Taxonomic studies on Hydrophilidae and other coleoptera residing in temporally limited heterotrophic systems

（腐敗・分解有機物環境に生息する甲虫類の分類学的研究）

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北海道大学　大学院農学院　環境資源学専攻　博士後期課程

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Abstract

Heterotrophic habitats, including decaying vegetation, dung, and carrion, act as nutritionally rich but temporally limited habitats in which various organisms function in the process of decomposition. The breakdown of detritus is necessary for mass removal and nutrient cycling and different species of insects, fungi, etc. play special roles in this process. Terrestrial hydrophilid beetles tend to specialize in such habitats and play roles in breaking up and consuming detritus and predating on fly larvae and other soft bodied invertebrates. Since a single microhabitat can contain many species of these rather small beetles, their identification can be difficult and many groups require taxonomic revision.

This thesis consists of taxonomic studies on several groups of hydrophilid beetles (Coleoptera: family Hydrophilidae) living in decaying organic material with an additional section on other beetles living in decaying material on beaches. The members of the genus *Sphaeridium* occurring in Europe and Asia are revised with descriptions of two previously undescribed species, *Sphaeridium* sp.1 and *S.* sp.2, one new synonymy of *S. reticulatum* into *S. severini*, sixteen new country and ten new regional records (*S. bipustulatum* from China, India, and Pakistan; *S. dimidiatum* from Cambodia and Laos and Halmahera, Sulawesi, Sumbawa, Ternate, and West Timur in Indonesia; *S. discolor* from Malaysia and Nepal and Kyushu, Japan and Queensland, Australia; *S. marginatum* from China; *S. quinquemaculatum* from Bhutan, Guam, and Laos; *S. seriatum* from Japan; *S. severini* from Thailand and Quangxi, China and Flores and Sulawesi, Indonesia, *S. substriatum* from North Korea; *S. vitalisi* from China, India, Indonesia, Nepal, and Taiwan). Members of the beach dwelling species of *Cercyon* from the Pacific region are also comprehensively revised with an analysis of the characters of the female genitalia and metafurca for diagnostic purposes. Keys, illustrations, habitus photos, and SEM are included for both *Sphaeridium* and *Cercyon* revisions. Hydrophilids collected from a fallen nest of the giant Asian honeybee *Apis dorsata dorsata* from Bogor Botanical Garden, Java, Indonesia, are also identified and analyzed taxonomically with habitus photos of all species and SEM images and genitalia illustrations for species lacking recent taxonomic treatment. One new country record for *Protosternum hainanensis* and two new regional records for *Noteropagus obliquus* and *N. occlusus* are included. Additionally, a new record of the Byrrhid genus *Microchaetes* (Coleoptera: Byrrhidae) from Japan with habitus photographs and genitalia illustrations and a revision of the Pacific tenebrionid genus *Phaleromela* (Coleoptera: Tenebrionidae) are included. The three confirmed

species of *Phaleromela* are redescribed with habitus photos, SEM images, and genitalia illustrations along with a key to species.

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Contents

Chapter I:

General Introduction

Introduction

Along with climate change, biodiversity loss is one of the great challenges we are currently facing globally. It is well accepted that biodiversity is necessary for the ecological systems we rely on for breathable air, food production, and clean water among other ecosystem services, but the recent acceleration in species extinction has led to increased urgency in researching the processes driving biodiversity and the most efficient methods for its conservation. While new findings in technologies in molecular biology and genetics provide invaluable tools to better understand life on earth, investment in alpha-taxonomy, or the discipline of naming, describing, and classifying organisms has, like biodiversity itself, been in decline over the last several decades (Kim and Byrne 2006). In order to measure biodiversity, a proper understanding of the number of species in a given system is necessary, and while even larger, more conspicuous organisms such as mammals and other vertebrates could perhaps still use taxonomic attention, smaller organisms, particularly those living in decomposer communities have been largely neglected.

Heterotrophic systems and the necrobiome

Heterotrophic systems, or the "necrobiome" include dead wood, leaf litter, carrion, dung, seaweed wrack, fruits, mushrooms and other types of dead organic material or "detritus." They represent unique microhabitats containing a high level of diversity within relatively small systems. Decomposers play a vital role in terrestrial and aquatic ecosystems, allowing for nutrient cycling and energy flow throughout systems. These systems consist of complex interactions between a variety of actors, including microbes, fungi, and invertebrates working at a variety of trophic levels to efficiently break down organic matter. Without these actors, the accumulation of dead matter would be much higher, and their organic components would not be as readily available to the next generation of autotrophic organisms (Nadeau *et al.* 2015). In fact, it is estimated that about 90% of plant biomass is not directly consumed by herbivores and would accumulate at extraordinary rates if not for the work of decomposers (Benbow *et al.* 2018).

Multiple ecological theories have been developed for describing the communities and processes at work in such heterotrophic systems, particularly with regard to carrion and dung systems which have been rather heavily studied due to their applications in forensics and agriculture respectively (Nadeau *et al.* 2015, Benbow *et al.* 2018). Succession, or the process of changing species composition within an ecological system over time, has been closely associated with studies on carrion since the late 1800s when it was first defined, birthing the field of forensic entomology (Michaud *et al.* 2015). Meta-population theory has also been used to explain the distribution of populations across spatially separated systems such as carrion and dung and aggregation and coexistence models have been used to explain the coexistence of similar and closely related species living in close proximity (Ives 1991, Hartley and Shorrocks 2002, Woodcock *et al.* 2002, Benbow *et al.* 2018).

More recently, researchers have attempted to create more wholistic frameworks integrating these concepts to understand a wide variety of decomposition systems. The detritus framework (Moore *et al.* 2004) focuses on the spatial and food chain dynamics of dead matter and the necrobiome framework (Benbow *et al.* 2018) attempts to synthesize previous models to create a general template for understanding these habitats. While these frameworks emphasize the importance of biodiversity within these systems, the taxonomic understanding of many groups represented within them however remains lacking.

Hydrophilidae and the necrobiome

Within the coleoptera, many members of the Staphiliniformes infraorder are commonly included within heterotrophic systems or "the necrobiome", including members of the families Staphylinidae, Silphidae, Histeridae, Ptilidae, and Hydrophilidae. The family Hydrophilidae consists of over 3000 described species worldwide (Short and Fikáĉek 2013), inhabiting a wide variety of aquatic, semiaquatic, and terrestrial ecosystems, from streams and ponds, to algal mats in water seepage, to plant litter and other decaying organic matter (Bloom *et al*. 2014). With a few exceptions, the larvae of hydrophilids are predators, often feeding on the larvae of other insects and other soft-bodied invertebrates, while the adults vary in their feeding habits which may include predation, herbivory or scavenging. Females produce silk from which they make egg cases which they often attach to various substrates but sometimes carry under their elytra or float on the surface of the water. They can often be differentiated from other beetle families by their relatively short antennae bearing a three-segmented club with a cuplike segment at the base, five-segmented tarsi on all legs, lack a notoplural suture, and often but not always bear a variably shaped process on the middle of the mesoventrite, between the mesocoxae (Hansen 1991, Tassell 2001, Archangelsky *et al.* 2016).

The terrestrial lineages represent some of the youngest but also most diverse clades within the family, with the tribe Megasternini representing the most specious group with over 580 described species in over 50 genera (Short and Fikáĉek 2013; Bloom *et al.* 2014; Jia *et al.* 2020). The Megasternini, along with sister tribe Sphaeridiini and other terrestrial groups tend to occupy moist heterotrophic habitats such as carrion, dung, decaying plant material and seaweed wrack (Archangelsky *et al.* 2016) and within these habitats, they play a variety of roles not only as direct consumers of decaying material but also as predators of other insect larvae during their own larval stage (Tassell 2001, Archangelsky *et al.* 2016). Along with other invertebrates, they also often help facilitate the availability of the decaying material to other organisms by tunneling through and consuming it, which may increase surface area and penetrability (Benbow *et al.* 2018).

While the presence of hydrophilids is well documented within studies of heterotrophic systems, many studies have focused mainly on other more prominent groups such as the typically larger scarabaeid dung beetles, the behaviorally charismatic burying beetles, and calliphorid blow flies which are commonly used in forensic analyses of corpses (Nadeau *et al.* 2015, Benbow *et al.* 2018). They are, however, often prominent members of many necrobiome communities such as dung, decaying vegetation, and seaweed, often with several sometimes closely related species occurring together in rather large numbers (Hanski 1980, Przewoźny and Bajerlein 2010, Suzumura *et al.* 2019) so more detailed understanding of their diversity is important for a more complete understanding of such habitats.

Developing taxonomic resources

Perhaps because they have often been considered a side thought in ecological studies and perhaps because the taxonomic relationships within some groups of hydrophilids are rather difficult to parse, the taxonomy of this diverse group along with diagnostic tools for identification of its members has been scattered until recently. In recent years, work on describing species and understanding the higher taxonomic relationships of terrestrial hydrophilids has accelerated thanks to the work of several prominent hydrophilid researchers (Hansen 1991, Fikáĉek 2010, Fikáĉek *et al.* 2012, Short and Fikáĉek 2013, Fikáĉek *et al.* 2014, Fikáĉek *et al.* 2018, Jia *et al.* 2020, Arriaga-Varela *et al.* 2021) but species determination often remains difficult for experts and nonexperts alike. Without comprehensive keys, accurate species identification requires a large amount of research through various literature, often written many years ago, in several different languages, and without photos and diagrams, which poses a considerable barrier to ecologists and other researchers who are not experts in taxonomy of the group. As a result, groups that lack detailed diagnostic materials are often generalized or misidentified in ecological research and while new species description is incredibly important for understanding the scope of biodiversity in a system, illustrated diagnostic tools are necessary for the application of taxonomic work towards ecological and conservation studies.

Thesis overview

The overall aim of this thesis is to provide taxonomic resources on hydrophilids (and other coleoptera) to support further ecological work on heterotrophic systems. It is comprised of three main sections corresponding to taxonomic projects on terrestrial hydrophilid species inhabiting different types of heterotrophic systems including dung, beach detritus, and the fallen nest of the Asian honeybee *Apis dorsata dorsata.* Additionally, an addition section on two other genera of coleoptera found on decaying material on beaches is also included.

Chapter two provides a revision of the coprophagous genus *Sphaeridium* occurring in Palearctic and Oriental Asia, and by extension, Europe (as all European species are also found in northern Asia). Many species of the genus, particularly those occurring in more southern regions lack redescription since their original descriptions and diagnostic material comparing more than a few species. The goal of this chapter is to fill this gap and provide fully illustrated descriptions and keys along with updated species distributions.

Chapter three revises the beach-dwelling species of the genus *Cercyon* occurring in the north Pacific region from Taiwan, through Far East Russia and Alaska to Baja California. With increasing interest in research on the narrow microhabitat of the upper beach, where nutrient occurs between marine and terrestrial ecosystems (Orr *et al.* 2005, Dufour 2011), this section also aims to provide diagnostic materials for hydrophilidae with an integrated key to species occurring both in the Far East and along the west coast of the Americas.

In chapter four, I identified the species of hydrophilids collected from a fallen hive of the Asian honeybee *Apis dorsata dorsata* found in the Bogor Botanical Gardens, Java, Indonesia. Species that lack recent treatment are redescribed and male genitalia are illustrated as available. This represents the first record of the interaction of hydrophilids on the decaying remains of a beehive.

Additionally, I have compiled work on two other groups of non-hydrophilid beetles collected from decaying material on beaches into a fifth chapter. Records of the Australian beetle *Microchaetes* (Coleoptera: Byrrhidae) which has been introduced in Japan since at least the 1990's were compiled along with a new record of the genus from Miyazaki prefecture as well as photos and illustrations of the male genitalia. The small transpacific genus of beach dwelling tenebrionids, *Phaleromela* (Coleoptera: Tenebrionidae) was also revised and provides an interesting case study on another detritivorous group with trans-pacific distribution.

In chapter six, I compare and discuss the beetle communities analyzed across all three heterotrophic systems and the biogeographic historical implications of my findings.

Chapter II:

Revision of the Asian species of *Sphaeridium* Fabricius, 1775 (Coleoptera: Hydrophilidae)

Introduction

The terrestrial water scavenger beetle genus *Sphaeridium* Fabricius, 1775 is represented by 43 species worldwide with 18 species previously described from the Palearctic and Oriental regions (Hansen 1991, Fikáĉek and Kopráĉek 2015). These beetles are commonly found living in fresh pats of dung from large herbivorous mammals such as horses, cattle, and buffalo but have also been reported from animal cadavers (Heo *et al.* 2011). They tend to be rather ubiquitous in animal dung where they are distributed and are often found living alongside many other coprophilous coleoptera including megasternine hydrophilids and other species of *Sphaeridium*. While many species of megasternini readily colonize somewhat old pats of dung, *Sphaeridium* tend to be found mainly on very fresh (1–2 days old) dung (Otronen and Hanski 1983) and are often among the first insects to colonize new pats.

Among the terrestrial hydrophilids, they have been known to be closely related to the megasternines which has been recently confirmed by molecular phylogenetic studies (Short and Fikâĉek 2013) and together these two sister groups form the youngest clade of the Hydrophilidae which dates back to the early Cretaceous (ca. 120 million years ago) (Arriaga-Varela *et al.* 2021). While the *Sphaeridium* have ecologically similar lifestyles to many species of megasternines, the tribe Megasternini differs from Sphaeridiini in being highly diverse, with over 550 species in 51 genera while *Sphaeridium* is the sole genus in the Sphaeridiini. They are also morphologically quite distinct from them not only in their on average larger size but also in the distinct shape of the mesoventral protrusion and the modified protarsus in males.

While most of the diversity of *Sphaeridium* is concentrated in the Afrotropical region, there still remains several undescribed species from the Oriental and Palearctic regions of Asia, particularly Indonesia and India (Suzumura *et al.* 2022). As of now, except for an illustrated key to the members of the genus occurring in Great Britain (Berge Henegowen and Foster 2019), there are few resources for identification of members of the Asian *Sphaeridium* and the lack of comprehensive and diagnostic literature on this group has made research on it quite difficult, resulting in frequent misidentifications. As such, there remain many problems with the taxonomy of the group including synonymies, errors in reported distributions, as well as several undescribed species. Further complicating matters, many species of *Sphaeridium* are rather widely distributed, particularly longitudinally across very large ranges and many of the northern species have been introduced in relatively recent times. In particular, three species, *Sphaeridium scarabaeoides*, *S. lunatum*, *S. marginatum*, and *S. bipustulatum* were introduced to the United States. Additionally, the species *Sphaeridium lunatum* is thought to have been introduced to Hokkaido relatively recently with the earliest record of the species being from the year 1990 (Suzumura 2020). Additionally, while this genus is very often included in studies on beetles inhabiting dung of livestock animals (Otronen and Hanski 1983, Finn and Gittings 2003, Holter 2004, Mroczyński and Komosiński 2014, Wassmer 2014, Anto and Vinod 2017), the lack of comprehensive diagnostic literature has led to frequent misidentification and misunderstanding of the diversity of the group.

In this manuscript, we have reviewed the Asian species of *Sphaeridium* (of which the European species are also included) and have written redescriptions with SEM images and illustrations of the male genitalia for all species with the exception of *S. flavomaculatum*, *S. daemonicum*, and *S. kolleri* which I was unable to obtain specimens of to examine directly. From my review, I have found 2 undescribed species (*S.* sp. 1and *S.* sp. 2), one new synonymy (*S. reticulatum* as a junior synonym of *S. severini*), as well as 19 new country records in Asia

(*S. bipustulatum* from China, India, and Pakistan; *S. dimidiatum* from Cambodia and Laos; *S. discolor* from Malaysia and Nepal; *S. marginatum* from China; *S. quinquemaculatum* from Bhutan, Guam, and Laos; *S. seriatum* from Japan; *S. severini* from Thailand; *S. substriatum* from North Korea; *S. vitalisi* from China, India, Indonesia, Nepal, and Taiwan) and 9 new regional records in Asia and Australia (*S. dimidiatum* from Halmahera, Sulawesi, Sumbawa, Ternate, and West Timur in Indonesia; *S. discolor* from Queensland in Australia; *S. severini* from Guangxi in China and Flores and Sulawesi in Indonesia).

History

Fabricius erected the genus *Sphaeridium* in 1775 into which he placed several new species of small, dark, round beetles in addition to four species of terrestrial hydrophilids and one species from the family Kateridae previously placed into the genus *Dermestes* by Linnaeus (Fabricius 1775). With the exception of *Sphaeridium scarabaeoides* Linnaeus, 1758 (syn. *Dermestes scarabaeoides*) all other species originally placed in the genus were later transferred to their respective groups. In the following years, Fabricius described three more European species, *S. bipustulatum* Fabricius, 1781, *S. marginatum* Fabricius, 1787, and *S. lunatum* Fabricius, 1792 as well as the first Oriental species, *S. quinquemaculatum,* Fabricius 1798.

In 1802, Latreille erected the family Hydrophilidae along with the subfamily Sphaeridiinae and tribe Sphaeriniini which he referred to as "Sphaeridiota" and Mulsant established the first detailed classification of the family Hydrophilidae and split the group into the sister tribes Sphaeridiini and Megasternini in 42 years later in 1844, though in his original classification, he included members of the genera *Cercyon* and *Coelostoma* in the Sphaeridiini.

Between the years of 1913 to 1933, Armand d'Orchymont described many of the known oriental *Spheridium* species including *Sphaeridium seriatum* Orchymont, 1913 and *S. flavomaculatum* Orchymont, 1924 from Indonesia, *S. severini* Orchymont, 1919 and *S. discolor* Orchymont, 1933 from India, *S. kolleri* Orchymont, 1925 from Laos, and *S. vitalisi* Orchymont, 1925 from China. These descriptions were included within publications compiling new species descriptions of hydrophilids and other coleoptera he had discovered during his expeditions to Asia.

Following the work of Orchymont, there was a long gap in work on the Oriental and Palearctic *Sphaeridium* until the description of *S. huijbregtsi* Berge Henegowen, 1986a from Papua New Guinea and a few years later of *S. densepunctatum* Berlov and Shatrovskiy, 1989 from the Russian Far East. More recently, *S. daemonicum* Fikáček and Kopáček, 2015 was described from Arunachal Pradesh, India and *S. sundense* Berge Henegowen, Suzumura and Budi, 2022 from Indonesia.

While the West European species of *Sphaeridium* were treated with a detailed key to species in Berge Henegowen and Foster (2019), a comprehensive revision of *Sphaeridium* on a wider scale has so far been lacking.

Timeline

1758 Linnaeus described *Sphaeridium scarabaeoides* under the name *Dermestes scarabaeoides* from Europe.

1775 Fabricius erected the genus *Sphaeridium* to accommodate *S. scarabaeoides* along with a number of other small round beetles

1781 Fabricius describes *S. bipustulatum* from Kiel, Germany.

1787 Fabricius describes *S. marginatum* from Germany.

1792 Fabricius describes *S. lunatum* from Germany.

1798 Fabricius describes *S. quinquemaculatum*, the first Oriental species of *Sphaeridium* from East India.

1802 Latreille erects the family Hydrophilidae along with the tribe Sphaeridiini (Sphaeridiota Latreille, 1802: 135)

1834 Gory describes *S. dimidiatum* from Java, Indonesia.

1838 Faldermann describes *S. substriatum* from the Caucauses.

1844 Mulsant establishes the first detailed classification of the family Hydrophilidae

1913 Orchymont describes *S. seriatum* from Sumatra, Indonesia.

1919 Orchymont describes *S. severini* from Kerala, India.

1924 Orchymont describes *S. flavomaculatum* from Iriyan Jaya, Indonesia.

1925 Orchymont describes *S. kolleri* and *S. vitalisi* from Laos.

1929 Orchymont describes *S. reticulatum* from Shandong, China.

1933 Orchymont describes *S. discolor* from Tamil Nadu, India.

1986a Berge Henegowen describes *S. huijbregtsi* from Iriyan Jaya, Indonesia.

1989 Berlov and Shatrovskiy describe *S. densepunctatum* from Primorski Krai, Far East Russia.

2015 Fikáček and Kopáček describe *S. daemonicum* from Arunachal Pradesh, India.

2019 Berge Henegowen and Foster publish A key to the British species of *Sphaeridium*.

2022 Berge Henegowen, Suzumura, and Budi describe *S. sundense* from Indonesia.

Materials and Methods

Several specimens were collected from Hokkaido University experimental farms in Sapporo and Yonemura Cheese Farm in Ebetsu, in Hokkaido, Japan. *Spaeridium* was only found in fresh dung pats and collected by hand before being preserved in 70–90% ethanol and later point mounted and identified in the laboratory using a stereomicroscope. Most specimens were mounted on their sides so that ventral characters would be easily visible for examination. Identification was based on external morphology and structure of genitalia.

