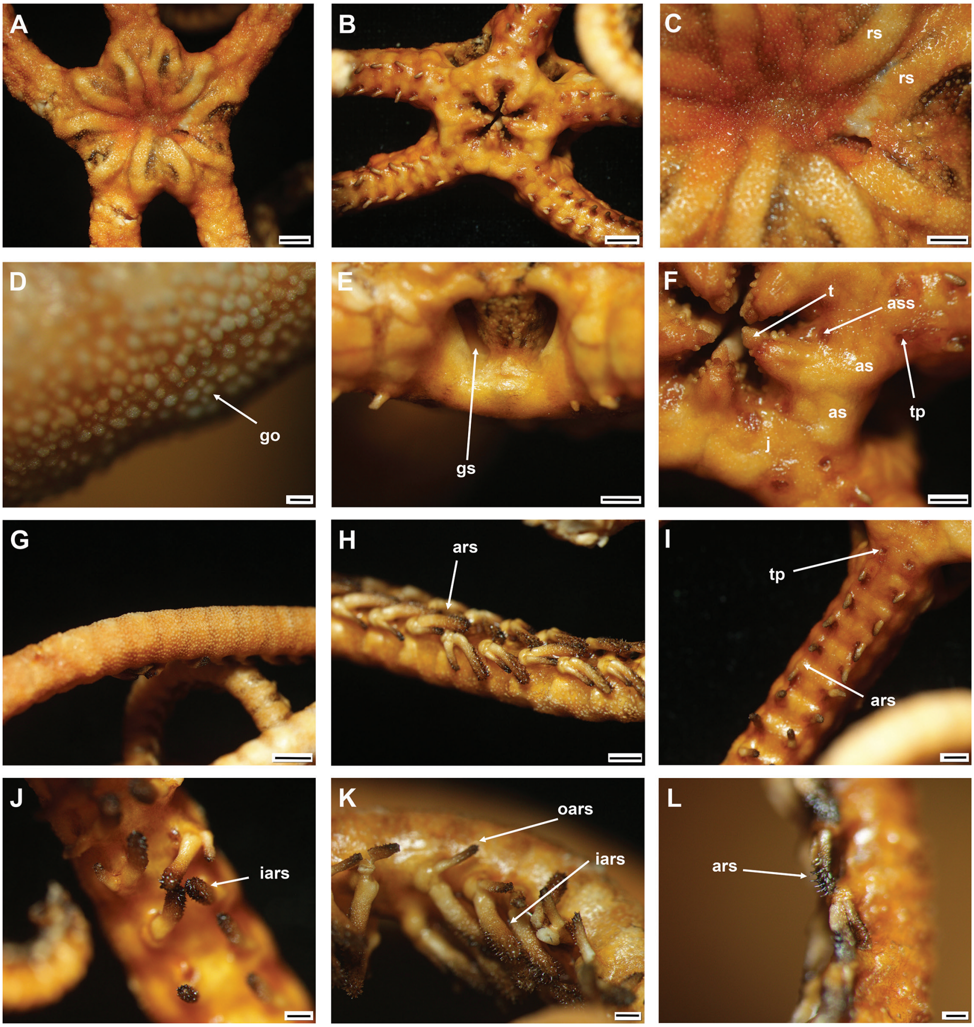

Figure 16. *Asteroschema* cf. *lissum* H. L. Clark, 1939 (IDSSE-EEB-SW0079) **A** dorsal view **B** ventral view **C** dorsal disc **D** skin on the disc **E** lateral disc **F** ventral disc **G** dorsal arm (middle) **H** lateral arm (middle) **I** ventral arm (proximal) **J** outer arm spine (proximal) **K** arm spines (middle) **L** arm spines (distal). Abbreviations: **as** adoral shield, **ass** adoral shield spine, **ars** arm spine, **go** granular ossicle, **gs** genital slit, **iars** inner arm spine, **j** jaw, **oars** outer arm spine, **ots** oral tentacle scale, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 2 mm (**A, B, G**); 1 mm (**C, E, F, H, I**); 500 μm (**J, K**); 200 μm (**D, L**).

with smooth to thorny tip (Fig. 16K). Both arm spines equal in length at distal end of arm, and compound hook with five or six secondary teeth (Fig. 16L).

Color. In live specimen, reddish brown but radial shields slightly lighter in color due to thin skin (Fig. 16).

Ossicle morphology. Lateral arm plate with two arm spine articular structures, with large muscle and nerve openings (Fig. 17A, B). Inner arm spine from proximal and middle half of arm cylindrical, with thorny tip (Fig. 17C). Distally, arm spine turns