Dissections of male genitalia were performed by relaxing specimens in boiled water for about 15 minutes before removing genitalia from the body either through a slit made between abdominal tergites or by removing the terminal two to four segments of the abdomen. Genitalia were then placed in 10% KOH solution for 20–30 minutes at 60˚C before muscle was removed in 70% ethanol and then dyed in lactic acid with 1–2 drops of acid fuchsine for three hours at 60˚C. They were then dehydrated in acetic salicylate (methyl salicylate 1: acetic acid 1) for 15 minutes at 60˚C, followed by xylene for about two minutes at room temperature before examination in α-terpineol under a dissecting microscope (Nikon SMZ645, Nikon SMZ800). α-terpineol was chosen because it has a relatively low refractive index and material can be preserved in it for an extended amount of time. Genitalia were preserved in Canada balsam resin on a small circle of glass glued to cardboard and attached to the specimen. Ratios were calculated as the average of the length of the inner margin of the parameres divided by the length of the phallobase.

General morphological illustrations of sclerotized structures besides the male genitalia were made by relaxing specimens of *Sphaeridium scarabaeoides* in boiled water for several hours and then immersing them in 10% KOH solution for about 20 minutes at 60˚C to soften connecting tissue. Structures of interest were then separated from the body and photographed with a Nikon Digital Sight DS-Fi1 on a Nikon SMZ745T stereomicroscope. These photoas along with photos of the male genitalia were later traced in Procreate on an iPad Air (3rd generation).

Habitus photos were taken with a Nikon Digital Sight DS-Fi1 on a Nikon SMZ745T stereomicroscope, SEM photos were taken with a JSM-6510 scanning electron microscope, and all photos were edited using Adobe Photoshop CS6.

I was unable to directly examine type material and specimens of three species, *Sphaeridium daemonicum* Fikáĉek and Kopráĉek, 2015, *S. flavomaculatum*, and *S. kolleri*

Orchymont, 1925 myself due to global events but I was able to work closely with Dr. Arno van Berge Henegowen who is located in Europe and had much easier access to European collection material. Photos provided in Figs. 46, 47, 75, 80 were provided by Dr. Berge Henegowen. I was able to compare photos and descriptions of the specimens in my care to his material and we were able to confirm the identities of the species described herein.

Specimens from the following collections were examined by myself:

SEHU	Laboratory of Systematic Entomology, Hokkaido University Museum, Hokkaido University, Sapporo, Hokkaido, Japan (M. Ôhara)
EUMJ	Ehime University Coleoptera Collection, Matsuyama, Ehime, Japan (H. Yoshitomi)
RMNH	Naturalis Biodiversity Centre, Leiden, The Netherlands

Specimens from the following collections were examined by Arno van Berge Henegowen for comparison:

ALBH	Personal collection of Arno van Berge Henegowen, Zoetermeer, The Netherlands
CNCI	Canadian National Collection of Insects, Ottowa, Canada
MNHN	Muséum d'Histoire Naturelle, Paris, France
MUDH	The Museon, The Hague, The Netherlands
NHMUK	The Natural History Museum London, London, United Kingdom
NMPC	National Museum of Natural History, Prague, Czech Republic
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
USNM	National Museum of Natural History,

	Washington DC, United States of America
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZMUC	University of Copenhagen, Zoological Museum, Copenhagen, Denmark

Characters of *Sphaeridium*

The tribe Sphaeridiini consists of the single genus *Sphaeridium* which is rather distinct among the terrestrial hydrophilids in both morphological characters as well as ecological habits. Recent molecular work has strongly supported the monophyly of the group (Short and Fikâĉek 2013, Bloom *et al.* 2014) though the taxonomic relationships of species within the genus is still unclear. The general morphology of the genus is examined in detail herein with comparison to characters of the sister tribe Megasternini of which most terrestrial hydrophilids are members.

In determining terminology to use for *Spheridium*'s unique characters, we worked to remain consistent to Hansen (1991) and Archangelsky *et al.* (2005) as well as Fikâĉek and Kopráĉek's (2015) description of the species *Sphaeridium daemonicum* Fikâĉek and Kopráĉek which represents the most recent description of a new species of *Sphaeridium* previous to our own *S. sundense* (Suzumura *et al.* 2022).

Body shape (Figs. 1-3)

The body shape in *Sphaeridium* species is wide oval and dorsoventrally convex but somewhat depressed in most species (Figs. 1, 3A). Though all species are longer than wide, some are quite wide and sometimes almost subquadrate. Compared to most genera of megasternines, *Sphaeridium* tend to be rather large in size, ranging from as small as 2.8 mm to over 8.0 mm in length and within coprophilous beetle communities, *Sphaeridium* is often the largest hydrophilid represented as the common genera of coprophilous megasternines do not typically exceed 3.0 mm in length.

Color (Figs. 4, 5)

The dorsal base color of Palearctic and Oriental *Sphaeridium* is piceous to dark testaceous in teneral specimens. The head is fully piceous in most species though *S. sundense* may have a slightly lightened spot on the middle of the frons. The pronotum is also piceous but either with a yellow lateral marginal stripe or in some *S. scarabaeoides* specimens, slightly lightened along apical corner. This yellow stripe may extend along only a part of the lateral margin or throughout and sometimes extends a short distance inward along the posterior margin. The coloration of the elytra is variable but all species bear a fulvous to almost whitish "apical spot" along the posterior margin of the elytra, often extending as a stripe along lateral margins to base. This apical spot can consist of a marginal stripe which extends a short distance anteriorly along the sutural margin (Figs. 4F–J, L) as in *S. sundense* and some specimens of *S. quinquemaculatum* or cover up to posterior about 1/3 of elytra as in *S. discolor* (Fig. 4E). Some species also bear one dark reddish to orange humeral spot on each elytra (Figs. 4A, B, F, H, J) though this spot is often divided into two spots in some smaller species such as *S. quinquemaculatum* and *S.* sp 1 (Figs. 4G, I, L). The species *S. quinquemaculatum* expresses a large range of dorsal color patterns (Figs. 4F-M), with two to four humeral spots which are often confluent with each other as well as with the apical spot which may be narrow or wide. In some specimens, these spots are so extensive and confluent that the elytra appear to have a fulvous to orange base coloration with five black spots as in Fig. 4K, justifying the species' name.

The ventral coloration tends to fall into two types, fully dark brown to piceous (Fig. 5A) or base color fulvous with variable dark spots on postmentum, lateral parts of pronotum, on center and sides of the metaventrite, and along each abdominal segment (Fig. 5B). In ventrally piceous specimens, legs can be piceous to dark brown, dark brown but fulvous on base and apex, or fulvous with variable dark brown spots at the center while ventrally fulvous specimens show only the latter coloration. The tibiae and tarsi are dark brown to testaceous in darker specimens and fulvous in lighter ones.

Head (Fig. 7)

The head is wide oval, slightly wider than long in dorsal and ventral views, weakly convex dorsally and strongly convex ventrally posterior to the eye, not abruptly narrowed behind eyes, and not ventrally deflexed. The dorsal surface (Fig. 7A) consists of the frontoclypeus which is the fused frons and clypeus which are undivided by a frontal stria or furrow. The remnants of the epicranial sutures are however discernable as narrow impunctate strips running from just anterior to the eyes and meeting at middle of frons. A very fine, often indiscernible suture may be present laterally but difficult to distinguish. In *Sphaeridium*, the lateral margins are not abruptly excised anterior to eyes as they are in the Megasternini and instead extend posteriorly into the eyes as an emargination. The surface of the frontoclypeus is not strongly convex and is densely and regularly punctate and the anterior margin is rather strongly convex and lacks a frontal suture.

The ventral side of head (Fig. 7C) is largely covered in dense setous punctures laterally behind eyes, on and posterior to submentum, and sometimes along gular sutures.

The gula is well developed, generally parallel sided in most species, sometimes weakly constricted anteriorly but not forming a triangle. The width is consistent in most species except for *S. discolor* in which it is distinctly wider posteriorly (Fig. 42A) and in *S. dimidiatum* in which it is very narrow (Fig. 39A). Anterior to the gula are two tentorial pits which may not be visible or obscured by pubescence in some specimens.

The compound eyes are not strongly variable. While visible dorsally, they are far more prominent when viewed ventrally where they are much more strongly convex. Anteriorly, they are strongly emarginate, a character that differentiates them from most members of the sister tribe, Megasternini. The emargination is formed from an extension of the anterior margin of the clypeus and is very slightly curved dorsally in many species.

Mouthparts (Figs. 7–9)

The labrum (Figs. 7A, 8A) is retractable but usually visible dorsally. Widest just anterior to base, the anterior margin is straight to weakly curved, lacking median convexity or emargination. The anterior margin bears a fringe of dense setae but the lateral margins lack setae or spines. The surface is finely and densely rugous (similar to microrugae in Fig. 6D) and has one to several rows of sparse setous punctures anteriorly.

The sclerotized portion of the mandibles is simple in shape and simply pointed, lacking denticles, gently and obliquely curved anterolaterally (Fig. 8C). The inner margin bears a brush of hairs referred to as the "prostheca" or "pecten medialis" which continues from near the apex to the molar. The molars are very asymmetrical with one being strongly convex and the other deeply concave. Their surfaces are covered in dense rows of zipper-shaped ridges which fit together and such that they form rows of minute holes. The ridges, also known as "tritors" function in grinding down food material and the holes are thought to function in drainage of fluid. (Beutel and Yavorskaya 2019, Hata and Edmonds 1983, Holter 2004). Laterobasally, the mandibulary condyle extends outward as an almost spherical knob.

The maxilla (Fig. 8D) consists of a small semicircular cardo, stipes palps, lacinia, and galea. The stipes is mainly visible ventrally and divided into basistipes and mediostipes (Archangelsky *et al.* 2016). The surface of the basistipes is sparsely covered in short setae while the middle of the inner part of the mediostipes is punctate. The lacinia is squeegee-shaped, short, about the same length as the subgalea, covered in short hairs, and projecting inward. The galea is flattened, the sclerotized portion forming a wide plate in females but is hollowed out in males and forming a membranous adhesion disc in males (Fig. 8Db). The sclerotized part extends apically along the inner margin in both sexes, the apical and outer margin bearing numerous long, apically hooked setae which are irregularly arranged on a membranous surface. The dorsal surface of the basal part bears many setae apically. The palpifer emerges dorsolaterally and is wide, teardrop shaped dorsally and bearing many stout setae consistent with those on dorsal surface of galea. The palp extends slightly beyond the apex of the galea, the first segment swollen with sparse short flat setae on surface, second weakly expanded apically with sparse punctation, and the terminal segment fusiform. The third segment is only slightly longer than the terminal segment.

The labial palpi (Figs. 8B, 9B) are short, not typically visible dorsally. The second and third segments are subequal in width but the second segment is slightly longer. The third segment is simple fusiform in shape. The palpifer is long, extending from the center anterolaterally and margined with a row of long dense hairs. The ligula is wide and extends laterally from the labial palpi, margined with a row of short setae which become longer at anterolateral margins.

The mentum (Figs. 7C, 8B, 9B) is rectangular to wide trapezoidal and does not conceal the labial palpi. The anterior margin is usually weakly emarginate and the surface is often abruptly depressed behind so that the anterior margin appears carinate though in some specimens, this margin appears more strongly convex. The lateral margins are weakly curved though not distinctly converging posteriorly and bear an irregular fringe of long setae. The surface is covered in dense and typically deep setous punctures and often transverse microrugae and granulate microsculpture.

The epipharynx (Fig. 9A) is densely covered in both dense pubesence and stout setae, somewhat resembling those of coprophagous scarabaeids in structure. The lateral margins are lined with dense lateral marginal setae which become confluent with the anterior parapedial setae which emerge from the anterolateral area of the ventral surface. Numerous stout setae extending from the anterolateral area towards the center comprise the “lateral bristle crest” which converges upon the “median bristle crest” which is comprised of a very dense brush of finer setae surrounded by coarse papillae. Posteriorly, the lateral areas are covered in minute sensillae and the central area posterior to the median bristle crest forms a weakly concave crepis lined with a dense row of hypopharyngeal lateral setae. The labial structure (Fig. 9B) corresponds to the ventral side of the labrum with a weaker median bristle crest between the palpifers as well as a lateral bristle crest running parallel to them. A longitudinal epipharyngeal process made up of another brush of dense hairs extends posteriorly and likely corresponds to the crepis.

Antennae (Figs. 7C, 22)

Antennae are about 2/3 width of head, insertion is on the ventral surface of the clypeus, anterior to the emargination of the eyes. The antenna is 8-segmented, geniculate and clubbed, consisting of scape, funicle, and club. The scape is elongate, slightly shorter than the other segments combined, and bearing one to many fine setae along the weakly concave surface of the anterior margin. The pedicel is trapezoidal in shape, stout, about 1.5x as long as wide and bearing a single small seta on the posterior apex. Segments 3–5 form the funicle and are of increasingly shorter and wider form apically. The terminal three segments form the club which is compact in most species but is weakly serrate/lamellate in *S. discolor* (Fig. 22L) and *S. severini* (Fig. 22I). Its surface is densely pubescent with sparse longer setae. The terminal segment is abruptly narrowed at apical about 2/5ths, often appearing as two segments.

Thorax (Figs. 1, 2, 3A–B, 10–11, 23, 24)

The pronotum is sutrapiziform in dorsal view and convexity is consistent with the elytra (Fig. 1). The disc is evenly convex, densely punctured, and usually without discernable microsculpture except in *S. dimidiatum* which has dense granulate and reticulate microsculpture and *S. severini* which only has very faint coriaceous microrugae. Species vary in the shape of the lateral margin and posterolateral corners (Fig. 23) which may form a 90˚ or oblique angle or be emarginate as in *S. discolor* (Fig. 23D) and *S. dimidiatum* (Fig. 23C). The lateral marginal beading continues from around the anterior margin and either ends at the posterolateral angle or may continue a short distance along the posterior margin. In species with emarginate posterior angles, it ends just before the emargination. The lateral margin also may or may not bear an even row of small, short spines which are often only visible laterally or ventrolaterally.

The posterior margin is sinuate and strongly rounded medially though in some species, it is strongly sinuate while in others, more weakly so.

The scutellum (Figs. 10A–B, 24) is triangular with lateral sides weakly to strongly curved.

The proventrite (Figs. 2, 11A) is well-developed, medially extending some distance posteriorly between the procoxae, culminating in a point which often but not always bears a terminal spine (*S. dimidiatum* lacks such a spine as can be seen in Fig. 39C and *S. lunatum* has a spine produced subapically on the ventral surface as in Fig. 58C). The shape can vary from weakly tectiform in many species to weakly convex in others. The surface is covered in granulate microsculpture and fine dense pubesence as well as three or more spines in most species (excluding *S. dimidiatum* which has long spine-like setae instead) located posteromedially, usually between the procoxae. These spines tend to be arranged in a row along the midline in many species but may also cover a wider area.

The procoxal cavities are round, continued anterolaterally as a short slit between the hypomeron and proventrite, and appear open posteriorly. The hypomeron is densely pubescent and has weakly defined anterior grooves for reception of the antennae which do not extend onto the proventrite.

Mesothorax (Figs. 2, 10A–B, 11C–F)

As with many other groups of the Hydrophilidae, the Sphaeridiini bear a process medially on the mesoventrite between the meso- and metacoxae (Fig. 11C–F). Hansen (1991) referred to this character as the "mesoventral carina or process" or "mesoventral plate" in groups such as the Cercyonini in which this process is raised to form a well-defined flat surface. In other, larger aquatic groups, it forms a narrow longitudinal "sternal keel" which extends posterior to the metacoxae and was recently shown by Matsushima (2021) to aid in swimming in the giant water scavenger beetle *Hydrophilus acuminatus*. While the function of this structure in terrestrial groups is still unknown, there seems to be quite a wide diversity of form across both aquatic and terrestrial lineages which provides a useful tool in identification of various groups within the family. In *Sphaeridium*, however, this structure has formerly lacked the proper attention that it deserves, with older descriptions either only mentioning it in general or omitting it altogether (Gory 1834, Orchymont 1919, 1925). In our analysis, we have found it to be rather complex in structure with several characters that are perhaps unique to the genus and as such, require specific terminology.

Unlike other related groups, the median part of the mesoventrite bears two paired structures of a "mesoventral process" directly anterior to and sometimes confluent with a "posterior lip" formed by a protrusion of the posterior margin of the mesoventrite which reaches between the mesocoxae, narrowly meeting the median anterior apex of the metaventrite. In most members of the sister tribe Megasternini, the mesoventral process lacks the recessed posterior lip and instead the raised part of the process contacts the metaventrite directly.

Because the mesoventral process in *Sphaeridium* is neither flat nor does it consistenly form a keel or carina across all species (though it may be narrow or keel-like in a few species), we will be referring to this structure simply as the "mesoventral process".

The general shape of the anterior protrusion of the process tends to take one of three general forms including fusiform (Fig. 11C), arrowhead-shaped (Fig. 11D), undefined (Fig.

11E), or triangular (Fig. 11F). The general shape is generally determined by the shape of the posterior margin of the process where it joins the posterior lip. In triangular forms, the posterior margin is horizontal and produced at about a 60° angle to the surface of the lip whereas in arrowhead forms, the median part of the posterior margin slopes into the surface of the lip, and if fusiform forms, the process protrudes posteriorly below the lip. In triangular and arrowhead-shaped forms, the posterolateral corners of the process extend as a carina or shelf and become confluent with the posterior margin of the mesoventrite lateral to the lip and separating the lip from the lateral areas of the mesoventrite.

The posterior lip may or may be distinctly separated from the rest of the mesoventrite by lateral shelves which are formed from the posteriolateral angles of the protrusion. In species in which it is separated, the surface of the lip is generally produced at a level lower than the surface of the adjacent lateral sections of the mesoventrite.

The mesoventral process in all species is spinose to some degree. Spines are most often "strong" by which we mean that they are relatively stout, at least at their bases, and rather stiff throughout. In rarer cases, as in *S. dimidiatum*, spines may be replaced with stout spine-like setae consistent with those on the proventrite, narrower from the base and less stiff throughout (Fig. 39B–C). The bases of spines may be produced from deep punctures or protrusions.

The ventral surface of the posterior lip may have some sparse, indistinct pubesence. In particular, the *quinquemaculatum* species group (*S. continens*, *S. himalabata*, *S. quinquemaculatum*) have long, slight pubesence emerging from the surface of the posterior lip and/or the posterior surface of the process which is almost vertical in these species (Figs. 49E–F, 51E–F, 53E–F). The lateral recessed areas of the mesoventrite may also be covered in shorter pubesence.

Elytra (Figs. 1, 3, 6)

The elytra are ovoid, weakly to moderately curved laterally. The base of each is generally convex basally and in most Asian species, the posterior apex is independently curved such that they separate slightly posteriorly, often exposing the tip of the pygidium dorsally (Figs. 1, 3). The suture has a wide margin posteriorly which is often raised but flat but sometimes simply convex. The sutural margin is continuous with the posterior and lateral beading though sometimes disappearing near posterior apex. In a few species, the posterior margin is modified in the female such that the beading is greatly widened posterolaterally in the female of *S. reticulatum* (Fig. 3Cb) while in *S. vitalisi*, the posterolateral marginal area inside of the beading is swollen (Fig. 3Cc). The surface is covered in dense punctures which are usually smaller and denser near the scutellum though. Striae are usually present and consist of uneven rows of larger punctures which are usually not connected by grooves except in some individuals of *S. vitalisi* Three types of microsculpture are present in different densities and combinations depending on the species:

Reticulate microrugae: short microrugae connecting to punctures and each other, forming a net-like pattern, often denser and more apparent posteriorly, as in Fig. 6B–C.

Radiating microrugae: microrugae appear almost like scratches which radiate from the base of the elytra around the scutellum, oriented longitudinally nearer the scutellum and suture and becoming more angled posterolaterally as in Fig. 6A.

Granulate microsculpture: microsculpture forms tiny bumps, appearing like leather as in Fig. 6C.