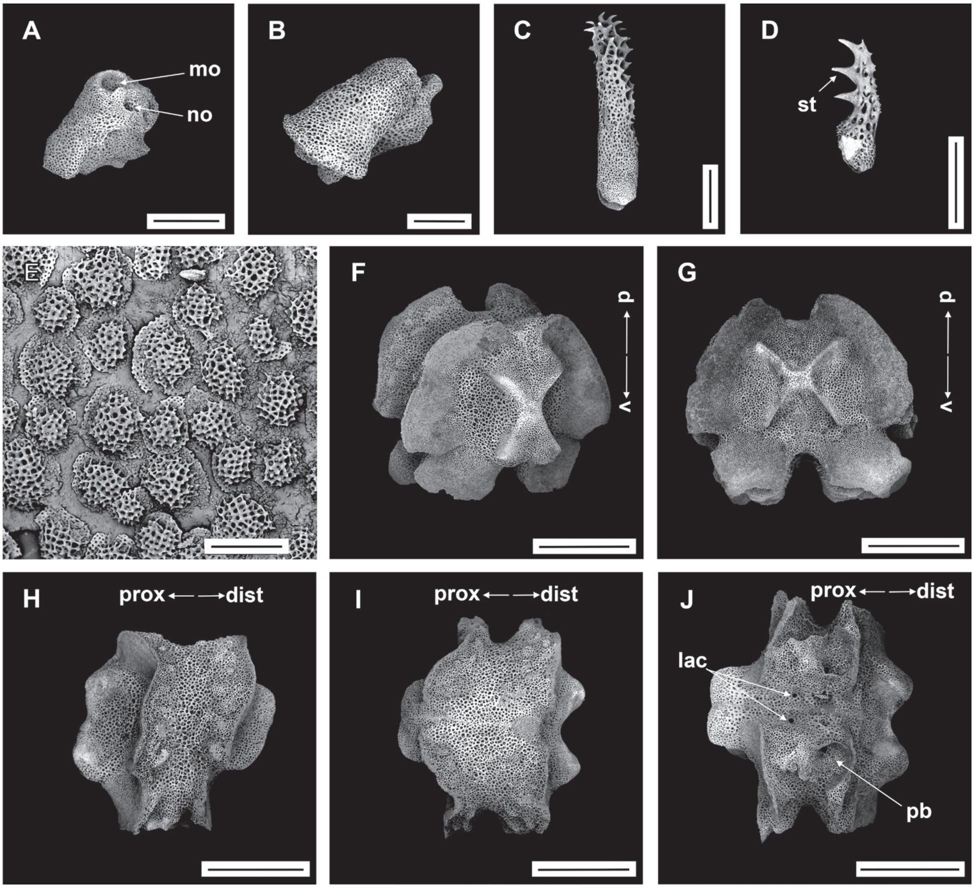

Figure 17. *Asteroschema* cf. *lissum* H. L. Clark, 1939 (IDSSE-EEB-SW0079) **A, B** lateral arm plate (external, internal) **C** outer arm spine (middle) **D** arm spine (distal) **E** skin from dorsal arm base (granular ossicles) **F–J** vertebrae **F** proximal view **G** distal view **H** lateral view **I** dorsal view **J** ventral view. Abbreviations: **d** dorsal, **dist** distal, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pb** podial basin, **prox** proximal, **st** secondary teeth, **v** ventral. Scale bars: 800 μm (**F–J**); 500 μm (**A, C**); 300 μm (**B, D**); 200 μm (**E**).

into compound hook with secondary teeth (Fig. 17D). Arm and disc concealed by less dense, wider, and short granular ossicles (Fig. 17E). Vertebrae with streptospondylous articulation, dorsally a median longitudinal furrow, ventrally with deep median longitudinal groove with lateral ambulacral canals, podial basins relatively small (Fig. 17F–J).

Distribution. 797–1515 m depth. Maldives, South China Sea, Northwest Pacific.

Remarks. *Asteroschema lissum* was first described by H. L. Clark (1939), with type locality Maldives waters in the Indian Ocean. This is the first redescription after the original description. The specimens from our collection were close to H. L. Clark's description but we noticed some differences, such as: characters of radial shields, and granular ossicles at ventral disc and base of arm. We hesitate to fully associate our specimens with *Asteroschema lissum* or propose a new species, due to uncertainty of these morphological variations. Some of these variations may be affected by size, maturity, and environment (holotype disc diameter 7.5 mm). *Asteroschema lissum* strongly resembles *A. hemigymnum*, *A. intectum*, and *A. sublaeve* by having similar granular density, and almost naked ventral disc and arms but differs in characters of the radial shields, start of second arm spine, granulation pattern on the disc and arm (Table 2). This is the first record of *A. lissum* from the South China Sea and the North Pacific Ocean, if it is indeed this species.

Genus *Asterostegus* Mortensen, 1933

Asterostegus maini McKnight, 2003
Figures 18, 19

Asterostegus maini McKnight, 2003: 386–389, figs 1, 2.
Astroceras elegans McKnight, 1989: 25 (non *Astroceras elegans* Bell, 1917).

Material examined. China • 2 specimens; South China Sea, near Xisha Islands archipelago, seamount; 16°47.79'N, 113°15.04'E; depth 602 m; 31 Mar. 2020; Collecting event: stn. SC009; 'Shenhaiyongshi' msv leg; preserved in -80 °C; GenBank: OK044303; IDSSE-EEB-SW0075; IDSSE-EEB-SW0076.

Description. IDSSE-EEB-SW0076: disc diameter 32.2 mm, length of arms 240–250 mm, height of arm base 9.8 mm (Fig. 18A–M).

Disc. Disc circular and slightly inflated radially, with sunken interradial margins (Fig. 16A). Radial shields elongated, narrow, raised above the disc, extending nearly toward the disc center (Fig. 18B, C). Distal half of radial shield periphery covered by 10–12 (0.44 to 0.75 mm in width) large, club-shaped granules (Fig. 18C). Most of these granules cluster on distal end of radial shield (Fig. 18C). Entire disc, including radial shields, covered by thick skin (Fig. 18A–C). Adoral shields with slightly ovoid outline (Fig. 18E, F). Teeth spearhead-shaped, accompanied by granular domed lateral oral papillae but not visible in wet specimen (Fig. 18D–F). Proximally, adoral shields separated by triangular plate (Fig. 18F) Oral shields absent, and single or double row of two to six rounded, square, or irregular oral interradial plates beyond adoral shields (Fig. 18E, F). One median plate located between distal end of adoral shields, and slightly proximal to rest of oral interradial plates (Fig. 18E, F). Lateral interradial surface of disc slightly vertical and covered by thick naked skin, two conspicuous genital slits inside a large opening (Fig. 18G).

Arms. Arms simple, strong, and not branching (Fig. 18A). Cross section of arm base slightly rectangular (7.2 mm in width and 8.5 mm high), but distal half of arm more cylindrical and narrower (Fig. 18H–J). Proximal to middle region of dorsal arm slightly flattened, ventral surface slightly arched, and lateral surface vertical (Fig. 18J, K). Whole arm concealed by thick skin (Fig. 18H–K). Lateral arm plate on proximal half of arms bears three to five club-shaped granules (0.4–0.6 mm in width) (Fig. 18H), decreasing in size and number along arm and vanishing on distal half of arm (Fig. 18I). Ventral arm covered by naked skin (Fig. 18K). First one to two tentacle pores lack arm spines; second or third pore with two or three arm spines, similar in size

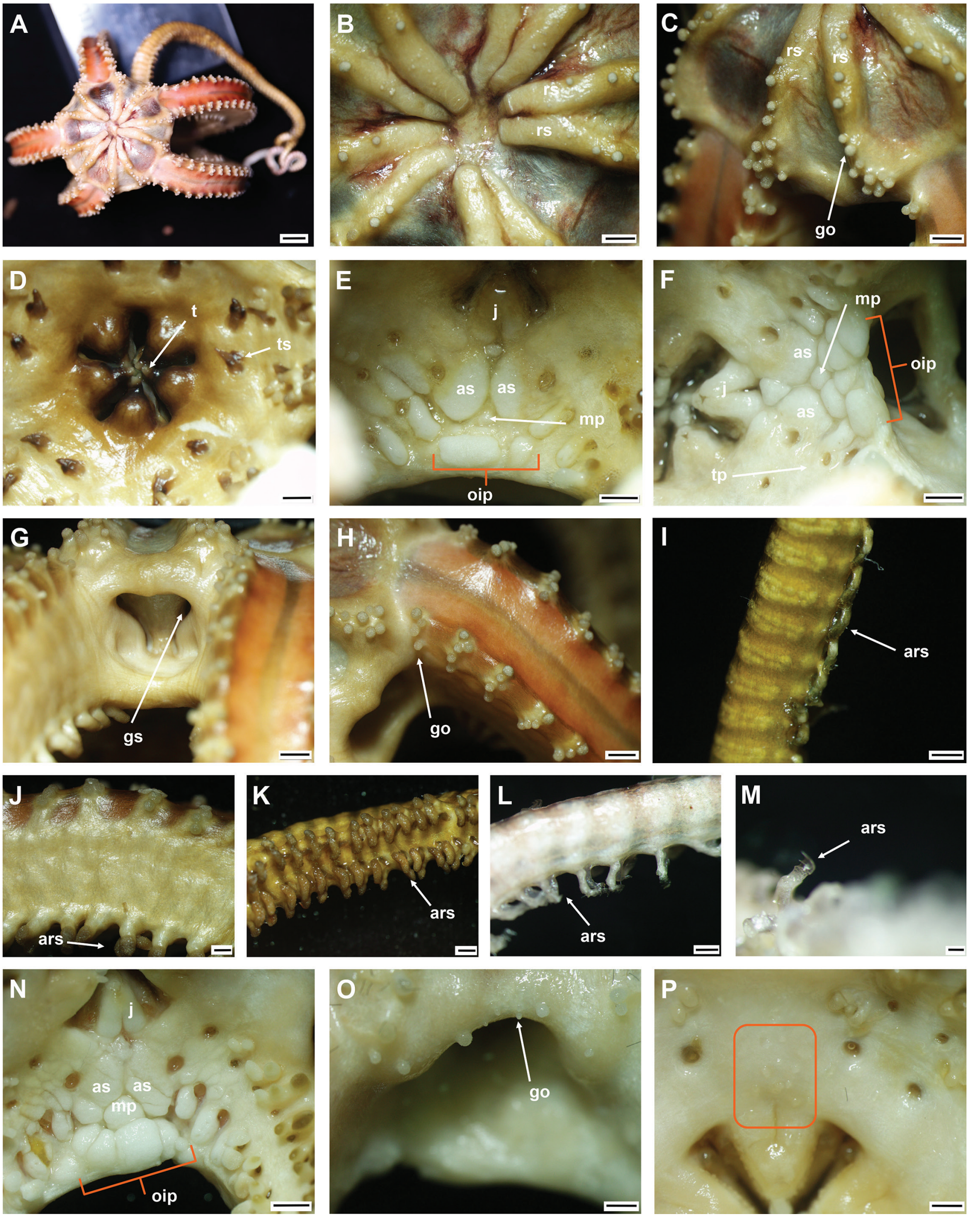

Figure 18. *Asterostegus maini* McKnight, 2003 (**A–M** IDSSE-EEB-SW0076 **N–P** IDSSE-EEB-SW0075) **A** dorsal view **B** center of dorsal disc **C** dorsal disc (distal end of radial shields) **D** ventral disc **E, F** oral frame **G** lateral disc **H** dorsal arm (proximal) **I** dorsal arm (distal) **J** lateral arm (proximal) **K** ventral arm (middle) **L, M** arm spines (distal) **N** oral frame **O** periphery of the disc **P** oral frame (small transparent ossicles). Abbreviations: **as** adoral shield, **ars** arm spine, **go** granular ossicle, **gs** genital slit, **j** jaw, **mp** median plate, **oip** oral interradial plate, **rs** radial shield, **t** teeth, **tp** tentacle pore, **ts** tentacle scale. Scale bars: 6 mm (**A**); 2 mm (**B–H, N**); 1 mm (**I–K, O, P**); 500 μm (**L**); 200 μm (**M**).