Hind wings (Fig. 10D)

The overall wing shape is rather narrowed apically with a distinct jugal lobe. Wing venation is highly reduced, with sclerotization restricted mainly to the anterior and basal areas. Of the sclerotized veins, the costa (C), subcosta (scp), and radius anterior (RA) are closely attained, the radius apically culminating in a wide pigmented radial cell (R), and the first branch of the radius (R_1) continues along the anterior margin a short distance subequal to the length of the radial cell. The fourth anterior radial branch (RA_4) is weakly present basally but extends mainly as a fold and fuses apically with the radial first radial posterior (RP_1). Also sclerotized is the radiomedial crossvein (r-m) which connects the radial cell to the radius posterior (RP) which reaches only a very short distance basally. The radiomedial loop (RML) connects the radius posterior to the media posterior (MP_{1+2}) which is strongly sclerotized from the base to where it fuses with the RML and has a sclerotized medial spur (MSP) extending posteriorly from the apical end. The third and fourth radial posterior veins (RP_{3+4}) are fused and weakly sclerotized, extending from the junction of the RML and MP_{1+2}. The cubitus (Cu) is sclerotized but extends only a short distance before splitting into a weakly sclerotized cubitus anterior (CuA) and more strongly sclerotized cubitus posterior (CuP) which fuses apically with the fused third and fourth anal anterior (AA_{3+4}). The fused third and fourth anal posterior (AP_{3+4}) extends posteriorly only as a fold.

Metaventrite (Figs. 2, 10C)

In both the Megasternini and *Sphaeridium*, the middle of the metaventrite is raised into a pentagonal "metaventral disc" or "metaventral field" which is often convex and medially bare of the dense pubescence that covers the lateral areas and metepisterna (Figs. 2, 11B). In *Sphaeridium*, the borders of the median disc are not distinctly demarcated from the surrounding lateral area with pubesence irregularly disappearing around its margins. The surface of the disc has a longitudinal furrow which is distinct on anterior 3/4ths to 4/5ths where it meets transverse furrows which are often not distinctly impressed but generally extend from the posterior angles of the disc anteromedially to meet at the longitudinal furrow. The longitudinal furrow either ends at the intersection with the transverse furrow or continues to posterior margin depending on the species. The surface of the disc is covered in dense but sometimes superficial microrugae (Fig. 6E) and the area anterior to the transverse furrows is uniformly punctured, though sometimes sparser medially. Punctation posterior to transverse furrows is present in many species but often reduced, particularly around the intersection of the furrows. In a few species including *S. dimidiatum*. *S. seriatum*, and *S. vitalisi*, punctation is completely absent posterior to the transverse furrows. The posterior margin of the disc also varies in shape between species and may be simply curved, angled, or emarginate. Some of the larger species including *S. lunatum*, *S. reticulatum*, *S. scarabaeoides*, and *S. vitalisi* have an even row of short stout setae emerging from the posterior surface of the disc.

The metepimera (Fig. 2) are elongate subquadrate and curved along the anterior and posterior margins with densely pubescent surface and strong, almost carinate beading along the anterior, posterior, and lateral margins.

The metafurca (Fig. 10C) is consistent with closely related groups, strongly sclerotized and rather stout, with wide stem and furcal arms. Within the genus, it is not strongly variable between species.

Legs (Figs. 2, 12, 13)

The legs of *Sphaeridium* species are rather flattened with apically expanded tibiae, particularly of the middle and hind legs.

The procoxa is modified, rather round and with anterodorsal surface covered in dense strong spines and fine long pubescence which vary in number and density depending on the species (Fig. 12D). This surface rolls up into the coxal cavity when the proleg is positioned anteriorly and is only visible when the leg is directed ventrally or posteriorly. The ventroposterior apex of the procoxa is produced as a small spine in most species (Figs. 58D, 60D) though in some of the smaller species, this spine may be produced only as a small bulge (Figs. 49D, 51D, 53D). The trochanter is somewhat elongate, with a row of stout setae running along the anteroventral surface and often continuing along the ventral margin of the profemora.

The profemora (Fig. 12A, D) is rather flat, its ventral surface is densely pubescent on basal about 4/5ths. The dorsal surface is also densely pubescent but bare on the basal about 1/4th and apical 1/6th. The posterior margins of both dorsal and ventral surfaces form ridges between which the posterior surface of the profemora is longitudinally concave, creating a tibial groove, particularly apically.

The protarsus (Figs. 12A, D, 13) in *Sphaeridium* show distinct sexual dimorphism. In the male, the first four segments are strongly shortened while the apical fifth segment is strongly expanded, with a large distinct empodium and strongly asymmetrical claws (Fig. 13A–B). The outer claw is very stout, strongly sclerotized, and often ending in sharp dorsal denticle while the inner claw is much finer and sharper. The shape of the fifth segment, particularly the relative width and shape of the outer apical margin, varies between species to some extent. The lower apical margin of the fifth segment may or may not be produced into a denticle or emarginate in some smaller species of the *quinquemaculatum* species group (Fig. 22E–G). The surface near the lower apical margin bears one or more very small setous punctures that are not easily visible except under high magnification. The number and position of these punctures vary within species (Fig. 25). In the female, the protarsus is not so strongly modified (Fig. 13C).

The mid- and hindlegs (Figs. 12B–C, E–F) are more similar in structure, with the femora being elongate ovoid and tibiae triangular, becoming more elongate apically. The ventral side of the femora is covered in setous punctures (Fig. 6D), the setae of which tend to be longer on the midleg and on the dorsal side, sparse pubescence is irregularly arranged along posterior margin. Both mid- and hind tibiae bear two rows of strong, stout spines along the outer margin, with one or two pairs of smaller stout spines preapically on inner margin. The ventral surface bears one or more strong ventral tibial spines, the number of which on the hind tibia is variable between species. Some variation within species is seen as well but species are constrained in the which numbers of spines are possible. The apical margin bears one very long, strong spine on inner angle along with a few other shorter strong spines ventrally and on outer angle as well a row of very short, blunt spines along the ventral margin. Between spines are numerous setous punctures.

Abdomen (Fig. 2A)

The abdomen is composed of five segments densely covered in pubesence. The first segment is not carinate medially as it often is in the Megasterniines. The ventral apical margin is simply curved except in some females of *S. vitalisi* in which it is irregularly emarginate or serrate medially (Fig. 20H).

Male genitalia (Fig. 14)

The male genitalia are of a simple trilobed type as in Fig. 14, consisting of a median lobe enclosed in the tegmen which can be divided into a basal piece connected to two lateral paramera. The basal piece is asymmetrical, a trait shared with some other members of the Sphaeridiinae (Archangelsky *et al*. 2016). The apical opening of the median lobe or "corona" of the median lobe is located on the ventral surface and the distance of the opening from the apex varies between species. The curvature of the median lobe also varies between species, with some being straight in lateral view while others are either weakly curved or angled apically or strongly curved throughout. The ninth tergite (Fig. 14A) is formed by a weakly sclerotized plate with an elongate median ridge and two lateral arms. It is connected by a membrane which surrounds the aedeagus and apically connects to the tenth tergite which is very weakly sclerotized.

Female genitalia (Figs. 15–17)

The female external genitalia are sclerotized and mainly formed from the eighth through tenth abdominal segments (Figs. 15–16). The eight abdominal segment forms the "valvifer", which is comprised of the mediotergite and medioventrite, and the laterotergite. The dorsal and ventral segments of the valvifer are strongly appressed and largely unmovable while the lateroterite folds up, forming a joint such that the valvifer and gonocoxite can be extended posteriorly. While the valvifer of *Sphaeridium* is rather wide and the mediotergite is almost circular, the same structure in the megasterniines tends to be thinner and more linear, appearing to form a more linear and seemingly continuous loop with the gonocoxite. The tenth abdominal highly reduced segment which often presents as two weakly sclerotized plates under the pygidium and is connected by thin membrane to the apical ends of the arms of the laterotergite.

The second abdominal segment forms the gonostylus and coxostylus which function as spinnerets for spinning silk cocoons in which their eggs are laid. Each coxostylus bears a long seta apically. Ventral to the gonostyli is a fine, membranous lamella referred to as the "median membranous piece" by Nasserzadeh *et al.* 2006. It surrounds the vaginal opening and extends into two points on each side, flanking the gonostylus.

Between the bases of the two gonocoxites and the right and left valvifer is an "articulating sclerite" (Figs. 15B, 16), a character also seen in many Histeridae and which in *Sphaeridium*, is variably triangular, wide posteriorly and tapering to a point anteriorly. The articulating sclerite seems to stabilize the gonocoxites and limit their range of movement (Lackner and Tarasov 2019).

The bursa copulatrix (Fig. 16) is rather short as compared to the female genitalia in the megasterniines and extends only slightly beyond the anterior end of the valvifer. The spermathecal gland duct emerges apically from the bursa and connects to a large, spherical sclerotized spermatheca and and even larger, elongate spermathecal gland. As in the littoral *Cercyon*, the spermatheca and gland vary very little between the different species in the genus (Suzumura *et al.* 2022). The common oviduct attaches ventrally to the bursa, just behind the medioventrite.

The internal female reproductive system (Fig. 17) resembles that of many other beetles, composed of a pair of ovaries composed of several ovarioles which join the common oviduct leading to the bursa copulatrix (Nasserzadeh *et al.* 2006). As in other members of the Hydrophilidae, *Sphaeridium* produce silk from large accessory glands (sometimes referred to as "colleterial glands") which is spun into egg cases or cocoons into which eggs are laid (Archangelsky *et al.* 2016). Two types of accessory glands are present as is also typical within the hydrophilids, the first of which are the lateral oviduct-derived accessory glands which are formed from the lateral oviducts and are present lateral to the ovaries, while the ovariole-derived glands are formed from one or more egg tubes of each ovary and are present medially on the dorsal and ventral surfaces of the ovaries (Hinton 1981).

Systematics

Key to species of *Sphaeridium* occurring in the Asian region.

1. Mesoventral protrusion fusiform, flattened, or carinate (Figs. 11C, E); body size variable.

…2

- Mesoventral protrusion triangular (Figs. 11D, F); body size small to medium.

…12

2. Anterior half of head light colored (Fig. 4G); head covered in microreticulation.

Sphaeridium flavomaculatum Orchymont, 1924

- Head entirely black; lacking discernable microsculpture.

…3

3. Ventral base coloration light, with variable dark markings (Figs. 5B, 20); dorsally without distinct humeral markings (Figs. 4E, 20).

… 4

- Ventral base coloration dark (Figs. 5A, 18, 19, 21); dorsal color variable.

…9

4. Size small, body length <5mm; abdominal segments each with a transverse dark stripe along base (Fikáček and Kopráček, 2015).

S. daemonicum Fikáček and Kopráček, 2015

- Size larger, body length usually >6mm; abdominal segments simply yellow or with a checkerboard pattern of dark spots (Figs. 5B, 20).

seriatum species group …5

5. More than two spines on the ventral surface of the hind tibiae.

…6

- One or two spines on the ventral surface of the hind tibiae.

…8

6. Scutellum narrow, about twice as long as wide.

S. kolleri Orchymont, 1925

- Scutellum rather wide, about 1.5x as long as wide.

…7

7. Posterior apex of mesoventral protrusion with two spines (Figs. 63E–F); male genitalia as in Fig. 64, sides of median lobe not constricted near apex of paramera, basal about 4/5ths weakly curved in lateral view, apical 1/5th strongly curved.

S. huijbregtsi Berge Henegowen, 1986

- Posterior apex of mesoventral protrusion with one spine (Figs. 65E–F); male genitalia as in Fig. 66, sides of median lobe weakly constricted constricted near apex of paramera, basal about 4/5ths straight in lateral view, angled at apical 1/5th.

S. seriatum Orchymont, 1913

8. Elytra without distinct striae which are never deeply grooved; mesoventral tablet squat, diamond shaped (Figs. 67E–F); metaventral disc wider than long (Fig. 67H); elytral beading distinctly widened posterolaterally in female; male protarsus with apical margin sinuate, ventral angle forming denticle (Fig. 25K); male genitalia as in Fig. 68.

S. severini Orchymont, 1929

- Elytra with distinct striae which are sometimes deeply grooved; mesoventral tablet longer, carinate (Figs. 69E–F); metaventral disc about as long as wide (Fig. 69H); elytral beading not widened posterolaterally but margin inside beading swollen in female; male protarsus angled, longest ventrally (Fig. 25L); male genitalia as in Fig. 70.

S. vitalisi Orchymont, 1925

9. Posterior angles of pronotum emarginate. Distributed in tropical and subtropical regions.

…10

- Posterior angles of pronotum complete. Distributed in temperate regions.
  scarabaeoides species group

…11

10. Emargination of posterior angles of pronotum small, as in Fig. 23C; lacking apical spine of proventrite (Figs. 39B–C); proventrite and mesoventral protrusion lacking spines,

instead with stout spine-like setae (Figs. 39B–C, E–F); male genitalia as in Fig. 40. Size medium, length 5.0-7.5mm.

Sphaeridium dimidiatum Gory, 1834

- Emargination of posterior angles of pronotum long, as in Fig. 23D; bearing apical spine of proventrite (Figs. 42B–C); proventrite and mesoventral protrusion with spines (Figs. 42B–C, E–F); male genitalia as in Fig. 43. Size medium to large, length 5.5–8mm.

Sphaeridium discolor Orchymont, 1933

11. Apical spot of elytra not extending along lateral margins of elytra; ventral coloration of femora dark, not distinctly lightened at base and apex (Fig. 21F); sides of median lobe of male genitalia parallel until near apex, tip forming an oblique angle (Fig. 59).

Sphaeridium lunatum Fabricius, 1792

- Apical spot of elytra extending along at least half of length of lateral margins of elytra; ventral coloration of femora variable but usually lighter, fulvous to testaceous with a dark spot at the center of each (Fig. 21H); sides of median lobe of male genitalia gently curved, gradually tapered to tip which is acute (Figs. 14B–C)

Sphaeridium scarabaeoides Linnaeus, 1758

12. Mesoventral protrusion about as long as wide (Fig. 11F).

quinquemaculatum species group …13

- Mesoventral protrusion longer than wide (Fig. 11D).

…15

13. Anterior apex of mesoventral protrusion not tuberculate (Fig. 49E–F), gently sloping towards body. Body size small, length 4.0–4.5mm. West Bengal, India.

Sphaeridium sp.2

- Anterior apex of mesoventral protrusion tuberculate, protruding ventrally (Figs. 51E–F, 53E–F). Body size variable.

…14

14. Sides of median lobe parallel on basal 3/4ths, apical 1/4th roundly tapered to tip; curved throughtout in lateral view (Fig. 52). Size small, length 3.3–5.5mm.

Sphaeridium quinquemaculatum Fabricius, 1798

- Sides of median lobe parallel to just before apex which is forms a right angle; basal half straight, weakly curved on apical half in lateral view (Fig. 54). Size small to medium, length 4.0–6.0.

Sphaeridium sp. 1

15. Pronotum with granulate microsculpture laterally (Fig. 76B); male genitalia as in Fig. 77; distributed only in Southeast Asia (Indonesia).

Sphaeridium sundense Suzumura, van Berge Henegowen and Budi, 2022

- Pronotum without apparent microsculpture; distribution more northern.

bipustulatum species group

…16

16. Coloration dark, lacking reddish humeral spots (Figs. 4D, 18C); male genitalia as in Fig. 29; size medium, length 4.7–7.0mm.

Sphaeridium densepunctatum Berlov and Shatrovskiy, 1989

- Coloration lighter, with reddish humeral spots (Figs. 4C, 18A, E, G); size small to medium.

…17

17. Posterior angle of pronotum oblique, not forming a right angle (Fig. 23B); male genitalia as in Fig. 33.

Sphaeridium substriatum Faldermann, 1838

- Posterior angle of pronotum forming a right angle (Fig. 23A).

…18

18. Elytral strial punctures distinct, surface glabrous, with or without superficial granulate microsculpture; female with beading distinctly continuing around apices of elytra.

Sphearidium bipustulatum Fabricius, 1781

- Elytral strial punctures indistinct or absent, surface appearing more mattte, with distinct granulate microsculpure; female with beading disappearing near apices of elytra.

Sphaeridium marginatum Fabricius, 1787

S. bipustulatum Group

(Figs. 4C–D, 5A, 6D–E, 18, 22A–C, 23A–B, 24A–D, 26–37)

Species included: *Sphaeridium bipustulatum*, *S. densepunctatum*, *S. marginatum*, *S. substriatum*.

Distribution. Northern; Europe, Asia, North America (introduced).

Diagnosis. Species of the *bipustulatum* group can be characterized by their mainly northern distribution, small size, and somewhat dark coloration. While the dorsal coloration in most species may or may not have reddish humeral spots, these spots are never distinctly delineated and the ventral coloration is always of the dark type (Figs. 4D–C, 5B, 18). The antennal club is compact and symmetrical. The mesoventral protrusion is always elongate triangular and lacks pubesence on the posterior lip which is separated from the surrounding mesoventrite by the posterolateral angles of the protrusion. The fifth segment of the male protarsus has the apical outer margin sinuate, convex centrally (Fig. 25A–D) and the sides of the median lobe of the male genitalia have a narrow thin "flange" which ends at or just beyond the corona and never reaches the apex.

Sphaeridium bipustulatum Fabricius, 1781

(Figs. 4C, 5A, 18A–B, 22A, 24A, 25A, 26, 27, 34)

Sphaeridium bipustulatum Fabricius, 1781: 78 (as "2pustulatum") – Germany, Kiel ["Kilia"]; Smetana, 1988: 131 (Description, North America distribution); Hansen, 1999: 311 (Catalogue, worldwide); Przewoźny, 2021: 37 (Catalogue, Palearctic); Sazhnev *et al.*, 2021: 272 (Species records, Far East Russia).

Sphaeridium marginatum var. *bipustulatum*: Gyllenhal, 1808: 101.

Dermestes haemorrhoum Schrank, 1781: 26. – Austria, Vienna – Syn: Kugelann, 1794: 541.

Sphaeridium quadrimaculatum Herbst, 1783: 30 ["*4-maculatum*"] (secondary homonym of *Dermestes quadrimaculatus* Schrank, 1781). – Germany, Berlin – Syn.: Smetana, 1978: 31.

Sphaeridium bimaculatum Herbst, 1783: 30; Herbst, 1792: 71. – Europe – Syn.: Smetana, 1978: 31 (syn. of *humerale* Westhoff: Ganglbauer, 1904: 271).

Dermestes testudinarius Fourcroy, 1785: 24 (secondary homonym of *Hister testudinarius* Degeer, 1774: 345) – France, Paris. – Syn. Olivier, 1790: (no.15) 5.

Sphaeridium marginatum Scriba, 1790: 164 (primary homonym of *Sphaeridium marginatum* Fabricius, 1787). – Germany, Darmstadt ["Darmstädter Gegend"] – Syn.: Mulsant, 1844: 153.

Sphaeridium daltoni Stephens, 1829: 156. – England, Yorkshire – Syn.: Smetana, 1978: 31.

Sphaeridium lunulatum Stephens, 1829: 155. – England – Syn.: Ganglbauer, 1904: 271.

Sphaeridium semistriatum Castelnau, 1840: 60. – France, Paris – Syn.: Mulsant, 1844: 154; Smetana, 1978: 31.

Sphaeridium renipustulatum Heer, 1841: 488 (ascribed to Megerle). – Switzerland, "Matt" – Syn.: Knisch, 1924: 121 (as "*renipustulatum* Stierlin").

Sphaeridium basalis Dalla Torre, 1877: 72. – Austria – Syn.: Zaitzev, 1908: 406.

Sphaeridium quadrimaculatum Marsham: Schilsky, 1889: 348 (as "4-pustulatum Marsh.").

Sphaeridium testaceum Heer, 1841: 488 (primary homonym of Sphaeridium testaceum Olivier, 1790 and *Sphaeridium testaceum* Fabricius, 1792). – Switzerland, (Geneva ["Genf"], Malans) – Syn.: Ganglbauer, 1904: 271; Smetana, 1978: 32.

Sphaeridium tauricum Motschulsky, 1849: 94. – S. Ukraine – Syn.: Ganglbauer, 1904: 271 (as syn. dub.); Zaitzev, 1908: 405

Sphaeridium humerale Westhoff, 1881: 61. – Germany, Westfalen – Syn.: Smetana, 1978: 3.

Redescription. Size small, length 4.8–6.0 mm, width 2.7–3.5 mm. Body shape broadly oval, not strongly compressed dorsoventrally.

Coloration not widely variable, usually as in Figs. 4B, 18A, head black, labrum black, pronotum black with narrow yellow stripe along lateral margins, not continuing around anterior or posterior angles; elytra base color black, with apical yellow spot which, if present, covers posterior about 1/5 of elytra, lateral margins with yellow stripe beginning at base or near base and continuing posteriorly to apex, joining apical spot if present, color of sutural interval continuous with surrounding elytra, with dark, indistinct reddish humeral spots; epipleuron fulvous, black near base. Ventral base color black, lightened on anterior and lateral areas of pronotum, posterior margins of abdominal segments, and area of metaventral field posterior to transverse sutures; legs reddish yellow, femorae darker brown at centers either gradually darkened or expressed as discrete spots (Fig. 5A, 18B). Mentum black, submentum dark brown to black, gula yellow, maxillary palps reddish, antennae brown.