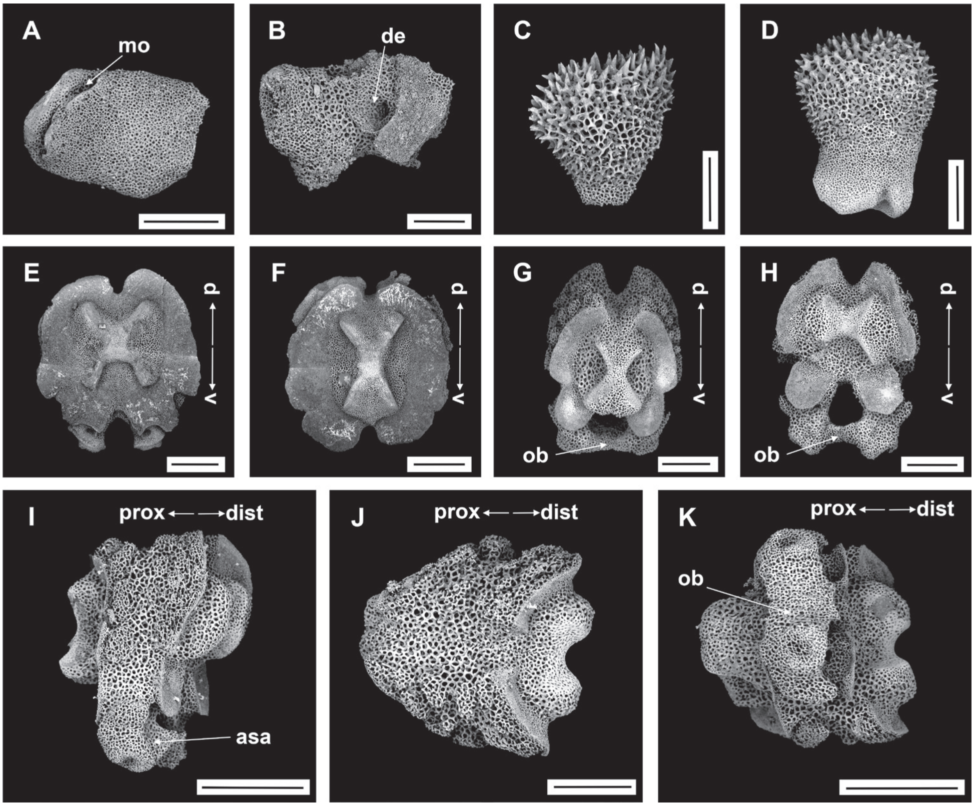

Figure 19. *Asterostegus maini* McKnight, 2003 (IDSSE-EEB-SW0076) **A, B** lateral arm plate (external, internal) **C, D** arm spine (middle) **E, F** vertebrae (middle) **E** proximal view **F** distal view **G–K** vertebrae (distal) **G** proximal view **H** distal view **I** lateral view **J** dorsal view **K** ventral view. Abbreviations: **asa** arm spine articular structure, **d** dorsal, **de** depression, **dist** distal, **mo** muscle opening, **ob** oral bridge, **prox** proximal, **v** ventral. Scale bars: 800 µm (**E, F**); 500 µm (**A, C, D, I, K**); 300 µm (**B, G, H, J**).

(Fig. 18D). At proximal end of arms, arm spines short, thick, ovoid with more or less rounded tip with rough surface, at middle of arms club-shaped, transversely flattened (Fig. 18J, K). Arm spines turn into hook with two to three secondary teeth at distal end of arms (Fig. 18L, M).

Color. In live specimen, dorsal disc interradially dark brown but radial shields light brown. Ventral and lateral disc whitish brown, dorsal surface of proximal and middle regions of arms bright brown/red. Lateral and ventral surface of arms whitish brown, granules creamy white (Fig. 18).

Ossicle morphology. Lateral arm plate with two arm spine articular structures, middle half of arm with large and wide, separated muscle and nerve openings, depression on inner side (Fig. 19A, B). Arm spines large, short, flattened, and club-shaped with thorny surface (Fig. 19C, D). Vertebrae with streptospondylous articulation. Vertebrae on proximal to middle half of the arm large, flat with deep ventral groove, no oral bridge (Fig. 19E, F). Vertebrae on distal half of arm slightly longer, dorsally large median longitudinal furrow, and deep median longitudinal groove on ventral side, with oral bridge (Fig. 19G, H).

Distribution. 417–602 m in depth. New Zealand (Cook Island), South China Sea.

Remarks. *Asterostegus maini* was first described by McKnight (2003), with type locality Cook Islands, South Pacific Ocean, and Okanishi and Fujita (2014) redescribed it. However, this is the first record of *Asterostegus maini* since the holotype. Here we recorded two specimens from the South China Sea (disc diameter 26 mm and 32.2 mm) and both are larger than the holotype (disc diameter 22 mm). Currently, three species belong to the genus *Asterostegus*: *A. maini* McKnight, 2003, *A. tuberculatus* Mortensen, 1933, and *A. sabineae* Okanishi & Fujita, 2014. *Asterostegus tuberculatus* differs from *A. maini* in granules being scattered across the whole disc including the radial shield, and only two to three stump-like granules on the dorsolateral arm plate (McKnight 2003; Okanishi and Fujita 2014). *Asterostegus sabineae* differs from *A. maini* in large stump-like granules on the radial shield, only one oral interradial plate, and one or two large stump-like granules on the dorsolateral arm plate (Okanishi and Fujita 2014). The number of oral interradial plates and their arrangement are highly variable within and between individuals (Fig. 18E, F, N). Previous studies on the holotype showed only one row with two to five interradial plates (McKnight 2003; Okanishi and Fujita 2014). However, in our specimens, these are arranged in one or two rows with two to seven interradial plates in total (Fig. 18E, F, N). Therefore, one of the key morphological characters in the genus *Asterostegus*, the arrangement of oral interradial plates has to be modified. One specimen from the present study (IDSSE-EEB-SW0075, 26 mm disc diameter) showed some morphological variations, such as: small granules on the periphery of the disc and on few small areas on the ventral disc (Fig. 18O, P). These granules are extremely small compared to those on the radial shields and arms. In the specimens from the present study, first arm spines started from second or third arm segment, but in the holotype, it started from the fourth arm segment. However, except for these small morphological variations, both specimens were similar to the holotype description.

Family Gorgonocephalidae Ljungman, 1867
Subfamily Gorgonocephalinae Döderlein, 1911
Genus *Astrodendrum* Döderlein, 1911

Astrodendrum cf. *sagaminum* (Döderlein, 1902)
Figures 20, 21

Astrodendrum sagaminum Döderlein, 1902: 321–322; 1911: 38–39, figs 2, 3–5, 7, 8; 1927: 32, 92; H.L. Clark 1911: 292–293; A. H. Clark 1916a: 185; Liao 2004: 109–111, fig. 52.

Material examined. China • 1 specimen; South China Sea, East side from Zhongsha Islands, seamount; 16°22.11'N, 116°06.60'E; depth 1619 m; 09 Aug. 2020; Collecting event: stn. SC028; ‘Shenhaiyongshi’ msv leg; preserved in -80 °C; GenBank: OK044304; IDSSE-EEB-SW0104.

Description. Disc diameter 62 mm (Fig. 20A, B).

Disc. Dorsal disc slightly inflated, swollen in the center (Fig. 20A, B). Radial shields elongated, tapered at proximal end, extending to center of disc (Fig. 20C, D). Entire disc covered by skin with conical ossicles of various size (0.4–0.7 mm high) and widely separated and scattered (Fig. 20C–E). Genital slits conspicuous, interradial margin covered by two rows of higher than wide conical ossicles (Fig. 20F, G). Ventral disc almost naked, but micro-granular ossicles visible on oral region (Fig. 18H). Oral area covered by smooth skin with few scattered small granular ossicles, exposing adoral and oral shield outlines (Fig. 20H). Oral plates flat, polygonal, and slightly in contact with adoral shields (Fig. 20H). Adoral shields short, square. Oral papillae and teeth spiniform (Fig. 20H), several vertical rows of teeth on dental plate (possibly tooth papillae at ventral edge).

Arms. Arms branched at least eight to nine times, flexible dorso-ventrally, flat ventrally, arched dorsally (Fig. 20I–N). Ventral arm surface covered by smooth skin; proximal half with widely scattered small, flat, polygonal granular ossicles (Fig. 20I–K). Dorsal arm surface covered by polygonal or domed plates and between these pedicellarial bands (Fig. 20L–O) that appear after second arm fork, covering whole lateral to dorsal area of arm, creating annulated appearance (Fig. 20L). First arm segment lacks spines, next four to six with two arm spines, thereafter two or three arm spines per segment (Fig. 20I–K). Ventral arm spines similar in size, smaller, unevenly pointed, distally turning into hooks with 2–3 secondary teeth (Fig. 20K, P, Q).

Color. In live specimen, whole specimen brown, but radial shields, oral regions, and ventral arms lighter than disc (Fig. 20).

Ossicle morphology. On middle half of arm, lateral arm plates with perforations on ventral side, large muscle opening and small nerve opening (Fig. 21A). Pedicellarial bands formed by approximately 12 articulating tubercles at curved distal end of baseplate and these articulations have a single foramen per tubercle for pedicellariae with one secondary tooth (Fig. 21B, C). Ventral arm spines on distal end of arm transformed into hook with two or three secondary teeth (Fig. 21D). Pedicellariae differ from ventral arm spine by having smooth apophysis (Fig. 21C, D). Vertebrae with streptospondylous articulation with smooth lateral furrows and paired openings in lateral side of vertebrae for lateral ambulacral canals, no oral bridge (Fig. 21F–N).

Distribution. 90–1300 m depth. South China Sea, Japan, East China Sea, Sri Lanka.