Dorsal surface of head with dense, uniform punctures separated by about their own diameter, interstices without apparent microscupture. Eyes of normal size, ventral interocular distance about 5.5x width of one eye, excised on anterior margin. Labrum largely exposed, anterior margin straight medially, with dense, flat golden pubesence anteriorly, surface covered in transverse microrugae. Antennal club symmetrical, compact (Fig. 22A).

Pronotum with distinctly bisinuate posterior margin; lateral margins evenly curved, without uniform row of small spines; marginal beading flat, slightly widened posteriorly, continuing around posterior angles; posterolateral corners forming a right angle (Fig. 23A), without emargination. Surface covered in dense, uniform punctures, consistent with those on head, interstices without apparent microsculpture.

Scutellum more than 2x as long as wide, sides almost straight; surface covered in dense punctures consistent to those on surrounding elytra, interspaces without apparent microsculpture (Fig. 24A). Elytra ovoid, sides gently rounded, apices rounded separately; sutural interval flat, slightly raised, continuous with marginal bead which is distinct around lateral and anterior margins. Surface covered in dense, uniform punctures separated by about their own diameter, interspaces appearing glabrous, with or without indistinct granulate microsculpture which may be more apparent posteriorly; traces of striae present though may be indistinct, represented by irregular lines of slightly larger punctures, interspaces flat. Posterolateral margins not swollen nor modified in female (Fig. 3Ca).

Pygidium flat to weakly tectiform, median suture distinct throughout.

Mentum as in Fig. 26A anterior margin weakly sinuate, mostly straight, carinate, impressed behind; lateral margins weakly curved; surface with deep, coarse setous punctures, interspaces with dense, conspicuous microrugae. Gula not distinctly narrow or wide, sides parallel to slightly widened posteriorly.

Proventral process as in Figs. 26B, C, convex, weakly tectiform posteriorly, bearing a large spine at posterior apex and 3–4 strong spines medially, anterior and lateral areas covered in sparse long golden pubesence.

Mesoventral process as in Figs. 26E–G, anterior protrusion elongate triangular, distinctly longer than wide; ventral and lateral surfaces covered in strong spines emerging from tubercles. Posterior lip about 1/2 length of anterior protrusion, triangular, apex rounded, slightly convex medially, surface glabrous, without pubesence, separated from lateral areas of metaventrite by posterolateral corners of anterior protrusion but not distinctly produced at a different level as metaventrite.

Midmetaventral field s as in Fig. 26H, lightly convex, wider than long, median furrow continuing to posterior margin, often more strongly impressed posterior to transverse furrows which are straight laterally, meeting at an obtuse angle but sometimes not strongly impressed; surface covered in uniform punctures, separated by about 2x their diameter, interspaces with dense microrugae, punctures and microscuplture continuing onto area posterior to transverse sutures; , posterior margin between metacoxae angled, shallowly emarginate medially, without row of hairs.

Procoxae with strong spines and sparse indistinct setae, with small but distinct dentiform process at internal posterior apex (Fig. 26D). Posterior margin of trochanters with strong row of golden spines continuing along posterior margin of femora. Male protarsus modified as in Fig. 25A, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 as long as other segments combined, much wider than tarsomere 4, with apical outer margin sinuate, ventral angle forming an angle though without pointed angular process. Hind tibiae each with one or two small strong spines on ventral surface (often with one spine on one leg and two spines on the other).

Abdominal 5th ventrite apex simply rounded, without emargination, without fringe of hairs.

Male genitalia as in Fig. 27, ratio of median lobe:tegmen = 1.35, straight from base to apical 1/7 which is weakly angled and curved when viewed laterally (Fig. 27D). Median lobe wide, sides straight from base to about apical 1/3 at which it is gradually widened and sinuately tapers to truncate apex which is relatively wide and flat at tip, corona located at about 1/8 length from tip (Fig. 27B); posterior margin of ventral opening truncate, weakly rounded (Fig. 27C). Paramera, wide throughout, ventral side tapered to apices, dorsal side wide, truncate with tips rounded, fringed with setae along inner margin. Accessory sclerite (9th ventrite) short, about 1/4 length of aedeagus, apex pointed, with distinct median ventral ridge; lateral arms subequal in length to paramera, apices bevelled truncate (Fig. 27A).

Distribution. Europe: Albania, Austria, Belarus, Belgium, Bosnia and Herzegovnia, Britain, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Poland, Romania, Serbia, Spain, Sweden, Switzerland, Turkey, Ukraine. Middle East: Armenia, Iran, Israel, Georgia, Syria. Africa: Algeria, Morocco. Asia: Afghanistan, **China [new record]** (Shandong), Russia (Irkutsk, Karelia, Khakassia, Krasnoyarsk, Kurgan, Leningrad, Moscow, North Ossetia-Alania, Omsk, Perm, Pskov, Primorsky Krai, Yakutia), Israel, **India [new**

record] (Kashmir, Sikkim), Kazakhstan, Mongolia, **Pakistan [new record]**, Tajikistan, Turkey Turkmenistan; North America (introduced). Map: Fig. 34.

Remarks. Very similar to *S. marginatum* and *S. densepunctatum* but differs from the former in the presence of much more distinct strial punctures and lack of distinct granulate microsculpture on the posterior portion of the elytra. While this microsculpture may be present in *S. bipustulatum*, it is much more superficially impressed and the elytra appear more glabrous. Additionally, the male protarsus is smaller compared with that in *S. marginatum* (Berge Henegowen and Foster 2019).

S. densepunctatum is also very similar externally but larger on average, has darker coloration, more distinctive radiating microrugae, is wider in habitus and with a narrower mesoventral protrusion, and the sides of the median lobe of the male genitalia are parallel whereas it is widened apically in *S. bipustulatum*.

A new distribution record from Shandong, China is much farther east than the previously known distribution range indicating that this species is dispersed much more widely than thought and follows distribution patterns similar to other northern species like *S. scarabaeoides* and *S. lunatum*.

Specimens examined. **Africa.** “N. Afrika, "Triest", Matsum. 28.VII.1902” (1♂). **Europe. Armenia:** Aragatzotn region, Talin, Nerkin Bazmaberd, 1650m, mountain steppe, in dung, 15.V.2000, leg. Khazaryan (4♂♂, 1♀). **Hungary:** “Budapest, Matsumura” (1♂); **Italy:** Roma/17.IV.1977// A. Tanaka coll., SEHU Japan, 2005; **Slovakia:** CSSR Slovakia, Chlmec, okr. Humenné, lgt. V. Týr, 21.4.90 (1♂, 1♀); same location but 6.IX.89 (1♂, 2♀♀). **China:** E. Shangdong, Liangshan, 1200m, X.2004 (1 female). **Pakistan:** Kawai, Khagan Y., 1450-1800m, 15.VI.1977, Wittmer, Brancucci [EUMJ] (1♀). **India:** Lederwat – Kolhai, (3050-3800m), Kashmir, 3.IX.1970, Y. Arita leg. [EUMJ] (1♀); Aru-Lederwat, (2740-3050m) Kashmir, 2.IX.1970, Y. Arita leg. [EUMJ] (1♀); Diukchu, 10.IX.1977, Sikkim, Bhakta B. [EUMJ] (1♀).

Sphaeridium densepunctatum Berlov and Shatrovskiy, 1989

(Figs. 4D, 18C–D, 22B, 24B, 25B, 28, 29, 35)

Sphaeridium densepunctatum Berlov and Shatrovskiy (in Shatrovskiy), 1989: 277. – Russian Fed., Far East, Primorskiy Kray [“Prim.”].

Redescription. Size medium, length 4.7–7.0 mm, width 3.3–4.0 mm. Body shape subquadrate, rather compressed dorsoventrally.

Coloration as in Figs. 4D, 18C, consistently dark, head black, labrum black, pronotum black with narrow reddish stripe along lateral margins, reaching but not continuing around anterior and posterior angles; elytra black to dark reddish on center of each elytra, lateral margins with very narrow reddish-yellow stripe beginning at base, widening slightly posteriorly and joining with apical spot which covers less than posterior 1/5 of elytra, color of sutural interval consistent with surrounding area, lacking distinct reddish humeral spots; epipleuron reddish. Pygidium dark brown to black, sometimes narrowly lightened along posterior margin. Ventral side black, reddish-fulvous on lateral areas of pronotum and along posterior margins of metaventral field and abdominal ventrites; legs reddish-fulvous, darkened on center of ventral surface of each femur (Fig. 18D); head black to reddish-black, mentum black, submentum and gula black, maxillary palps dark reddish, antennae dark reddish with dark brown club (Fig. 22B).

Dorsal surface of head with very dense, uniform small punctures separated by much less than their diameter, interstices without apparent microsculpture. Eyes of normal size, ventral interocular distance 6x width of one eye, greatly excised on anterior margin. Labrum exposed, anterior margin straight medially with dense flat golden pubesence anteriorly, surface covered in dense granulate microsculpture.

Pronotum with bisinuate posterior margin, medially strongly convex; lateral margins gently curved, with indistinct row of small blunt spines; marginal beading flat, narrow, ending just after posterior angles; posterior angles oblique, not emarginate (Fig. 23B). Surface covered in very dense uniform punctures separated by much less than their own diameter, consistent with those on head, interspaces without apparent microsculpture.

Scutellum about 2x as long as wide, sides almost straight (Fig. 24B). Elytra wide oval, almost subquadrate, sides gently rounded, apices rounded separately; sutural interval flat, slightly raised posteriorly, continuous with marginal beading which is distinct around lateral and posterior margin. Surface covered in very dense uniform punctures separated by much less than their own diameter, interspaces with close reticulate microsculpture; striae distinct, consisting of larger punctures closely arranged in slightly irregular rows, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Pygidium weakly tectiform, divided by median suture which is distinct to apex, apex obtusely angled.

Mentum as in Fig. 28A, anterior margin straight, beaded, surface depressed behind; lateral margins gently curved; surface with very dense deep coarse setous punctures, interspaces with irregular microsculpture. Antennal club symmetrical, compact.

Proventral process as in Fig. 28B–C, tectiform posteriorly, strongly raised, almost carinate along midline, bearing a large spine at posterior apex, with three to four long strong spines medially between coxae and with sparse indistinct pubesence on lateral areas.

Mesoventral process as in Fig. 28E–G, anterior protrusion triangular or arrow-shaped, longer than wide, ventral, lateral, and posterior surfaces covered in strong spines emerging from tubercles; without pubesence. Posterior lip of mesoventrite triangular, posterior apex rounded; longitudinally convex medially, about 1/3 length of protrusion, separated from lateral areas of mesoventrite by posterolateral angles of protrusion, produced at a lower level, lacking pubesence on surface.

Metaventrite with midmetaventral disc raised as in Fig. 28H, strongly convex anteriorly, flat posteriorly; median furrow continuing to posterior margin, transverse furrows only barely impressed centrally, meeting at an oblique angle, area around intersection impressed; surface covered in coarse uniform puctures separated by about 2x their own diameter except on and just posterior to impressed intersection, interspaces with superficial microsculpture. Posterior margin between metacoxae gently rounded, straight to very weakly emarginate medially.

Abdominal apex simply rounded, without emargination, without emargination, posterior margin without fringe of hairs.

Procoxae with strong spines interspersed with long sparse pubesence; with short but distinct dentiform process at internal posterior apex. Posterior margin of trochanters with row of very short spines which continue along femur where they are much bigger. Male protarsus modified as in Fig. 25B, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 almost as long as other segments combined, a little wider than tarsomere 4, with apical outer margin obliquely angled, apex of ventral margin slightly produced into small blunt spine (Fig. 28D). Hind tibiae each with 1–2 small strong spines on ventral surface.

Male genitalia as in Fig. 29, ratio of median lobe:tegmen = 1.25, straight until apex which is only slightly curved when viewed laterally (Fig. 29D). Median lobe wide, sides parallel until apical 1/4 at which it is gently tapered to a rounded to truncate tip; corona located at about apical 1/9; posterior margin of ventral opening truncate, anteriorly emarginate. Paramera very wide, dorsal side almost parallel throughout, apices oblique, membranous inner portion pointed, distinctly longer than ventral sclerotized part (Fig. 29B). Accessory sclerite (9th ventrite) a little less than 1/3 length of aedeagus, apex expanded and truncate, with distinct median ventral ridge; lateral arms subequal slightly shorter than paramera, apices truncate (Fig. 29A).

Distribution. Russia: Primorsky Krai. China: "North China", Heilongjiang Province. Map: Fig. 35.

Remarks. Very similar to *S. bipustulatum* though often a little larger in size, wider in habitus and with a wider, shorter mesoventral keel. In the male genitalia, the median lobe of the male genitalia of *S. densepunctatum* is somewhat narrower and not gradually widened from base nor as tapered at apex as in *S. bipustulatum* and the apices of the paramera are oblique where they are truncate in *S. bipustulatum*. Additionally, the dorsal punctation is denser in *S. densepunctatum* though I find this character to be difficult to differentiate the two as the difference is not strongly apparent.

Specimens examined. **Russia:** Primorsky, 22.VI.1997, M. Ôhara, human excrement/Russian Far East, "мальцевская", Cape Churkin, Vladivostok (3♀♀, 2♂♂). **China:** Yablonia [Yabulizhen, Harbin, Heilongjiang], East-Manchuria, VII.1940. Coll. A.S. Loukashkin/Nakane Coll. SEHU Japan 1999 (1♂).

Sphaeridium marginatum Fabricius, 1798

(Figs. 4C, 5A, 6D–E, 18E–F, 24C, 25C, 30, 31, 36)

Sphaeridium marginatum Fabricius, 1787: 43. – Germany, Sachsen, Halle ["Halae Saxonum"]; Hansen, 1999: 314 (Catalogue, worldwide); Alekseev and Bukejs, 2013: 27 (Species records, Far East Russia); Sazhnev *et al.*, 2021: 272 (Species records, Far East Russia); VanDyk *et al.*, 2020 (online records, North America); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Dermestes marginatus: Marsham, 1802: 66.

Redescription. Small to medium, body length 5.0–6.7 mm. Body shape oval, not strongly compressed dorsoventrally.

Coloration as in Figs. 4C, 18E, head black, labrum black to dark brown; pronotum black with even narrow yellow stripe along lateral margins, ending right before posterior margin;

elytral coloration with little variation, base color black, with two large dark reddish humeral spots which may be indistinct in some individuals, yellow apical spot present, covering up to about apical 1/5th though reduced to a narrow marginal stripe in some individuals; epipleuron dark brown, fulvous along lateral margin. Pygidium dark brown, sometimes lightened along posterior margin. Ventral side base color black; mentum and submentum black, gula yellow, maxillary palps and antennal segments fulvous to brown, antennal club dark brown; fulvous on lateral areas of pronotum and along posterior margins of abdominal ventrites; legs fulvous to testaceous, with a darkened spot at center of each femora (Figs. 5A, 18F).

Dorsal surface of head with dense uniform punctures separated by less than their diameter, interstices without apparent microsculpture. Eyes normal size, ventral interocular distance about 6x width of one eye, deeply excised on anterior margin. Labrum exposed, anterior margin straight medially, with dense and flat golden pubesence anteriorly, surface covered in dense transverse microrugae, with 3–4 rows of fine hairs on anterior half. Antennal club compact.

Pronotum with bisinuate posterior margin; lateral margins weakly curved, with row of small spines; marginal beading narrow, ending at posterior corners; posterior corners forming right angles, lacking emargination (as in Fig. 23A). Surface covered in dense uniform punctures separated by less than their diameter, slightly larger than those on head, interspaces without discernable microsculpture.

Scutellum about 2x as long as wide, sides straight; surface covered in dense punctures consistent to those on surrounding elytra, interspaces without apparent microsculpture (Fig. 24C). Elytra ovoid, sides weakly rounded, almost straight medially, apices rounded separately; sutural interval slightly raised posteriorly but flat throughout, ending at or just beyond apices; marginal striae starting on posterolateral area of margin, continuing anteriorly and around base to scutellum. Surface covered in dense uniform punctures consistent with those on pronotum, interspaces with distinct dense granulate microsculpture and sparse microreticulation; striae indistinct, larger strial punctures not strongly apparent, not evenly aligned, without grooves but interspaces sometimes weakly convex. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Apex of pygidium visible dorsally; flat to weakly tectiform, divided by median suture which is not distinct to apex, apex rounded, slightly emarginate medially.

Mentum as in Fig. 30A; anterior margin carinate, straight medially, very slightly bisinuate; lateral margins gently curved; surface with uniform deep coarse setiferous punctures, interspaces with dense, conspicuous microrugae except sometimes along posterior margin. Gula not distinctly narrow or wide, sides parallel to slightly wider posteriorly.

Proventrital process as in Fig. 30B–C, tectiform, bearing a large spine at posterior apex, and 5–7 strong spines medially on posterior 3/5, laterally with fine pubesence and setae close to median stout spines.

Mesoventral process as in Fig. 30E–G, anterior protrusion triangular, distinctly longer than wide, with strong spines on surface and sides, becoming smaller laterally, anterior apex sloping towards body, lateral and posterior surfaces with long, sparse pubesence; posterior lip about 2/3 length of protrusion, separated from surrounding mesoventrite by posterolateral corners of process, produced at a lower level, surface raised along midline, without pubesence.

Midmetaventral disc raised as in Fig. 30H, flat medially, about as long as wide, median furrow continuing to posterior margin; transverse furrows only impressed centrally, straight laterally, not meeting at an angle, area around intersection weakly impressed; surface covered in fine setous punctures except on and around impressed intersection, particularly posterior intersection, interspaces with dense microrugae. Posterior margin between metacoxae weakly but distinctly emarginate, with hairs produced from ventral surface along margin.

Apex of fifth abdominal ventrite simply rounded, without emargination, posterior margin without fringe of hairs, bare medially.

Procoxae with strong spines interspersed with abundant long yellow pubesence near anterior margin (Fig. 30B–C); with distinct dentiform process at internal posterior apex (Fig. 30D). Posterior margin of trochanters with irregular row of spines of increasing size continuing along anterior margin of femur. Male protarsus modified, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 almost as long as segments 1–4 combined, S5 distinctly wider than S4, with apical outer margin rounded with an emargination on ventral apical corner, without pointed angular process. Hind tibiae usually with one or two small moderately strong spines on ventral surface.

Male genitalia as in Fig. 31, ratio of median lobe:tegmen = 1.32; basal 3/4ths straight when viewed laterally, apical 1/4 bent dorsally, apex bent ventrally (Fig. 31D). Median lobe wide, with sinuate, widened from base to just beyond paramera, then irregularly narrowed to wide truncate apex; corona located at about apical 1/9 length (Fig. 31B); posterior margin of ventral opening narrowed, extending to near tip, anterior margin concave (Fig. 31C). Paramera wide, basal 3/4ths wide dorsally then narrowed to apex, ventrally wide throughout and truncate apically, without long pubesence.

Distribution. Europe: Albania, Austria, Belarus, Belgium, Bosnia Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, England, Finland, France, Georgia, Germany, Greece, Hungary, Ireland, Italy, Latvia, Macedonia, Malta, Netherlands, Norway, Poland, Portugal, Romania, Slovenia, Spain, Switzerland, Sweden, Ukraine. Russia: Adygea, Crimea, Irkutsk, Krasnodar, Khakassia, Smolensk. Africa: Algeria, Egypt, Morocco, Tunesia. Asia: **China (Xinjiang) [new record]**, Cyprus, Iran, Israel/Palestine, Lebanon, Syria, Tajikistan, Turkey, Uzbekistan. Map: Fig. 36.

Remarks. This species is very similar to *S. bipustulatum* but differs from it in the lack of distinct strial punctures and presence of distinct granulate microsculpture on the posterior portion of the elytra (granulate microscultpure may be present in *S. bipustulatum* but is much more superficially impressed). Additionally, the male protarsus is larger compared to that of *S. bipustulatum* (Berge Henegowen and Foster 2019).

Specimens examined. **Czech Republic:** Boheme IX.1937, Trutnov, Coll. Pospisil [EUMJ] (1♂). **Hungary:** Budapest, Matsumura// Sphaeridium bipustulatum F/ det. F.L. Jia 2003 (1♂). **France:** [FR-06-MO-023] Aveyron (12), St-Léons, alt. 750m, nr. Millau, 44º13'08.3"N 2º58'57.1"E, 30.V.2006, M. Ôhara (from cow dung) (1♂, 1♀); [FR-06-MO-009] Haute-Corse (2B), Furiani, alt. 1m. sand beach, 42º38'34.3"N 9º27'32.4"E, 24.V.2006, M. Ôhara (2♀♀). **China:** Boro Horo Shan, Jining Ining-H-Sien, 44˚06'SS, 81˚56'VD, Snizek leg. (1♀).