Remarks. The specimen is similar to the holotype description by Döderlein (1902), and the redescriptions of Döderlein (1911, 1927), Liao (2004) and Okanishi and Fujita (2018), but showed some morphological variations especially on the disc (Fig. 20). Therefore, we hesitate to fully associate our specimen with *Astrodendrum sagaminum*. All descriptions mentioned granules on both dorsal and ventral disc, but in the present specimen, the dorsal disc is covered with widely separated conical stump-like granules and the ventral disc is covered with widely scattered micro-polygonal ossicle plates in naked skin. However, Baker (1980) mentioned that the granular pattern on the disc

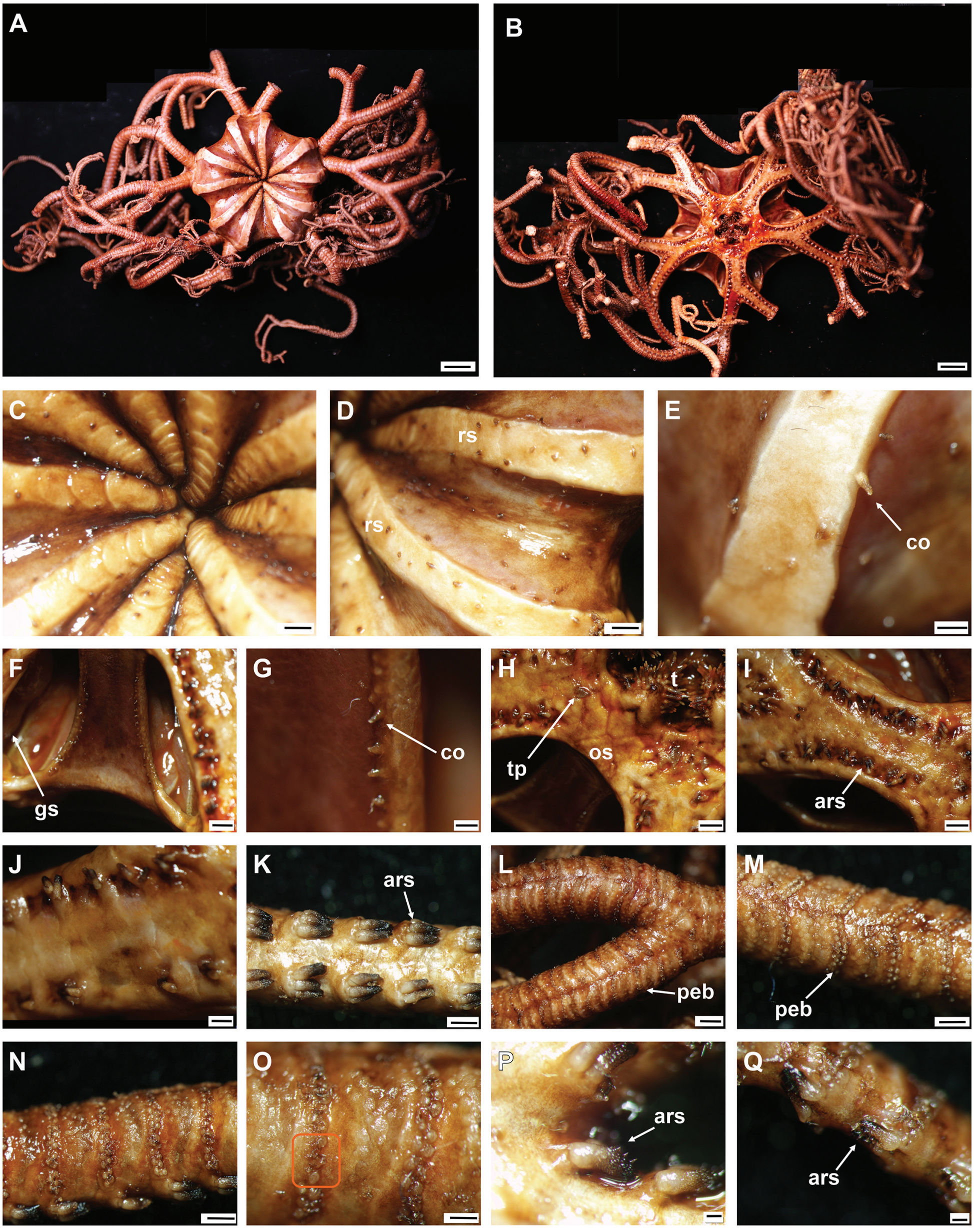

Figure 20. *Astrodendrum* cf. *sagaminum* (Döderlein, 1902) (IDSSE-EEB-SW0104) **A** dorsal view **B** ventral view **C** dorsal disc (center) **D** dorsal disc (distal edge) **E** radial shield **F, G** ventral disc **H** oral frame **I, J** ventral view of arm base **K** ventral view of after second arm branch **L, M** dorsal view of second arm branch **N** lateral view of arm (middle) **O** lateral view of arm (pedicellariae with baseplate) **P, Q** variations of arm spine on distal end of the arm. Abbreviations: **ars** arm spine, **co** conical ossicles **gs** genital slit, **os** oral shield, **peb** = pedicellarial band, **rs** radial shield, **t** teeth, **tp** tentacle pore. Scale bars: 16 mm (**A, B**); 2 mm (**C, D, F, L**); 1 mm (**E, H–K, M, N**); 500 µm (**G, O**); 200 µm (**P, Q**).

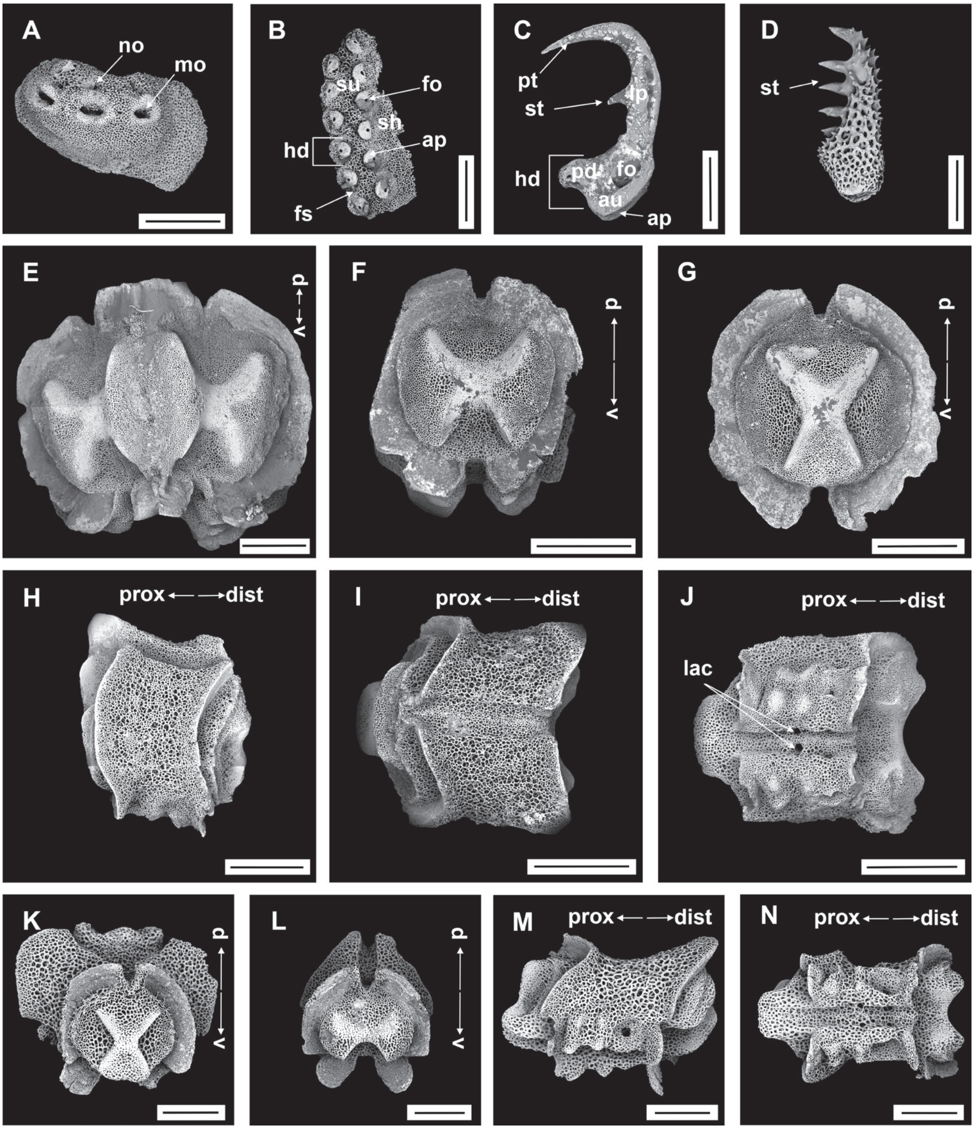

Figure 21. *Astrodendrum* cf. *sagaminum* (Döderlein, 1902) (IDSSE-EEB-SW0104) **A** lateral arm plate (middle) **B** plan view of baseplate **C** pedicellariae **D** arm spine on distal end **E–J** vertebrae on middle half of arm **E** proximal view of branch vertebrae **F** proximal view **G** distal view **H** lateral view **I** dorsal view **J** ventral view **K–N** vertebrae on distal end of arm **K** distal view **L** proximal view **M** lateral view **N** ventral view. Abbreviations: **ap** articular pad of the base, **au** auricle, **d** dorsal, **dist** distal, **fo** foramina of the base, **fs** fossa between adjacent tubercles, **hd** head of the apophysis, **lac** lateral ambulacral canals, **mo** muscle opening, **no** nerve opening, **pd** pedicel of the apophysis, **prox** proximal, **pt** primary tooth of the blade, **sh** sheath of the baseplate, **su** sulcus of tubercle head, **v** ventral. Scale bars: 800 µm (**E–J**); 500 µm (**A, B**); 300 µm (**K–N**); 200 µm (**D**); 80 µm (**C**).

was not a suitable morphological feature to delimit species in the genus *Gorgonocephalus*. This is the first record of *Astrodendrum sagaminum* from the South China Sea, if this is indeed that species.