Sphaeridium substriatum Faldermann, 1838

(Figs. 4C, 5A, 11D, 18G–H, 22C, 23B, 24D, 25D, 32, 33, 37)

Sphaeridium substriatum Dejean, 1821: 51. – nom. nud.; Hansen, 1999: 316 (Catalogue, worldwide); Berge Henegowen, 2019: 1 (Description); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Sphaeridium atratum Ragusa 1891: 136. – Italy, Sicily ["Sicilia"] – Syn.: Hansen 1999: 316.

Redescription. Small to medium, body length 4.4–6.0mm, width 2.8–3.4mm. Body shape slightly elongate oval, not strongly compressed dorsoventrally.

Coloration as in Figs. 4C, 18G, head black, labrum black to dark brown; pronotum black, variably lightened along lateral margins, without narrow marginal stripe though weakly testaceous on beading, with narrow marginal stripe from anterior angle to anterior to posterior angle, or variably shortened and/or interrupted, not extended inward along anterior or posterior margins; elytral coloration with little apparent variation, base color black, humeral areas completely black or indistinctly reddish at centers, with large yellow apical spot covering apical 1/2–1/3 with anterior margin oblique laterally, meeting lateral margin at an angle, not extended anteriorly along margins; epipleuron black to dark testaceous anteriorly, fulvous posteriorly. Pygidium dark brown. Ventral side base color black; mentum and submentum black, lightened on gula, maxillary palps and antennal segments testaceous, antennal club dark brown; fulvous along lateral areas of pronotum, light area wider anteriorly; legs fulvous to light testaceous with a darkened spot at center of each femora (Figs. 5A, 18H).

Dorsal surface of head with dense, uniform punctures separated by about their own diameter or a little less, except around smooth epicranial sutures, interstices without apparent microsculpture. Eyes of normal size, excised on anterior margin. Labrum exposed, anterior margin straight medially, with dense flat goldent pubesence anteriorly, surface covered in dense transverse microrugae, anteriorly with 3–4 rows of fine setous punctures. Antennal club elongate, symmetrical, compact (Fig. 22C).

Pronotum with bisinuate posterior margin; lateral margins rounded, without row of small spines (may have some spines irregularly arranged along margin); marginal beading narrow, flat, continuing around anterior margin, ending just behind posterior angles; posterior angles forming a slightly oblique angle, lacking emargination (Fig. 23B). Surface covered in dense deeply impressed punctures separated by much less than their own diameter, slightly larger than those on head, interspaces without apparent microsculpture.

Scutellum elongate, more than 2x as long as wide, sides weakly rounded; surface covered in dense punctures consistent to those on the surrounding elytra, interspaces without apparent microsculpture (Fig. 24D.) Elytra elongate ovoid, sides weakly rounded, apices rounded separately; sutural interval not raised posteriorly, flat to weakly convex, continuous with marginal beading which is narrow but distinct apically, only slightly widened anteriorly, continuing around humeral angles to scutellum. Surface covered in dense uniform punctures consistent with those on pronotum, interspaces with sparse reticulate microsculpture, glabrous; striae distinct, though larger strial punctures not evenly alighned, without grooves, interspaces flat. Posterolateral margins not distinctly swollen, not modified in female (as in Fig. 3Ca).

Pygidium largely visible dorsally; weakly tectiform, divided by median suture which is distinct near apex, apex rounded to weakly angled, slightly emarginate medially.

Mentum as in Fig. 32A, anterior margin weakly carinate, bisinuate, concave, lateral margins weakly curved, surface with uniform deep coarse setiferous punctures, interspaces with dense conspicuous microrugae except sometimes along lateral and posterior margins. Gula not distinctly narrow or wide, sides parallel to slightly curved.

Proventrital process as in Figs. 32B–C, tectiform, forming a large spine at posterior apex, and bearing 3 strong stout spines posteriorly along median line, and several smaller spines anterior to these spines, laterally and anteriorly with dense short pubesence.

Mesoventrital process as in Fig. 32E–G, anterior protrusion triangular to fusiform, distinctly longer than wide, posteriorly continuous with posterior lip along median line, ventral surface with 6–8 long strong spines produced from tubercles, lateral surfaces with many smaller stout spines, lacking pubesence; posterior lip about 1/2 length of anterior protrusion, apex rounded, separated by surrounding mesoventrite by posterolateral corners of process, produced at a lower level, surface lacking pubesence.

Midmetaventrital disc raised as in Fig. 32H, convex, about as long as wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow continuing to posterior margin, transverse furrows weakly discernable laterally, straight to weakly curved laterally, meeting at an oblique angle, area around intersection not strongly impressed; surface covered in coarse deep setous punctures except around intersection of furrows and just behind transverse furrows, though present along posterior margin, interspaces with dense microrugae. Posterior margin between metacoxae curved to obliquely angled, distinctly emarginate medially.

Apex of fifth abdominal ventrite weakly angled to strongly rounded, without emargination, posterior margin without fringe of hairs.

Procoxae with strong spines interspersed abundant long yellow pubesence, with long dentiform process at internal posterior apex (Fig. 32D). Posterior margin of trochanters with irregular row of short spines continuing along posterior margin of profemora. Male protarsus modified as in Fig. 25D, with tarsomeres 1–5 weakly shortened and slightly widened and tarsomere about as long as segments 1–3 combined, segment 5 slightly wider than segment 4, with apical margin rounded, with ventral apical corner forming a pointed angular process; tip of claw denticulate. Hind tibiae almost always each with one small strong spine on ventral surface put may have two spines on one or both legs in rare cases.

Male genitalia as in Fig. 33, ratio of median lobe:tegmen = 1.27; basal 2/3 straight, apical 1/3 weakly curved in lateral view (Fig. 33D). Median love with sides parallel on basal 2/3, weakly constricted at around apical 1/3, then swollen before roundly converging at apex which bears a small but distinct truncate protrusion; corona located at about apical 1/10 (Fig. 33B); posterior margin of ventral opening located just anterior to corona, anterior margin emarginate (Fig. 33C). Paramera moderately wide, tapered to tips, dorsal and ventral surfaces about the same width except near tips at which ventral surface becomes narrower, dorsal surface with fringe of short pubesence on inner margin. Acessory sclerite (9th ventrite) about 1/4 length of aedeagus, apex pointed, median ridge fine, arms slightly shorter than paramera (Fig. 33A).

Distribution. Europe: Azerbaijan, Armenia, Austria, Azores, Bosnia Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, France, Germany, Greece, Hungary, Italy, Lithuania, Macedonia, Montenegro, Poland, Slovakia, Ukraine, United Kingdom. Russia: South European Territory, East Siberia, Far East, West Siberia. Africa: Algeria, Egypt, Tunisia. Asia: China (Liaoning, Inner Mongolia, Shanxi), Iran, Israel, Kashmir, Kazakhstan, Mongolia, **North Korea [new record]**, Tajikistan, Turkmenistan, Turkey. Map: Fig. 37.

Remarks. Originally described as a variety of *S. bipustulatum*, *S. substriatum* can be differentiated from the former by the posterior angle of the pronotum which forms an oblique angle (Fig. 23B) as opposed to a right angle as in *S. bipustulatum* (Fig. 23A). Additionally, the strial punctures of the elytra are more distinct and the shape of the median lobe of the male aedeagus is narrower and not widened before apex (Fig. 33). Despite these differences, this species can be included in the *bipustulatum* group of species which also includes *S. densepunctatum* and *S. marginatum* and is defined by the small body size, “arrowhead” shape of the mesoventral protrusion which is distinctly longer than wide (Figs. 11D, 26E–F, 28E–F, 30E–F, 32E–F), and mainly northern, Palearctic distribution.

Specimens examined. **Asia. China:** Yablonia, East Manchuria, VII.1940, A. S. Loukashkin leg. (1♂, 2 exs.); [Huangtuling] Xu. Liaoning Sh. 16.IX.1985, Jing Ke Li leg. (1♀); Zhang Jia Ying Zi, Keshiketeng Qi, Inner Mongolia, 5–25.VII.2005 (1♀). **North Korea**: KangUon-Do, UonSan City, AnByon-Gun, Pisan-ri, 22.VII.2008, Changdo Han leg. [EUMJ] (1♂, 1♀); KangUon-Do, PopTong-Gun, Yohe-Ri, Rimzin Riverside, 23.VII.2008, Changdo Han leg. [EUMJ] (2♀♀). **Europe. Armenia:** Kotayk region, Gehadir, 1650m, mountain steppe, under stone, 16.IV.2000, A. Amiryan leg. (2♂♂, 3♀♀). **Poland:** Grunwald, Olszynek, 29.VIII.2004, M. Ôhara leg. (2♂♂).

S. daemonicum Group

(Figs. 4E, 38)

Species included: *Sphaeridium daemonicum*

Distribution. India and Myanmar

Diagnosis. This group can be differentiated from other Asian species by its smaller size and light ventral coloration. While similar to members of the *seriatum* species group, *S. daemonicum* is smaller and lacks the checkered pattern of dark spots on the abdominal ventrites.

Sphaeridium daemonicum Fikáček and Kopráček, 2015

(Figs. 4E, 38)

Sphaeridium daemonicum Fikáček and Kopráček, 2015: 647.

Comprehensive description available in Fikáček and Kopráček (2015).

Distribution. India (Arunachal Pradesh), Myanmar. Map: Fig. 38.

Remarks. This species appears similar to *S. kolleri* but differs in the following: *S. daemonicum* is smaller, about 4.2 mm as compared to *S. kolleri* which is over 6mm and the number of spines on the hind tibia is 2 in *daemonicum* whereas it is up to 5 in *kolleri* (Berge Henegowen, personal communication 2022).

S. dimidiatum Group

(Figs. 4F, 5A, 11E, 21A–B, 22K, 23C, 24M, 25M, 39–41)

Species included: *Sphaeridium dimidiatum*

Distribution. Southern, Asia.

Diagnosis. This very distinctive species can be differentiated from the other Asian *Sphaeridium* by the short emargination on the posterior angle of the pronotum as well as by the distinct lack of strong spines on the medial area of the proventrite and mesoventral protrusion. Instead, this species bears strong, erect setae and the posterior apex of the proventrite lacks a terminal spine which is present in all other Asian species though sometimes produced on ventral surface just before apex. Additionally, the gula is very narrow and the mesoventral protrusion is quite flattened and not distinctly delineated from the surrounding mesoventrite. The male protarsus is not strongly widened, with the fifth segment barely wider than the preceding segments, though the outer claw is still much wider than the inner claw and strongly denticulate.

Sphaeridium dimidiatum Gory, 1834

(Figs. 4F, 5A, 11E, 21A–B, 22K, 23C, 24M, 25M, 39–41)

Sphaeridium dimidiatum Gory, 1834: pl. 20 (illustration); 1842: 73 (description). – Indonesia, Java; Hansen, 1999: 313 (Catalogue, worldwide); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Sphaeridium dimidiatum Castelnau, 1840: 60 (primary homonym of *Sphaeridium dimidiatum* Gory, 1834). – Indonesia, Java – Syn.: Orchymont, 1913: 13.

Sphaeridium cameroni Orchymont, 1926: 202. -–India, Uttar Pradesh, Siwalik R., Mohand – Syn: Hansen, 1999: 313; Orchymont, 1933: 297 (as *dimidiatum* “var. color”).

Redescription. Size small to medium, length 5.0–7.5 mm, width 3.5–4.1 mm. Body shape oval, not strongly compressed dorsoventrally.

Coloration as in Fig. 4D, 21A, with little variation; head black, labrum black; pronotum black with narrow yellow stripe along lateral margins, continuing around anterior angle but not reaching middle of anterior margin, ending just before posterior angles; elytra black, yellow apical spot covering posterior about 1/3, reaching more than halfway anteriorly along lateral margins, lacking reddish humeral spots; epipleuron reddish black on anterior half, yellow on posterior half. Pygidium black to dark brown, narrowly lightened along posterior margin. Ventral base color black, lightened on lateral margins of pronotum and posterior margins of abdominal ventrites; legs reddish-yellow, darkened at center of femora (Fig. 21B). Mentum black, submentum black to dark brown, gula lightened posteriorly, maxillary palps yellow, antennae yellow with dark brown club.

Dorsal surface of head with very dense, uniform small punctures separated by about their own diameter, interstices with superficial granulate microsculpture. Eyes slightly large, ventral interocular distance about 4.5x width of one eye, greatly excised on anterior margin. Labrum exposed, anterior margin straight medially with dense flat golden pubesence anteriorly, surface covered in microrugae. Antennal club elongate, symmetrical, not compact (Fig. 22K).

Pronotum with bisinuate posterior margin; lateral margin evenly curved, without row of spines; marginal beading narrow, slightly convex, continuing around anterior margin, ending at posterior angles; posterior angles with small, short emargination (Fig. 23C). Surface covered in small uniform punctures separated by about their own diameter, consistent with those on head, interspaces with superficial granulate microsculpture which is more apparent laterally.

Scutellum elongate, almost 3x as long as wide, sides gently curved (Fig. 24M). Elytra oval, not subquadrate; apices not strongly rounded; sutural intervals flat, slightly raised, ending at apex of elytra, not or barely continuous with lateral marginal beading, which is very narrow posteriorly, almost disappearing. Surface appearing somewhat matte, covered in dense uniform punctures separated by about their own diameter, consistent with those on head and pronotum, interspaces with distinct granulate microsculpture, microreticulation, and radiating microrugae; without apparent striae, not even as misaligned larger punctures, interspaces flat. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Pygidium flat, not tectiform, divided by median suture only distinct posteriorly, apex rounded, sometimes weakly emarginate medially, only tip exposed in dorsal view.

Mentum as in Fig. 39, anterior margin straight to concave, weakly carinate, depressed medially and behind; lateral margins curved; surface with sparse shallow setous punctures the setae are rather long and golden, interspaces with dense, conspicuous microrugae. Gula distinctly narrow.

Proventral process as in Figs. 39B–C, tectiform, weakly but distinctly raised along midline though not carinate, forming a sharp, acute posterior apex but lacking a terminal spine, surface lacking strong spines but with erect long strong curved golden pubesence, lateral areas with weaker pubesence.

Mesoventral process as in Figs. 11E, 39E–G, form distinct, anterior protrusion weakly fusiform, surface weakly convex, not protruding, almost flat, not strongly protruding above level of posterior lip, surface covered in setae-like golden spines which are distinctively less stout as those in other species, laterally pubescent, posterior lip crescent-shaped, confluent with protrusion, separated from lateral areas by posterior margin of protrusion.

Midmetaventral field as in Fig. 39H, about as long as wide, flat medially, lateral margins not distinctly separated from lateral areas, median furrow shallowly impressed to transverse furrows, not continuing to posterior margin, transverse furrows weakly impressed, meeting at an oblique angle; surface irregularly covered in fine setous punctures separated by about 2x their diameter though becoming denser anteriorly and laterally, interspaces with fine dense granulate microsculpture, area posterior to transverse furrows weakly concave, with microsculpture but lacking punctures. Posterior margin between coxae angled, sometimes with small weak emargination medially.

Apex of 5th abdominal ventrite simply rounded, without emargination, hair reaching margin.

Procoxae with short strong spines and long, golden pubescence which is longer than the spines (Fig. 39B–D); with very short, indistinct dentiform process at internal posterior apex. Posterior margin of trochanters with row of stout golden setae which continues along posterior margin of profemora. Male Protarsus weakly modified as in Fig. 23M, with tarsomeres 1–4 slightly widened and shortened, and tarsomere 5 about as long as tarsomeres 1–3 combined, only slightly wider than tarsomere 4, with apical margin rounded, apex of ventral margin simply rounded, not at all produced into an angle or spine. Each hind tibia with 1–2 small strong spines on ventral surface (usually with two spines on each).

Male genitalia as in Fig. 40, ratio of median lobe:tegmen = 1.31, strongly curved in lateral view (Fig. 40D); median lobe narrow, widest at basal 1/3, parallel throughout apical 2/3, roundly tapered on apical 1/10, tip with truncate protrusion; corona located at apical about 1/9 (Fig. 40B); posterior margin of ventral opening acute, extending to near tip (Fig. 40C). Paramera strongly tapered to tips, which are pointed, internal margin lacking dense pubesence. Accessory sclerite (9th ventrite) rectangular, wider than long, not extending posteriorly medially, posterior margin sinuate, almost horizontal, without apparent median ridge, lateral arms distinctly shorter than paramera (Fig. 40A).

Distribution. **Cambodia [new record]**, India (Bihar, Kerala, Tamil Nadu, Uttar Pradesh, Sikkim), Indonesia (Java, **Halmahera**, **Sulawesi**, **Sumbawa**, **Ternate**, **West Timur [new records]**), **Laos [new record]**, Sri Lanka, Thailand. Map: Fig. 41.

Remarks. Extremely unique within the Asian *Sphaeridium*, this species is distinctive not only in the small emargination of the posterior angles of the pronotum but also in many ventral characters. Both proventrite and mesoventral protrusion lack strong spines and instead have strong erect spine-like setae and the apex of the proventrite is bear, lacking a terminal spine. The mesoventral protrusion is not defined from the surrounding mesoventrite, its sides gently sloping and posteriorly almost becoming confluent with the posterior lip (Figs. 39E–F).

Specimens examined. **Cambodia:** Siempang, Soeng Treng province, 9–25.IV.2006 (1♀). **India:** "Dzongri, 15.X.1977, 3000m/Sikkim, Bhakta B.“ (2♂♂); "Mangon, 2.IX.1977/Sikkim, Bhakta B." (1 female);"Lage Shap (“Legship?”), 5/600m 14.IV./Sikkim, 78 Bhakta B.“ (1♀); “Kalimpong Umg. XI.1976, Bhakta Bahadur” [EUMJ] (1♂, 1♀). **Indonesia:** “[SB-06-MO-034] Indonesia: Sumbawa., 08°48’50”N 117°19’45”E, Desa Tatebal, Kecamatan Ropang, Kabupaten Sumbawa Besar, Propinsi Nusa, Tenggara Barat (NTB) 9.XI.2000, M.Ôhara” (2♂♂, 1♀, 1ex.); “[SB-06-MO-037] Indonesia: Sumbawa., 08°45’48”N 117°50’15”E, ca. 5 m. Desa Sukajaya, Kecamatan Plampang, Kabupaten Sumbawa Besar, Propinsi Nusa Tenggara Barat (NTB, 11.XI.2000, M. Ôhara” (2♂♂); “[TI-03-MO-027], 09°57’34”N 124°09’01”E, [West Timor: Indonesia], Desa Boentuka, alt 100m, Kecamatan Batuputih, Kabpaten Timur Tengah, Selaten, Propinsi Nusa, Tenggara Timur (NTT), 1.II.2003, M.Ôhara” (1♀); “Indonesia, [HA-06-MO-032] Halmahera, Desa Acango, Kec. Jalido, Kab. Halmaehra Barat, 26.VIII.2006, M. Kon leg. Collected from cow (Bali sapi) dung under palm trees” (2♂♂, 2♀♀); “Indonesia, [HA-06-MO-034] Halmahera, 01°07’47”N 127°28’24”E, Desa Akeramo, Kec. Sahu timor, Kab. Halmahera Barat, 26.VIII.2006, M.Ôhara, collected from cow (Bali sapi) dung” (1♀); “Indonesia, [HA-06-MO-042] Halmahera, 01°50’16”N 127°50’26”E, Desa Toweka Kec. Galela, Kab. Halmaehra Utara, 29.VIII.2006, M.Ôhara leg. collected from cow (Bali sapi) dung under palm trees” (4♂♂, 1♀); “Indonesia, [HA-06-MO-043] Halmahera, 01°48’52”N 127°48’20”E, Desa Igobula, Kec. Galela, Kab. Halmaehra Utara, 29.VIII.2006, M.Ôhara, cow (Bali sapi) dung” (2♂♂, 1ex.); “Indonesia, [TE-06-MO-044] Ternate Is., 00°45’24”N 127°20’16”E, Desa Gambesi, Kec. Pulau Ternate, Prop. Malku Utara, 30.VIII.2006, M.Ôhara leg. collected from cow (Bali sapi) dung” (1♂); “[SU-06-MO-002] Indonesia: Sulawesi, 01°50’16”N 127°50’26”E/ Cagar Alam, Bantimurung, alt. 40m, Kabupaten Maross, near Makassar, Propinsi, Sulawesi Selatan (South Sulawesi), 27.X.2006, M.Ôhara" (2♀♀), "Indonesia, "[SU-06-MO-050] Sulawesi Is., 01°15'08"N 124°48'19"E, Desa Leilern, Kec. Sonder Kab. Minahasa, Prop. Sulawesi Utara, 31.VIII.2006, M.Ôhara leg., collected from cow (Zebu) dung" (1♂); "Indonesia, "[SU-06-MO-058] Sulawesi Is., 00°48'08"N 124°12'49"E, Desa Inuai, Kec. Pasi, Kab. Bulaang Mongondow, Prop. Sulawesi Utara, 2.IX.2006, M.Ôhara leg. collected from cow (Zebu) dung, open land" (2♂♂, 2♀♀); "Indonesia, [SU-06-MO-059] Sulawesi Is., 00°59'13"N 124°14'01"E, Desa Nona Panduang, Kec. Polgar, Mongondow, Kab. Bulaang Mongondow, Prop. Sulawesi Utara, 2.IX.2006, M.Ôhara, collected from cow (Zebu) dung, open land and under palm trees" (1♀); "Indonesia, [SU-06-MO-054] Sulawesi Is., 00°01'18"N 123°56'33"E, Desa Doloduo, Kosinggolan, Kec. Dumoga Barat, Kab. Bolang Mongondow, Prop. Sulawesi Utara, 1.IX.2006, M.Ôhara, collected from cow (Bali sapi, Zebu) dung, open land" (1♀). **Laos:** "[LAOS] Piarhat, W. Vientiane 50km Vientiane Prov., 22.IV.2007, Katayama Y. leg." [EUMJ] (3♂♂, 1♀). **Sri Lanka:** "CEYLON., XII.1881-IV. 1882, G. Lewis leg./Presented from Brit. Mus. Nat. Hist. to M. CHŪJÔ, 1961, through E.B.BRITTON" [EUMJ] (1♀).