Discussion

The molecular phylogenetic trees of these species of Gorgonocephalidae and Euryalidae were in agreement with previous studies (Okanishi and Fujita 2013; Christodoulou et al. 2019; O'Hara et al. 2019). Previous molecular studies indicated that intraspecific genetic distance ranges approximately from 0.5% to 6.4%, with a mean of 2.2%, but species from the family Euryalidae usually showed less than 2% mean genetic distance (Okanishi et al. 2011, 2018; Okanishi and Fujita 2013; Boissin et al. 2017). In this study, we focused on the genera *Asteroschema*, *Asterostegus*, and *Astrodendrum*. In addition, we included species from the genus *Ophiocreas* due to their similar morphology to *Asteroschema* species. The species in the genus *Asteroschema* were difficult to analyze only morphologically due to great similarity in most morphological characters. Previous studies divided *Asteroschema* into three groups according to ossicle shape on the disc and arms, but still many species within these groups are hard to identify. In this study, we successfully managed to obtain the COI and 16S sequences from only one of the proposed new species, *Asteroschema shenhaiyongshii* sp. nov., which suggests a close relationship to *A. bidwillae* according to genetic distance (2.56%), but *A. shenhaiyongshii* sp. nov. is pentamerous and shows no signs of fission. It also has dense granular ossicle coverage on the ventral disc and ventral arm surface (Suppl. material 2: Table S2; Fig. 6). Therefore, we consider these two as sibling species. According to the present study, we suggest a species complex within *Asteroschema tubiferum* due to morphological variations between specimens from the South China Sea and New Zealand. However, we found significantly low genetic distances between the specimens identified as *A.* cf. *lissum*, *A. tubiferum*, *A. rubrum*, and *A. salix* (2.79±0.66% SE) (Suppl. material 2: Table S2). Therefore, understanding key morphological differences and intraspecific genetic distance range are important to delimit *Asteroschema* species. *Asteroschema* cf. *lissum* was recognized here as intermediate species between *A. salix* and *A. tubiferum* due to genetic distance values between these species. In the ML tree of the family Euryalidae, all *Ophiocreas* species cluster with *Asteroschema oligactes*, *A. migrator*, *A. edmondsoni*, *A. ajax*, and *A. horridum.* All these *Asteroschema* species have conical ossicles or annular bands on the arms. These two clades may correspond to one of these genera each or one of them may belong to both genera (making them synonymous) and the other to a putative new genus, but since the type species of both genera have not been sequenced yet, it is impossible to decide. Thus, the present study concurs with previous molecular studies in the hypothesis that *Asteroschema* may be polyphyletic, but may instead be paraphyletic with the genus *Ophiocreas*, and the present morphological differentiation between these two genera can be questioned (Okanishi and Fujita 2013; Christodoulou et al. 2019; O'Hara et al. 2019). A comprehensive morphological and molecular taxonomic revision, including examination of type specimens of all *Asteroschema* and *Ophiocreas* species is needed to understand the key morphological characters and genetic differences. We tentatively place our new species in *Asteroschema*, but acknowledge that they may later be found to belong in *Ophiocreas*.

The genus *Asterostegus* includes only three species, and is closely related to *Astroceras*, but a previous phylogenetic analysis recognized it as monophyletic and belonging in the family Euryalidae (Okanishi and Fujita 2013). The interspecific genetic distance (3.09±0.75% SE) within the genus *Asterostegus* was low and similar to other Euryalidae species (Suppl. material 2: Table S2). The genetic distance of the genus *Gorgonocephalus* was significantly lower than in *Asteroschema*. The molecular phylogenetic analysis of *Astrodendrum* and *Gorgonocephalus* showed two main clades, and previous studies showed that *Gorgonocephalus* may be polyphyletic (Okanishi and Fujita 2013; Christodoulou et al. 2019; O'Hara et al. 2019). In the present study, *Astrodendrum* cf. *sagaminum* clustered with *Gorgonocephalus sundanus* and *G. pustulatum*. The type species *Gorgonocephalus caputmedusae* (Linnaeus, 1758) clustered with *G. chilensis*, *G. eucnemis*, *G. arcticus*, and *G. tuberosus* (Fig. 3, Suppl. material 3: Table S3). We suggest that *A. sagaminum* should belong in the genus *Gorgonocephalus*, or alternatively, *Gorgonocephalus* could be split into two genera, but a more thorough study with more genes and more specimens should be performed, before this step is taken.

Most of the species from the present study were collected from deep water in the South China Sea. Previous studies from the South China Sea recorded only few *Asteroschema* species, but found no representatives of the genera *Astrodendrum* and *Asterostegus*. According to the present study, the ophiuroid diversity of the South China Sea may be higher than previously known and future expeditions to the South China Sea deep-sea seamounts may discover even more species. The present study suggests a wider distribution of Euryalida species from the South-Pacific to the North-Pacific regions than previously expected.

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Supplementary material 1

Table S1

Authors: Hasitha Nethupul, Sabine Stöhr, Haibin Zhang

Data type: Primers (text)

Explanation note: COI and 16S primers and PCR cycles used in this study (Hoareau and Boissin 2010; Okanishi and Fujita 2013).

Link: https://doi.org/10.3897/zookeys.1090.76292.suppl1

Supplementary material 2

Table S2

Authors: Hasitha Nethupul, Sabine Stöhr, Haibin Zhang

Data type: Genetic distance % (COI)

Explanation note: Genera *Asteroschema*, *Ophiocreas* and *Asterostegus*, pairwise distance values based on 592 bp mitochondrial COI sequences, calculated using the Kimura 2-parameter method with 1,000 bootstrap replicates (Value in blue color represent Standard Error). Abbreviations: AUS Australia, CAN Canada, CS Caribbean Sea, JAP Japan, MAD Madagascar, NCA New Caledonia, NWP Northwest Pacific, NZ New Zealand, PAO Pacific Ocean, SCS South China Sea.

Link: https://doi.org/10.3897/zookeys.1090.76292.suppl2

Supplementary material 3

Table S3

Authors: Hasitha Nethupul, Sabine Stöhr, Haibin Zhang

Data type: Genetic distance % (COI)

Explanation note: Genera *Gorgonocephalus* and *Astrodendrum*, pairwise distance values based on 730 bp mitochondrial COI sequences, calculated using the Kimura 2-parameter method with 1,000 bootstrap replicates (Value in blue color represent Standard Error). Abbreviations: AN Antarctic Sea, AUS Australia, CAN Canada, JAP Japan, NZ New Zealand, SCS South China Sea, SWE Sweden.

Link: https://doi.org/10.3897/zookeys.1090.76292.suppl3