S. discolor Group

(Figs. 4F, 21C–D, 22L, 23D, 24N, 25N, 42–44)

Species included: *Sphaeridium discolor*

Distribution. Southern, Asia.

Diagnosis. This species can be distinguished from other Asian species by the long emarginations on the posterior angles of the pronotum and the very wide gula. It differs from *S. dimidiatum*, the only other species with emarginate pronotal posterior angles, not only in that the emarginations are much longer but also in that the antennal club is asymmetrical and weakly lamellate as well as the proventrite and mesoventral protrusion bear numerous strong spines whereas those of *S. dimidiatum* lack spines but have strong setae instead.

Sphaeridium discolor Orchymont, 1933

(Figs. 4F, 21C–D, 22L, 23D, 24N, 25N, 42–44)

Sphaeridium discolor Orchymont, 1933: 298 [India, Tamil Nadu, Uttar Pradesh]; Hansen, 1999: 313 (Catalogue, worldwide); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Sphaeridium dimidiatum Nakane, 1954, in Nakane *et al.*, 1954: 25–26 [misidentification: Tokara Takarajima]; revised in Jia and Ôhara (2004).

Redescription. Size medium to large, length 5.5–8.0mm, width 3.5–4.5mm. Body shape wide oval to subquadrate, moderately compressed dorsoventrally. Coloration as in Figs. 4F, 21C, with little variation; head black, labrum reddish black, prontoum black with narrow yellow-white stripe along lateral margins, not continuing around anterior angles and ended at excavation of posterior corner; elytra black on anterior half, with posterior half covered by yellow-white apical spot); epipleuron reddish on anterior area, yellow posteriorly; pygidium black to dark brown, sometimes narrowly lightened along lateral margins. Ventral base color black, lightened on gula, anterior half and along lateral margins of pronotum, and sometimes slightly lightened along ventral margins of abdominal ventrites; legs reddish brown, femora may be lightened near base and/or apex (Fig. 21D); mentum black or dark reddish, maxillary palps yellow on first segment and apical half of apical segment and reddish brown on second segment, antennae yellow with dark brown club.

Dorsal surface of head with dense uniform small punctures separated by less than their own diameter, interstices without apparent microsculpture. Eyes of normal size, ventral interocular distance about 6x width of one eye, greatly excised on anterior margin. Labrum exposed, anterior margin straight medially with dense flat golden pubesence anteriorly, surface covered in microrugae. Antennal club compact, not symmetrical, weakly lamellate (Fig. 22L).

Pronotum with sinuate posterior margin; lateral margins evenly curved, with row of very small spines; marginal beading wide, flat, continuing around anterior and posterior angles, continuing along anterior margin, posterior angles with long, distinct excavation on which beading is abruptly narrowed (Fig. 23D). Surface covered in very dense, uniform small punctures, consistent with those on head, interspaces without apparent microsculpture.

Scutellum elongate oval, more than 2x as long as wide, with sides rounded (Fig. 24N). Elytra wide, oval, apices rounded separately; sutural interval flat, continuous with marginal beading which is distinct around apex. Surface covered in dense, uniform small punctures separated by their own diameter or less, interspaces with superficial granulate microsculpture and reticulate and radiating microrugae; lacking apparent striae but with distinct radiating microsculpture; interspaces flat. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Mentum as in Fig. 42A, anterior margin straight or slightly rounded medially, not carinate, medially weakly depressed; lateral margins slightly angled, surface with sparse fine uniform punctures and dense transverse microrugae.

Proventral process convex, not distinctly raised along midline, bearing a large spine at posterior apex, surface covered in about 22 large strong spines medially and numerous long strong golden setae anteriorly and laterally (Fig. 42B–C).

Mesoventral process as in Fig. 42E–G, anterior protrusion, fusiform to teardrop-shaped, about 2x as long as wide, distinctly raised but almost flat on ventral surface, surface covered with about forty long, stout spines; posterior lip short, forming a flange around posterior margin of anterior protrusion, posterior margin rounded, continuous with lateral areas of mesoventrite, not separated by posterolateral angles of protrusion. Lateral areas with short indistinct pubesence lateral to process.

Midmetaventral disc raised as in Fig. 42H about as long as wide, surface convex throughout, lateral margins not distinctly separated from surrounding lateral areas, median furrow reaching transverse sutures, transverse sutures not strongly impressed, perpendicular to median furrow, posterior margin rounded to slightly angled; surface covered in sparse, shallow punctures separated by 4–5x their own diameter, interspaces with dense, granulate microsculpture, area posterior to transverse suture with only microsculpture. Posterior margin between metacoxae angled, with sparse irregular setous punctures near margin.

Apex of 5th abdominal segment simply rounded, without emargination, posterior margin without fringe of hairs.

Procoxae with numerous strong spines and very sparse indistinct long golden pubesence posteroventrallly (Fig. 42B), with long distinct dentiform process at internal posterior apex (Fig. 42D). Posterior margin of trochanters with uniform row of long spines which continues along posterior margin of profemora. Male protarsus modified as in Fig. 25N, with tarsomeres 1–4 shortened and widened and tarsomere 5 as long as other segments combined, distinctly wider than tarsomere 4, with apical outer margin strongly angled, apex of ventral margin produced into short blunt spine. Each hind tibia with 1–3 small strong spines on ventral surface but most commonly with 2 spines on both.

Male genitalia as in Fig. 43, ratio of median lobe:tegmen = 1.2, basal 4/5ths straight, apical 1/5 weakly angled ventrally in lateral view (Fig. 43D); median lobe wide, parallel-sided until apex which is rounded with a indistinctly truncate tip but lacking an apparent protrusion; coronal located near tip at about apical 1/10 (Fig. 43B), posterior margin of ventral opening truncate, rounded (Fig. 43C). Paramera rather narrow, tapered to rounded tips, internal surface finely pubescent but lacking fringe of hairs. Acessory sclerite (9th ventrite) about 2/7th length of aedeagus, apex roundly pointed, median ridge strong, lateral arms about 3/4 length of paramera (Fig. 43A).

Distribution. **Asia:** China (Guandong, Guangxi), India (Bihar, Tamil Nadu, Uttar Pradesh, West Bengal), Indonesia (Flores, Sulawesi, Sumba, Timor), Japan (Ryukyus, **Kyushu [new record]**), **Malaysia [new record]**, **Nepal [new record]**, Philippines, Taiwan. **Australia** (northern territory, **Queensland [new record]**, introduced). Map: Fig. 44.

Remarks. S. discolor can be easily distinguished from other Asian *Sphaeridium* from the long excavation of the posterolateral angles of the pronotum. While *S. dimidiatum* also has emarginate pronotal angles, they are much shorter and less apparent. This species had been previously recorded in Japan as the result of a misidentification by Nakane in which it had been recorded as *S. dimidiatum*. The mistake was later corrected in Jia and Ôhara (2004).

Specimens examined. **Australia:** Mt. Carbine, Queensland, 3.II.1996, Y. Nishijima// Nishijima Coll. SEHU Japan, 2014 (2♀♀). **China:** S. Guangxi, Ningming County, Shilang Mt., 1600m, X.2005, Yi et al. leg. (1♂, 1♀); Border of Guangdong and Fujian, Zaoyang vill. about 1300m, Jiolin County, XII.2005, Jin et al. leg. (1♀). **Indonesia: Sulawesi:** [SU-06-MO-050] 01º15'08"N 124º48'19"E, Desa Leilem, Kec. Sonder, Kab. Minahasa, Prop. Sulawesi Utara, 31.VIII.2006, M. Ôhara leg., collected from cow (Zebu) dung (7♂♂, 4♀♀); [SU-06-MO-051] 01º14'13"N 124º47'02"E, DS. Sonder Kawang Koan, Kab. Minahasa, Prop. Sulawesi Utara, 31.VIII.2006, M. Ôhara leg., collected from cow (Zebu) dung (3♂♂, 3♀♀); [SU-06-MO-054] 00º01'18"N 123º56'33"E, Desa Doloduo, Kosinggolan, Kec. Dumoga Barat, Kab. Bolang Mongondow, Prop. Sulawesi Utara, 1.IX.2006, M. Ôhara, collected from cow (Bali Sapi, Zebu) dung, open land (1♀); [SU-06-MO-058] 00º48'08"N 124º12'49"E, Desa Inuai, Kec. Pasi, Kab. Bulaang Mongondow, Prop. Sulawesi Utara, 2.IX.2006, M. Ôhara leg., collected from cow (Zebu) dung, open land (2♂♂, 2♀♀); **Flores:** [FL-03-MO-009] 08º39'64"S 121º19'49"E, Desa Labolewa, Kec. Aesesa, Kab. Ngada, Prop. Nusa Tenggara Timur (NTT), 25.I.2003, M. Ôhara (7♂♂, 5♀♀). **Japan: Kagoshima:** Sumiyô-Mura, Aoku, 3.X.2001, Kunoki Seiichiro leg. Label made by Satô, 2021// Yasuda Coll., SEHU Japan, 2021 (2♂♂, 2♀♀). **Amami Oshima:** 20.VII.1964, M. Nagai et al. (2♂♂, 4♀♀). **Iriomote:** 6.IV.1968, I. Iwata// Nakane Coll. 1999 (1♂); 13–16.V.1974, H. Hayakawa// *Sphaeridium dimidiatum* Gory, Det. T. Nakane// Nakane Coll. SEHU Japan, 1999 (2♀♀); Uehara, 20.XI.1983, leg. T. Moriyama (1♂♂, 4♀♀); 19–20.X.1988, M. Ôhara leg. (2♀♀); Shirahama-rindô,13.IV.1993, M. Ôhara leg. (6♂♂); Hirakubo-saki, 16.IX.1993, M. Ôhara leg. (3♂♂, 4♀♀); Yaeyama-gun, Taketomo-cho, Komi, 13.III.2017, Endô Masaki leg. Label made by Satô, 2020 (1♀). **Kuroshima:** Hori (cow dung), 24º14'50"N 123º59'58"E, 8.XII.2008, M. Ôhara, [KU-08-MO-051] (4♂♂, 6♀♀); nr. Kuroshima-tôdai (cow dung), 24º13'13"N 124º00'27"E, 8.XII.2008, M. Ôhara, [KU-08-MO-052] (2♂♂, 3♀♀). **Tokara-Takarajima:** 23.VII.1923, K. Maeda// H. Takizawa Coll., SEHU Japan, 2012 (1♂♂, 1♀♀); 26.V.1953// Nakane Coll. SEHU Japan, 1999 (3♂♂, 1♀); 29.V.1953// Nakane Coll., SEHU Japan, 1999 (1♂, 1♀); 30.V.1953// Nakane Coll., SEHU Japan, 1999 (1♂); 31.V.1953// Nakane Coll., SEHU Japan, 1999 (1♂, 2♀♀). **Malaysia:** Sabah, Liwagu Trail, 1500m, Kinbaru, 29.VIII.1998, M. Kon leg. (1♂). **Nepal:** Narayani, Takagi S.// Adhabar, 25.X.1975 (1♂). **Philippines:** Mindoro, Mt. Halcon, IV.2005 (16♂♂, 8♀♀); Mindoro, Mt. Halcon, V.2005 (8♂♂, 16♀♀); Nueva Vizcaya, Luzon, IV.2005 (10♂♂, 17♀♀). **Taiwan:** Taipei City// 14.X.1976, M. Kiuchi (3♂♂, 2♀♀,); Koupi, Hsinhua, Tainan County// 7.XI.1976, M. Kiuchi (7♀♀); Koupi, Hsinhua, Tainan County// 8.XI.1976, M. Kiuchi (6♂♂, 7♀♀); Jui-sui, Hualian County// 8.X.1976, M. Kiuchi (1♀); Puli, Nantou County// 8.X.1976, M. Kiuchi (1♀); Wushe, Nantou County// 30.X.1976, M. Kiuchi (1♀); Rokki, 30.IV.1982, leg. M. Ôhara// Nakane Coll., SEHU Japan, 1999 (1♂, 1♀); Songkang, 2000m, Nantou pref., 14.IV.1986, M. Ôhara leg. (2♂); Lan-yu Is., 18–22.IV.1986, M. Ôhara leg. (1♀).

S. flavomaculatum Group
(Figs. 4G, 45)

Species included: *Sphaeridium flavomaculatum*

Distribution. Indonesia

Diagnosis. This species is likely more primitive than the other Asian species of *Sphaeridium*. It can be easily distinguished by the coloration of the head which is yellow on the anterior half and pronotum in which the lateral yellow stripes extend narrowly along the anterior margin. It is also the only Asian species which has apparent granulate microsculpture on the head.

Sphaeridium flavomaculatum Orchymont, 1924
(Fig. 4G, 45)

Sphaeridium flavomaculatum Orchymont, 1924: 28. Indonesia, Irian Jaya, Memberamo River; Berge Henegowen, 1986: 255 (Distribution and key).

Original description in Orchymont (1924). Key to species occurring in West Papua in Berge Henegowen (1986).

Distribution. Indonesia (West Papua). Map: Fig. 45

Remarks. I was unable to examine specimens of this rare species but according to the abovementioned references, it is unique in the Asian fauna in the coloration of the head which is yellow on the anterior half and the apices of the elytra which are more closely joined than the other species in which they are separately rounded. Additionally, the surface of the head and lateral areas of the pronotum have reticulate microrugae in interspaces between punctures. This species is likely more primitive than the other Asian species (Berge Henegowen, personal communication 2022).

S. kolleri Group
(Figs. 4E, 5B, 46–48)

Species included: *Sphaeridium kolleri*

Distribution. Laos

Diagnosis. This species is likely close to the members of the *S. seriatum* species group but can be differentiated from them by its smaller size, lighter ventral coloration, narrow scutellum, and wide male genitalia with a rounded apex.

Sphaeridium kolleri Orchymont, 1925
(Figs. 4E, 5B, 46–48)

Sphaeridium kolleri Orchymont, 1925: 155. – Laos, Pak Lay.

Redescription. Medium to large, body length of paratype about 6.7 mm, width 4.1 mm. Body shape subquadrate, sides of elytra subparallel, weakly compressed dorsoventrally.

Coloration as in Figs. 4H, 46, head black; pronotum black with wide yellow stripe along lateral margins, reaching posterior margin; elytra base color black, anterior half reddish black, margin narrowly yellow posteroapically, connected to wide apical spot covering about 2/5 surface of elytra; epipleuron yellow. Ventral side base color yellow; mentum black, submentum and gula yellow, maxillary palps and antennal segments yellow; median part of mesoventrite except keel black; femora fulvous, darkened on center; trochanters dark fulvous; tibiae testaceous, spines testaceous; tarsi testaceous (Fig. 5B).

Dorsal surface of head with dense uniform punctures separated by more than their diameter, interstices without apparent microsculpture (Fig. 47A). Eyes large, ventral interocular distance 5x width of one eye, excised on anterior margin.

Pronotum with strongly bisinuate posterior margin; lateral margins gently and evenly curved, with even row of small spines; marginal beading wide, flat, continuing around anterior margin, ending before posterior angles; posterior corners forming a distinctly oblique angle, lacking emargination (Fig. 23B). Surface covered in dense uniform punctures separated by about their own diameter, though denser medially, interspaces without discernable microsculpture.

Scutellum narrow, about than 2.5x as long as wide, sides weakly curved; surface covered in dense fine punctures, consistent with surrounding elytra, interspaces without apparent microsculpture. Elytra subquadrate, sides weakly rounded; sutural interval slightly raised posteriorly, weakly convex, continuous with marginal beading, the inner margin of which disappears for a short distance near apex and which is narrow posteriorly widening laterally and anteriorly, continuing around humeral angles to scutellum. Surface covered in dense punctures separated by about their own diameter, with radiating and reticulate microrugae and irregular superficial granulate microsculpture on middle and posterior; with distinct strial punctures, with weak grooves, interspaces weakly convex. Posterolateral margins not swollen, not modified in female.

Pygidium not visible dorsally.

Mentum as in Fig. 47B, anterior margin carinate, concave behind, lateral margins weakly curved, surface with coarse setiferous punctures, interspaces with dense transverse microrugae except sometimes along anterior margin. Gula not distinctly narrow or wide, sides parallel to slightly curved.

Proventral process as in Fig. 47C, convex anteriorly, weakly tectiform posteriorly, bearing a spine at posterior apex, and with about 4 large spines medially on posterior half and many spines of reducing size laterally from central line, laterally glabrous, with few sparse hairs.

Mesoventral process distinctly longer than wide, covered in slender spines, posterior apex with two spines; posterior lip about 1/2 to 2/3 length of protrusion, not separated from surrounding mesoventrite postero-lateral angles of protrusion, surface flat, posterior apex rounded, without pubesence on surface.

Midmetaventral disc raised as in Fig. 47D, flat medially, about as long as wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow continuing to posterior margin; transverse furrows unimpressed, often only discernable centrally, area around intersection weakly impressed; surface covered large uniform punctures and dense microrugae, glabrous at center.

Apex of fifth abdominal ventrite simply rounded, without emargination, with row of short hairs along margin.

Procoxae with strong spines interspersed with very few sparse light hairs near ventral and lateral margins; with distinct dentiform process at internal posterior apex (Fig. 47C). Posterior margin of trochanters with row of long spines along anterior ventral margin, smaller spines also present out of row, row continuing along posterior margin of mesofemorae. Male protarsus slightly enlarged but terminal segment not strongly widened towards apex and exterior claw not strongly enlarged, same length as but about 3x as wide as inner claw. Hind tibiae with 3–5 moderately strong spines on ventral surface.

Male genitalia as in Fig. 46C, ratio of median lobe:tegmen = 1.2; slightly bent in lateral view. Median lobe with sides straight parallel, apex strongly rounded; dorsal and ventral surface smooth; corona located near tip, at about 1/12 length from tip. Paramera wider, apically pointed.

Distribution. Laos. Map: Fig. 48.

Remarks. I did not examine the species myself but v. Berge Henegowen examined type specimens in BMNH and the d'Orchymont collection in Brussels and was able to confirm the validity of the species. The description was written based on communications with, and photos taken by v. Berge Henegowen.

This rare species is so far only known from Pak Lay in Laos. Along with *seriatum* and *huijbregtsi*, this species has more than two spines on the ventral surface of each hindleg but can be distinguished from them by its smaller size, narrow scutellum, and much wider male genitalia.

Specimens examined. Holotype: "LECTO-/TYPE// TYPE// Laos/ Pak Lay./ 2.VIII..1918/ R.V. de Salvaza// Indo-China/ B.M.1924-315// A. d'Orchymont/ design. Shatrovskiy 1986// Sphaeridium/ kolleri Orch. Holotype/ v. Berge Henegowen/ 1989." (Examined by v. Berge Henegowen).

S. quinquemaculatum Group

(Figs. 4I–O, 5A, 11F, 19, 22D–F, 24E–G, 25E–G, 49–57, 79B, 80B, D, F)

Species included: *S. quinquemaculatum, S.* sp. 1, *S.* sp. 2

Distribution. Asia.

Diagnosis. The species of the *quinquemaculatum* group can be differentiated from other Asian species by their small size and the mesoventral process of which the protrusion is as long as wide and the posterior lip bears fine pubesence.

Sphaeridium quinquemaculatum Fabricius, 1798
(Figs. 4I–O, 5A, 11F, 19C–D, 22E, 24F, 25F, 51, 52, 56, 79B, 80B, D, F)

Sphaeridium quinquemaculatum Fabricius, 1798: 39 (as "5maculatum"). – East India ["India orientali"]; Hansen, 1999: 315 (Catalogue, worldwide); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Sphaeridium vicinum Castelnau, 1840: 60. – Syn. Orchymont, 1913: 11.

Sphaeridium tricolor Walker, 1858: 209 (secondary homonym of Dermestes tricolor Fourcroy, 1785). – Sri Lanka ["Ceylon"] – Syn.: Sharp, 1890: 357.

Sphaeridium chinense Frivaldszky, 1889: 197. – China, Jiangsu, Nanjing ["Jenking" (=Nanking), cf. Orchymont, 1913] – Syn. Orchymont, 1913: 11.

Redescription. Size very small to small, length 3.5–5.5 mm, width 2.3–3.6 mm. Body shape wide oval, not subquadrate, rather convex dorsoventrally.

Coloration as in Figs. 4I–O, 19C, 79B, highly variable; head black, labrum black to dark brown; pronotum black with yellow stripe along lateral margins, narrower medially, wider anteriorly and posteriorly, not ending just anterior to posterior margins, sometimes extended inward along anterior margin; elytral coloration highly variable, base color usually black to dark brown with 2–4 reddish orange humeral spots and a yellow apical spot which may present as a narrow or wide stripe along lateral and posterior margins and about posterior 1/4–1/3 elytral suture or as a wide area covering posterior 1/2–1/3 of elytra and with a black to dark brown spot at center on each elytra, less commonly, base color yellow with 2 dark brown to reddish humeral spots, one large black spot on center of disc, including scutellum and contacting base, and two black spots posteriorly; epipleuron yellow. Pygidium dark brown, yellow along posterior margin. Ventral side base color black to dark brown; mentum and submentum black, gula yellow, maxillary palps and antennal segments yellow, antennal club dark brown; lateral areas of pronotum, and along posterior margins of abdominal ventrites; legs dark yellow with a darkened spot at center of each femora (Fig. 5A, 19D).

Dorsal surface of head with dense, uniform punctures separated by less than their diameter, interstices without apparent microsculpture. Eyes normal size, ventral interocular distance about 5x width of one eye, excised on anterior margin. Labrum exposed or retracted under clypeus, anterior margin straight medially, with dense flat golden pubesence anteriorly, surface covered in dense transverse microrugae. Antennal club symmetrical, not compact, slightly weakly serrate (Fig. 22E).

Pronotum with distinctly bisinuate posterior margin; lateral margins evenly curved, without row of small spines; marginal beading narrow, slightly widened and becoming flat posteriorly, ending at posterior corners; posterior corners slightly oblique, lacking emargination (as in Fig. 23B). Surface covered in dense uniform punctures separated by less than their diameter, slightly larger than those on head, interspaces without discernable microsculpture.

Scutellum about 2x as long as wide, sides weakly rounded; surface covered in dense punctures consistent with those on surrounding elytra, interspaces without apparent microsculpture (Fig. 24F). Elytra ovoid, sides strongly rounded, apices rounded; sutural interval raised posteriorly, surface flat throughout, barely continuous with marginal beading which is very narrow posteriorly, widened anteriorly. Surface covered in dense uniform punctures consistent with those on pronotum, interspaces with distinct granulate microsculpture, sparse microreticulation, and sometimes longitudinal microrugae; striae distinct, though larger strial punctures not evenly aligned, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (as in Fig. 3Ca).

Pygidium flat to weakly tectiform, divided by median suture which is distinct to apex, apex rounded, slightly emarginate medially.

Mentum as in Fig. 51A, anterior margin weakly curved, marginal carina wide, flat, distinctly impressed behind; lateral margins almost straight, surface with uniform deep coarse setiferous punctures, interspaces with dense, conspicuous transverse microrugae except sometimes along posterior margin. Gula not distinctly narrow or wide, sides parallel to slightly wider posteriorly.

Proventral process as in Figs. 51B–C, 80B, tectiform, bearing a large spine at posterior apex, and two to three strong stout spines at about 1/2 length along longitudinal median line, rather distant from terminal spine, laterally with dense whitish to golden pubesence and a few sparse setae close to median stout spines.

Mesoventral process as in Fig. 11F, 51E–G, 80D, F, anterior protrusion triangular, about as long as wide, with strong spines on surface and sides, lateral and posterior surfaces with long sparse pubesence, anterior apex protruding; posterior lip about 2/3 length of protrusion, separated from surrounding mesoventrite by posterolateral corners of process, produced at lower level, surface weakly convex, with long golden pubesence.

Midmetaventral disc raised as in Fig. 51H, convex, slightly longer than wide, median furrow continuing to posterior margin, transverse furrows which are only discernable centrally, straight laterally, meeting at an oblique to 90˚ angle, area around and especially posterior to intersection impressed; surface covered in fine setous punctures, interspaces with dense microrugae. Posterior margin between metacoxae weakly but distinctly emarginate.

Apex of fifth abdominal ventrite simply rounded, with weak emargination, posterior margin without fringe of hairs.

Procoxae with strong spines interspersed with abundant long yellow pubesence; with or without dentiform process at internal posterior apex but if present, it is indistinct, small, and blunt (Fig. 51D). Posterior margin of trochanters with irregular row of spines increasing in size apically with long golden pubesence. Male protarsus modified as in Fig. 25F, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 about as long as previous segments combined, S5 distinctly wider than S4, with apical outer margin rounded with a small emargination on ventral apical corner, without pointed angular process. Hind tibiae usually with 1 small strong spine on ventral surface but may have two spines on one or both legs in rarer cases.

Male genitalia as in Fig. 52, ratio of median lobe:tegmen = 1.25; straight on basal 1/2, weakly curved on apical 1/2 when viewed laterally (Fig. 52D). Median lobe with sides parallel to apical about 1/5 at which they gently curve to meet at an apical angle, with a distinct protrusion at tip; corona located at about 1/7 length from tip (Fig. 52B); posterior margin of ventral opening ending at corona, truncate, anterior margin straight (Fig. 52C). Paramera narrow, pointed apically, dorsal surface thin, membranous, with fringe of short hairs along inner length. Accessory sclerite (9th ventrite) short, about 1/4 length of aedeagus, apex truncate to irregularly rounded, median ridge fine, arms slightly shorter than paramera (Fig. 52A).

Distribution. **Bhutan [new record]**, China (?), **Guam [new record]**, India (West Bengal), Indonesia (Java, Sumatra), Japan, **Laos [new record]**, Nepal, Philippines, Saudi Arabia, Sri Lanka, Taiwan. Map: Fig. 56.

Remarks. Originally thought to be distributed widely across Asia, detailed inspection of the male genitalia has revealed that it is in fact a complex containing at least three closely related species, *S. quinquemaculatum*, *S.* sp.1 and *S.* sp.2. *S.* sp.2 can be easily distinguished from *S. quinquemaculatum* and sp.1 by the lack of apical tubercle on the mesoventral protrusion and the male genitalia which has distinct lateral projections on the median lobe. *S. quinquemaculatum* and *S.* sp.1 are however much closer, differing only in average size and the shape of the apex of the median lobe which is tapered as in Fig. 52 in *quinquemaculatum* and parallel almost to tip which is angled in sp. 1 (Fig. 54). Except for the area around Thailand

and Laos, there seems to be a geographic divide between these two species with *S.* sp. 1 occurring throughout mainland China and S. *quinquemaculatum* occurring from Pakistan, through India, and across the island nations of Southeast Asia as far east as the Ryukyu islands in southern Japan. It was also likely introduced to Tinian in the Mariana Islands. None of the specimens examined were from mainland China but more data is needed to confirm whether or not it occurs there.

It is additionally quite similar to the newly described species *S. sundense* which can be found throughout Indonesia. It can however be differentiated by the pronotal coloration which does not extend somewhat inward along the posterior margin in *S. quinquemaculatum* as it does in *S. sundense*, as well as by the mesoventral protrusion which is about as long as wide and bearing fine pubesence on the posterior lip (Fig. 51E–G, 80D, F) as opposed to longer than wide and lacking pubesence on the posterior lip as in *S. sundense* (Fig. 76D, 80C, E) (Suzumura *et al.* 2022).

Specimens examined. **Bhutan:** Sarbhang, 300m, 31.VIII.1981, Bhakta B. leg. (1♂, 1♀) [EUMJ]. **Guam:** Umatac, Guam Is., Mariana Iss., 31.VII.2009, Y. Kusui leg.//decaying bamboo shoot (1♀). **India:** West Bengal, Pedong, 12.VII.1981, Bhakta B. leg. (3♂♂) [EUMJ]; Odisha, Cuttack, 21.VI.1989 (1♀); Delhi, 2.IX.1995 (2♀♀). **Indonesia: Flores:** [FL-03-MO-006] Desa Baramari, Kec. Nanguala, Kab. Ende, Flores, Prop. Nusa Tenggara Timur (NTT), -08˚47'88"N 121˚33'58"E, 25.I.2003, M. Ôhara leg. (4♀♀); [FL-03-MO-009] Desa Labolewa, Kec. Aesesa, Kab. Ngada, Flores, Prop. Nusa Tenggara Timur (NTT), -08˚39'64"N, 121˚19'49"E, 25.I.2003, M. Ôhara leg. (1♂); [FL-03-MO-010] Desa Sipizena, Kec. Detusoko, Kab. Ende, Flores, Prop. Nusa Tenggara Timur (NTT), -08˚43'96"N 121˚44'52"E, 26.I.2003, M. Ôhara leg. (1♂); [FL-03-MO-011] Desa Koanara, Kec. Wolowaru, Kab. Ende, Flores, Prop. Nusa Tenggara Timur (NTT), -08˚44'99"N 121˚51'02"E, 26.1.2003, M. Ôhara leg. (4♂♂, 1♀); **Halmahera:** [HA-06-MO-032] Desa Acango, Kec. Jailolo, Kab. Halmahera Barat, 26.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung, under palm trees (2♂♂, 5♀♀); [HA-06-MO-033] Desa Tedeng, Kec. Jailolo, Kab. Halmahera Barat, 26.8.2006, M. Ôhara leg., cow (Bali sapi) dung, under palm trees (5♂♂, 2♀♀); [HA-06-MO-034] Desa Akeramo, Kec. Sahu Timor, Kab. Halmahera Barat, 01˚07'47"N 127˚28'24"E, 26.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung (9♂♂, 17♀♀); [HA-06-MO-35] Desa Akediri, Kec. Jailolo, Kab. Halmahera Barat, 26.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung, under palm trees (5♂♂, 17♀♀); [HA-06-MO-037] Desa Binagara, Kec. Wasile selatan, Kab. Halmahera Timor, 00˚44'53"N 127˚48'13"E, 27.VIII.2006, M. Ôhara leg, cow (Bali sapi) dung, (10♂♂, 18♀♀); [HA-06-MO-

038] Desa Ngimadudera, Kec. Malifut, Kab. Halmahera Utara, 01˚05'39"N 127˚46'35"E, 28.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung (3♂♂); [HA-06-MO-039] Desa Tahani, Kec. Malifut, Kab. Halmahera Utara, 01˚08'14"N 127˚49'05"E, 28.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung (1♀); [HA-06-MO-041] Desa Pune, Kec. Galela, Kab. Halmahera Utara, 01˚48'55"N 127˚50'45"E, 29.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung, under palm trees (1♂); [HA-06-MO-42] Desa Toweka, Kec. Galela, Kab. Halmahera Utara, 01˚50'16"N 127˚50'26"E, 29.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung, under palm trees (6♂♂, 7♀♀); [HA-06-MO-043] Desa Igobula, Kec. Galela, Kab. Halmahera Utara, 01˚48'52"N 127˚48'20"E, 29.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung (4♂♂, 4♀♀); [HA-06-MO-044] Desa Gambesi, Kec. Pulau Ternate, Prop. Malku Utara, 00˚45'24"N 127˚20'16"E, 30.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung (6♂♂, 9♀♀); [HA-06-MO-046] Desa Bula, Kec. Pulau Ternate, Prop. Malku Utara, 00˚50'59"N 127˚20'44"E, 30.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung, under palm trees (3♂♂, 2♀♀); [HA-06-MO-048] Desa Tobololo, Kec. Pulau Ternate, Prop. Malku Utara, 00˚51'21"N 127˚20'46"E, 30.VIII.2006, M. Ôhara leg., cow (Bali sapi) dung (2♂♂, 4♀♀); **Java:** [JA-00-MO-001] Desa Cimenyan, Kec. Sukamakmur, Jonggol, Kab. Dati Il Bogor, Jawa Barat (West Java), -06˚32'50"N 107˚03'49"E, 25.X.2000, M. Ôhara leg. (2♂♂, 1♀); **Kalimantan Timur:** [KL-07-MO-008] Des. Kandolo, Kec. Teluk Pandan, Kab. Kutai Timur, -00˚18'10.2"N 117˚26'27.4"E, 12.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (3♂♂, 1♀); [KL-07-MO-010] Des. Sangatta, Kec. Sangatta, Kab. Kulai Timur, -00˚28'23.4"N 117˚31'12.9"E, 13.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (3♂♂, 3♀♀); [KL-07-MO-013] Des. Teluk Pandan, Kab. Pandan, Kab. Tukai Timur, -00˚14'45.0"N 117˚29'21.8"E, 14.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (2♀♀); [KL-07-MO-014] Des. Telihan (RPH), Kec. Bontang Barat, Kab. Bontang, 14.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (1♂, 2♀♀); [KL-07-MO-020] Des. Karya Merdeka, Kec. Samboja, Kab. Kutai Kartanegara, -01˚01'13.6"N 116˚57'16.1"E, 17.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (2♀♀); [KL-07-MO-021] Des. Wonotirto, Kec. Samboja, Kab. Kutai Timur, -00˚01'07.8"N 117˚03'36.9"E, 17.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (3♀♀); [KL-07-MO-028] Des. Karya Merdeka RT09, Kec. Samboja, Kab. Kutai Kartanegara, -01˚03'04.2"N 116˚56'52.6"E, 18.XI.2007, M. Ôhara leg., cow dung (Bali sapi), open land (4♀♀); [KL-07-MO-029] Des. Kampoh Timur, Kec. Balikpapan, -01˚14'14.1"N 116˚51'24.1"E, 18.XI.2007, M. Ôhara leg., (11♂♂, 17♀♀); **Lombok:** [LO-00-MO-027] Desa Lendang Andus, Kec. Sekotong, Prop. Nusa Tenggara Barat (NTB), 120m, -08˚44'39"N 116˚04'56"E, 6.XI.2000, M. Ôhara leg. (2♂♂, 2♀♀); **Sulawesi:** Bontongan, 29.XII.1999, M. Satô leg. (1♂, 1♀) [EUMJ]; Cagar Alam Bantimurung,Kab.

Maros, near Makassar, Prop. Sulawesi Selatan (South Sulawesi), 40m, -05˚01'08"N 119˚40'38"E, 27.X.2000, M. Ôhara leg. (2♀♀); [SU-00-MO-005] Desa Tung, Kec. Barru, Kab. Barru, Prop. Sulawesi Selatan, 2m, -04˚25'27"N 110˚36'46"E, 28.X.2000, M. Ôhara leg. (2♂♂, 2♀♀); Desa Bojo, Kec. Melusetasi, Kab. Parepare, Prop. Sulawesi Selatan (south Sulawesi), -04˚05'38"N 119˚36'57"E, 31.X.2000, M. Ôhara leg. (1♀); [SU-06-MO-050] Desa Leilern, Kec. Sonder, Kab. Minahasa, Prop. Sulawesi Utara, 31.VIII.2006, M. Ôhara leg., cow (Zebu) dung, open land (17♂♂, 5♀♀); [SU-06-MO051] Desa Sonder Kawang Koan, Kab. Minahasa, Prop. Sulawesi Utara, 01˚14'13"N 124˚47'02"E, 31.VIII.2006, M. Ôhara leg., cow (Zebu) dung (5♂♂, 5♀♀); [SU-06-MO-054] Desa Doloduo, Kosinggolan, Kec. Dumoga Barat, Kab. Bolang Mongondow, Prop Sulawesi Utara, 00˚01'18"N 123˚56'33"E, 1.IX.2006, M. Ôhara leg., cow (Bali sapi, Zebu) dung, open land (6♂♂, 3♀♀); [SU-06-MO-055] Desa Hosio, Kec. Dumoga Barat, Kab. Bolang Mongondow, Prop. Sulawesi Utara, 00˚32'23"N 124˚00'25"E, 1.IX.2006, M. Ôhara leg., cow (Bali sapi) dung, open land (1♂, 1♀); [SU-06-MO-056] Desa Ibolean, Kec. Dumoga Barat, Kab. Bolang Mongondow, prop. Sulawesi Utara, 00˚33'51"N 124˚01'31"E, 1.IX.2006, M. Ôhara leg., cow (Zebu) dung, open land (8♂♂, 6♀♀); [SU-06-MO-057] Desa Bubuhgon, Imande, Kec. Dumoga, Barat, Kab. Bolong Mongodow, Prop. Sulawesi Utara, 2.IX.2006, M. Ôhara leg., cow (Zebu) dung, open land (3♂♂, 7♀♀); [SU-06-MO-058] Desa Inuai, Kec. Pasi, Kab. Bulaang Mongondow, Prop. Sulawesi Utara, 00˚48'08"N 124˚12'49"E, 2.IX.2006, M. Ôhara leg., cow (Zebu) dung, open land (6♂♂, 9♀♀); [SU-06-MO-059] Desa Nona Panduang, Kec. Polgar Mongontow, Kab. Bulaang Mongondow, Prop. Sulawesi Utara, 00˚59'13"N 124˚14'01"E, 2.IX.2006, M. Ôhara leg., cow (Zebu) dung, open land and under palm trees (2♀♀); [SU-06-MO-060] Desa Sapa, Kec. Tenga, Kab. Minhasa Selatan, Prop. Sulawei Utara, 01˚10'43"N 124˚24'21"E, 2.IX.2006, M. Ôhara leg., cow (Zebu) dung, open land, (1♂, 1♀); [SU-06-MO-061] Desa Kalase, Kec. Pineleng, Kab. Minahasa, Prop. Sulawesi Utara, 2.IX.2006, M. Ôhara leg., cow (Zebu) dung, open land (3♂♂); [SU-06-MO-062] Desa Alatengahe, Kec. Bantimunung, Kab. Maros, Prop. Sulawesi Selatan, -05˚00'11"N 199˚36'43"E, 3.IX.2006, M. Ôhara leg., cow (Bali sapi) dung, open land (1♀); [SU-06-MO-063] Desa Bonte Bonte, Kec. Mantimunung, Kab. Maros, Prop Sulawesi Selatan, -4˚55'41"N 119˚07'02"E, 3.IX.2006, M. Ôhara leg., cow (Bali sapi) dung, open land (1♂, 2♀♀); [SU-06-MO-064] Desa Samangki, Kec. Simbang, Kab. Maros, Prop. Sulawesi Selatan, -05˚02'43"N 119˚42'43"E, 3.IX.2006, M. Ôhara leg., cow (Bali sapi) dung, open land (2♂♂); **Sumba:** [SM-03-MO-012] Desa Watumbaka, Kec. Pandawai, Kab. Sumba timur, Prop. Nusa Tenggara Timur (NTT), 28,30.I.2003, M. Ôhara and S. Hartini (2♀♀); [SM-03-MO-013] Desa Lupah Watumbaka, Kec. Pandawai, Kab. Sumba Timur, Prop. Nusa Tenggara Timur (NTT), -

09°38'75"N 120°24'14"E, 29.I.2003, M. Ôhara leg., Flight intercept trap (3♂♂, 1♀, 3ex.); [SM-03-MO-014] Desa Watuhadang, Kec. Umalulu, Kab. Sumba timur, Prop, Nusa Tenggara Timur (NTT), -09°56'16"N 120°38'50"E, 29.I.2003, M. Ôhara leg. (6♀♀); [SM-03-MO-020] Kec. Kamajawa, Kab. Kota Waingapn, Sumba timur, Prop. Nusa Tenggara Timur (NTT), -09°40'55"N 120°12'19"E, 30.I.2003, M. Ôhara leg., (1♀); [SM-03-MO-022] Desa Pametikarata, Kec. Lewa, Kab. Sumba timur, Prop. Nusa Tenggara Timur (NTT), -09°41'99"N 119°52'68"E, 30.I.2003, M. Ôhara leg. (2♂♂); **Sumbawa:** [SB-00-MO-035] Desa Batudulang, Kec. Batulanteh, Kab. Sumbawa Besar, Prop. Nusa Tenggara Timur (NTT), -08°35'31"N 117°16'38"E, 10.XI.2000, M. Ôhara leg. (5♂♂, 6♀♀); **West Sumatra:** Bukit Gompong, Sukrami, NE 20m from Padang, 19.VIII.1998, M. Ôhara leg., cow dung (1♂); **West Timor:** [TI-00-MO-039] Desa Tonlonggeru, Kec. Bolo, Kab. Bima, Prop. Nusi Tenggara Timor (NTT), -08°29'48"N 118°32'43"E, 11.XI.2000, M. Ôhara leg. (1♂); [TI-03-MO-002] Desa Penfui, Kec. Central Kupang, Prop. Nusi Tenggara Timor (NTT), -10°10'01"N 123°39'49"E, 23.I.2003, M. Ôhara leg. (1♂); [TI-03-MO-003] Desa Baumata (Fenonisa), Kec. Central Kupang, Prop Nusa Tenggara Timur (NTT), -10°11'48"N 123°40'20"E, 23.I.2003, M. Ôhara leg. (4♂♂); [TI-03-MO-026] Kelurahan Takari, Kec. Takari, Kab. Kupan, Prop. Nusa Tenggara Timur (NTT), 09°58'62"N 124°01'04"E, 1.II.2003, M. Ôhara leg. (2♀♀); [TI-03-MO-027] Desa Boentuka, Kec. Batuputih, Kab. Timur Tengah Selaten, Prop. Nusa Tenggara Timur (NTT), -09°57'34"N 124°09'01"E, 1.II.2003, M. Ôhara leg. (2♂♂, 3♀♀); [TI-03-MO-029] Desa Oekabiti, Kec. Amarasi, Kab. Kupang, Prop. Nusa Tenggara Timur (NTT), 10°10'30"N 123°49'46"E, 2.II.2003, M. Ôhara leg. (3♂♂, 2♀♀). **Japan: Iriomote Is.:** 13–16.VII.1974, H. Hayakawa leg. (1♂, 2♀♀); 6.IV.1968, I. Iwata leg. (1♂); Uehara, 20.XI.1983, M. Maegata leg. (2♂); Uehara, 20.XI.1983, Y. Moriyama leg. (2♀♀); Shirahama-rindo, 13.IX.1993, M. Ôhara leg. (9♂♂, 4♀♀); **Ishigaki Is.:** Shiraho Is., 16.V.1975, Y. Notsu leg. (1 male); Kabira, 25.III.1980, H. Okamura leg. (4♂♂, 3♀♀); Hirakubo-saki, 16.IX.1993, M. Ôhara leg. (4♂♂, 4♀♀); Okawa-bokujo, 16.IX.1993, M. Ôhara leg. (2♂♂, 1♀); Omoto, 25.III.2005, T. Kitano and Y. Satôh leg. (17♂♂, 13♀♀); **Kuroshima Is.:** Hori, 24°14'50"N 123°59'58"E, 9.VII.2008, M. Ôhara leg., cow dung (25♂♂, 17♀♀); **Yonaguni Is.:** Minami Bokujo, 25.X.2002, Y. Kikuhara leg. (1♂, 1 ex.). **Pakistan:** Hyderabad, 5.XI.1989 (2♂♂); Hyderabad, 29.III.1992 (1♀). **Philippines:** Mactan Island (near Cebu Island), Buyong Maribago Lapu-lapu city, near Tambuli Beach Villa, 3.IV.1996, S. Shimano leg. (1♂). **Sri Lanka:** "Ceylon", XII–IV. 1881–1882, G. Lewis leg. (2♀♀, 3 exs.) [EUMJ]; "Ceylon", Bentota, 21.VII.1973, Brancucoi leg. (5♂♂, 9♀♀) [EUMJ]. **Thailand:** Pathum Thani prov., Khlong 5, Khlong Luang district, 14°07'19.2"N 100°42'43.3"E, 17.IV.2013, M. Ôhara leg. from cow dung (1♀); Surat Thani prov., Tan Is., off Samui Is., 09°22'26.1"N 99°57'03.7"E, 17.IV.2013, under buffalo dung (1♀).

Sphaeridium sp. 1

(Figs. 4N–O, 5A, 19E–F, 22F, 24G, 25G, 53, 54, 57)

Description. Small to medium, body length 4.0–6.0 mm, width 2.5–3.5 mm. Body shape broadly oval, not strongly compressed dorsoventrally.

Coloration as in Figs. 4N–O, 5A, 19E, head black, labrum black to dark brown; pronotum black with yellow stripe along lateral margins, narrower medially, wider anteriorly and posteriorly, not ending just anterior to posterior margins, sometimes extended inward along anterior margin; elytral coloration with some variation, base color black, with four fulvous to dark reddish spots which may be indistinct in some individuals and are widely separated to confluent on each elytra, the two posterior spots may be divided by a stria and are occasionally confluent with lateral yellow marginal stripe which is narrow on anterior 1/3 at which it is abruptly widened and confluent with yellow apical spot which covers apical 1/3–1/8, yellow area continuing anteriorly along suture to posterior 1/3–1/2, or in rare cases, base color black, with two light reddish humeral spots, a yellow apical spot covering apical about 1/2 enclosing two small black spots; epipleuron dark brown anteriorly and fulvous posteriorly, completely dark brown, or completely fulvous. Pygidium dark brown, fulvous along posterior margin. Ventral side base color black; mentum and submentum black, gula yellow, maxillary palps and antennal segments fulvous to brown, antennal club dark brown; fulvous on lateral areas of pronotum and along posterior margins of abdominal ventrites and sometime on center of gula; legs fulvous to testaceous, with a darkened spot at center of each femora (Figs. 5A, 19F).

Dorsal surface of head with dense uniform punctures separated by less than their diameter, interstices without apparent microsculpture. Eyes normal size, ventral interocular distance about 5.5x width of one eye, excised on anterior margin. Labrum exposed, anterior margin straight medially, with dense and flat golden pubesence anteriorly, surface covered in dense transverse microrugae. Antennal club elongate, compact, slightly serrate (Fig. 22F).

Pronotum with bisinuate posterior margin; lateral margins evenly curved, without uniform row of small spines (may have a few irregularly spaced minute spines along margin); marginal beading narrow, slightly widened and becoming flat posteriorly, ending at posterior corners; posterior corners forming right angles (Fig. 23A), lacking emargination. Surface covered in dense uniform punctures separated by less than their diameter, slightly larger than those on head, interspaces without discernable microsculpture.

Scutellum about 2x as long as wide, sides weakly rounded; surface covered in dense punctures consistent to those on surrounding elytra, interspaces without apparent microsculpture (Fig. 24G). Elytra ovoid, sides strongly rounded, apices rounded separately; sutural interval raised posteriorly but flat throughout, continuous with marginal beading which is very narrow posteriorly, widened anteriorly. Surface covered in dense uniform punctures consistent with those on pronotum, interspaces with distinct dense granulate microsculpture, sparse microreticulation, and sometimes with longitudinal and radiating microrugae; striae distinct, though larger strial punctures not evenly aligned, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Pygidium only slightly visible dorsally; flat to weakly tectiform, divided by median suture which is distinct to apex, apex rounded, slightly emarginate medially.

Mentum as in Fig. 53A, anterior margin carinate, gently curved, very slightly bisinuate; lateral margins gently curved; surface with uniform deep coarse setiferous punctures, interspaces with dense, conspicuous microrugae except sometimes along posterior margin. Gula not distinctly narrow or wide, sides parallel to slightly wider posteriorly.

Proventrital process as in Figs. 53B–C, tectiform, bearing a large spine at posterior apex, and bearing two to four strong spines about 1/2 length along longitudinal median line, laterally with dense golden pubesence and sparse setae close to median stout spines.

Mesoventral process as in Fig. 53E–G, anterior protrusion triangular, about as long as wide, with strong spines on surface and sides, anterior apex protruding, lateral and posterior surfaces with long, sparse pubesence; posterior lip about 2/3 length of protrusion, separated from surrounding mesoventrite by posterolateral corners of process, produced at a lower level, surface weakly convex, with long golden pubesence.

Midmetaventral disc raised as in Fig. 53H, weakly convex medially, about as long as wide, median furrow continuing to posterior margin; transverse furrows only discernable centrally, straight laterally, meeting at an oblique angle, area around intersection impressed; surface covered in fine setous punctures except on impressed intersection, interspaces with dense microrugae. Posterior margin between metacoxae weakly but distinctly emarginate, without row of hairs.

Apex of fifth abdominal ventrite simply rounded, without emargination, posterior margin without fringe of hairs, bare medially.

Procoxae with strong spines interspersed with abundant long yellow pubesence, with small, indistinct dentiform process at internal posterior apex. Posterior margin of trochanters with irregular row of spines of increasing size apically with long golden pubesence. Male protarsus modified as in Fig. 25G, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 almost as long as segments 1–4 combined, S5 distinctly wider than S4, with apical outer margin rounded with a small emargination ventral apical corner, without pointed angular process (Fig. 53D). Hind tibiae usually with one small moderately strong spine on ventral surface but may have two spines on one or both legs in rarer cases.

Male genitalia as in Fig. 54, ratio of median lobe:tegment = 1.33; weakly curved when viewed laterally (Fig. 54D). Median lobe with sides simple, parallel until near apex which is angled at about a right angle, with a small protrusion at the tip, corona located near tip, at about 1/12 length from tip (Fig. 54B); posterior margin of ventral opening truncate, weakly curved (Fig. 54C). Paramera narrow, pointed apically, dorsal surface thin, membranous, with fringe of long hairs along inner length. Accessory sclerite (9th ventrite) short, about 1/5 length of aedeagus, apex rounded, median ridge fine, arms subequal in length to paramera (Fig. 54A).

Distribution. China (Fujian, Guangdong, Guangxi, Guizhou, Shandong, Tibet, Yunnan), Laos, Myanmar, Thailand. Map: Fig. 57.

Remarks. Previously misidentified as *S. quinquemaculatum* which is very similar externally and likely closely related but differs mainly in the shape of the male genitala but also in being on average larger than *S. quinquemaculatum*. There is a clear geographical separation between these two species as well, with *S.* sp. 1 occurring on the mainland of the Asian continent north and east of the Himalaya mountain range throughout continental China while *S. quinquemaculatum* occurs south of the Himalayas through Nepal and India and across the island nations of Southeast Asia as far east as the Ryukyu Islands in Southern Japan and Tinian in the Mariana Islands.

Specimens examined. **China:** Tibet: Zuogong, 11.VII.2006//contributed by Masahiro Kon, 2007 (1♀); East Tibet, Jiaka, about 4000m, Zhuogong County, VIII.2005. He et al. leg. (2♂♂, 6♀♀). Anhui: Mt. Huangshan, 5–18.VI.2007 (1♀). Fujian: Dongliushian, 1500m, Wuping just on the triangular area on Jiangi, Fujian, and Guangdong three province border, III.2005 (2♂♂, 11♀♀). Guangdong: Zaoyang vill. About 1300m Jiaoling County, XII.2005, Leg. Jin et al. (13♀♀, 19♂♂). Guangxi: Ningming County, Shilang Mt., 1600m, X.2005, Yi et al. leg. (7♂♂, 9♀♀). Guizhou: Gaoingshan, 1700m, Tianzhu, East Guizhou, IX.2005, Tong, et al. (1♀). Qinghai: Guoluosha, collected in ca. 4000m, Jiuzhi, VIII.2005, Li et al. leg. (1♂). Shandong: Mt. Huangshan, Anhui, 5–16.VI.2007. Yunnan: (near border Vietnam and Laos) Huang Lian Shan, 2600m, Laizhou IX.2005 (6♂♂, 4♀♀); Mt. Yinpanshan (atl. 2748m), Fuyuan County, 1–18.VI.2007 (1♂, 2♀♀). Province unspecified: Zhejiang, Fujian border, 2006// contributed by Masahiro Kon (5♂♂, 10♀♀); Border of Jiangsu, Zhejiang, and Anhui, VI.2005(4♂♂, 1♀). **Laos:** Ban Saleui, Xam Neua, 30–31.III.2005, J. Yamasako leg. [EUMJ] (1♂, 2♀♀); same label except 16–18.VI.2005 [EUMJ] (1 ex.); Myanmar-Laos border, 2005 (2♂♂, 4♀♀). **Thailand:** Phuping Palace, nr. Doi Suthep, North Thailand, 1980, Coll. N. Nishikawa (1♂).

Sphaeridium sp.2

Figs. (5A, 19A–B, 22D, 24E, 25E, 49, 50, 55)

Description. Size small, body length about 4.0–4.5 mm, width 2.5–2.8 mm. Body shape subquadrate, slightly compressed dorsoventrally.

Coloration as in Figs. 4L, 19G, head black, including clypeus anterior to epicranial suture; labrum dark brown with lateral margins lightened; pronotum black with yellow stripe along lateral margins, this stripe wider near anterior angles; elytra black to dark brown with marginal yellow stripe which is narrowest on anterior 2/5, widened at middle 1/5, and again narrowed on posterior 2/5, though not as narrow as anterior portion. Apical spot present as an extension of the marginal stripe up about 1/3 length of elytral suture. Elytra may also be orangish anteromedially, fading to yellow posteriorly and posterolaterally, with five black spots: two humeral, two spots apically on disc, and one rectangular medial spot which reaches basal margin, the two apical spots often narrowly confluent with the medial spot, narrowly darkened along suture but sutural interval consistent with surrounding area (this coloration may fade to the darker color in specimens preserved in ethanol). Epipleuron yellowish. Pygidium dark brown, lightened along posterior and lateral margins and along median suture posteriorly. Ventral side base color dark brown to black, lightened on lateral areas of pronotum and along posterior margins of metaventrite and abdominal ventrites, bright yellow on center of gula. Legs yellowish but darkened at bases and femora slightly darkened at centers (Figs. 5A, 19H). Mentum dark brown to black, maxillary palps and antennal segments fulvous, antennal club dark brown; submentum dark brown to black, gula yellow. Maxillary palpi fulvous to light brown; antennae fulvous except club which is dark brown.

Dorsal surface of head with dense uniform punctures separated by a little less than their diameter, interstices without discernable microsculpture. Eyes of normal size, ventral interocular distance about 6x width of one eye, excised on anterior margin. Labrum exposed, anterior margin straight medially, with dense and flat golden pubesence anteriorly, surface covered in dense transverse microrugae. Antennal club elongate, symmetrical, not compact (Fig. 22D).

Pronotum with bisinuate posterior margin; lateral margins gently curved, without distinctive row of short spines; marginal beading narrow anteriorly, slightly widened posteriorly; posterior corners forming right angles (Fig. 23A). Surface covered in dense uniform punctures separated by a little less than their diameter, consistent with those on head, interspaces without distinctive microsculpture.

Scutellum more than 2x longer than wide, sides sides curved, widest at about anterior 1/3 (Fig. 24E); surface with middle covered in uniform punctures separated by about their own diameter, less dense than puctures on surrounding area of elytra, interspaces without apparent microsculpture, smooth along margins. Elytra subquadrate, lateral sides weakly curved, almost parallel, apices rounded separately. Sutural interval flat, slightly raised posteriorly, continuous with marginal beading which is very narrow posteriorly, widened anteriorly, continuing around humeral angles to scutellum. Surface covered in dense uniform punctures separated by about their own diameter, though much denser around scutellum, a bit larger than those on pronotum and head, interspaces with distinct dense granulate microsculpture, sparse microreticulation, and indistinct longitudinal and radiating microrugae; striae distinct at center, though larger strial punctures not evenly aligned, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Pygidium weakly tectiform, median suture distinct throughout.

Mentum as in Fig. 49A anterior margin gently curved, very slightly bisinuate; lateral margins gently curved; surface with uniform deep coarse setiferous punctures separated by about 2x their diameter, interspaces with dense transverse microrugae except sometimes along posterior margin. Gula not distinctly narrow or wide, sides parallel to slightly widened posteriorly.

Proventral process as in Fig. 49B–C, narrow between procoxae, weakly tectiform posteriorly, bearing a large spine at posterior apex, and bearing two small strong spines situated close together along longitudinal median line at about apical 1/3, laterally with a few weaker spines and somewhat sparsely pubescent.

Mesoventral process as in Fig. 49E–G, anterior protrusion triangular, about as long as wide, anterior and lateral sides gently sloping, anterior apex not protruding; with strong spines on surface and sides, lateral surfaces with 2–3 long hairs; posterior lip about 4/5 length of protrusion, separated from surrounding mesoventrite by posterolateral corners of process, produced at a lower level, surface flat to weakly convex, with sparse long, golden pubesence.

Midmetaventral disc raised as in Fig. 49H, convex, wider than long, median furrow continuing to posterior margin, transverse furrows only discernable centrally, straight laterally, not meeting at an oblique angle, area around intersection impressed; surface covered in fine setous punctures except on impressed intersection, interspaces with dense microrugae. Posterior margin between metacoxae weakly but distinctly emarginate, without row of hairs.

Abdominal apex of fifth ventrite simply rounded, without emargination.

Procoxae with strong spines interspersed with abundant long yellow pubesence, with or without minute dentiform process at internal posterior apex (Fig. 49D). Posterior margin of trochanters without row of spines but with row of sparse setae instead. Male protarsus modified as in Fig. 25E, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 almost as long as segments 1–4 combined, S5 distinctly wider than S4, with apical outer margin sinuate with ventral apical corner angled, surface near angle with two small setous puctures. Hind tibiae with one to two small moderately strong spines on ventral surface.

Male genitalia as in Fig. 50, ratio of median lobe:tegment = 1.3; straight on basal 1/2, weakly curved on apical half when viewed laterally (Fig. 50D). Median lobe with subapical lateral swellings at about 1/5 length from tip, appearing almost spike-like in some specimens, lateral sides basal to swellings weakly convex, apical to swelling parallel to apex which is curved to a small protrusion at the tip; corona located just apical to lateral swellings (Fig. 50B); posterior margin of ventral opening rounded (Fig. 50C). Paramera narrow, pointed apically, dorsal surface thin, with fringe of long hairs along inner margin. Accessory sclerite (9th ventrite) about 2/5 overall length, apex rounded, median ridge, fine, narrow, lateral arms slightly shorter than paramera (Fig. 50A).

Distribution. Currently only known from the type locality, of Pedong, West Bengal in northeast India.

Remarks. Very similar to *S. quinquemaculatum* and *S.* sp.1 but can be differentiated from them by the slightly wider mesoventral keel that gradually slopes anteriorly and lacks a small protrusion at the anterior apex as found in *S. quinquemaculatum* and *S. continens* (Figs. 51E–F, 58E–F).

Type material. Holotype: Darjeeling District, India, Bhakta B. leg.// Pedong, 12.VII.1981 [EUMJ] (1 male). Paratypes: Same locality [EUMJ] (1♂, 1♀).

S. scarabaeoides Group

(Figs. 1–2, 3a, Ca, 4A–B, 5A, 7–10, 11A–C, 12–14, 16–17, 21G–F, 22N–M, 24O–P, 25O–P, 58–62)

Species included: *Sphaeridium lunatum, S. scarabaeoides*

Distribution. Northern, Europe, Asia, North America (introduced)

Diagnosis. This group can be differentiated from others by their large size and northern distribution. The mesoventral protrusion is fusiform in both species, with the posterior lip not separated from the surrounding mesoventrite by posterolateral angles of the protrusion. The proventrite is convex and has numerous strong spines medially and the posterior surface of the metaventral disc bears an even row of stout hairs. The ventral coloration is dark which also sets it apart from other large Asian species of the *seriatum* group with the exception of *S. discolor*, but the species of the scarabaeoides group lack the emargination of the posterior angle of the pronotum as is characteristic of *S. discolor*.

Sphaeridium lunatum Fabricius, 1792

(Figs. 4B, 21E–F, 22N, 24P, 25P, 58, 59, 61)

Sphaeridium lunatum Fabricius, 1792: 78. – Germany [“Germania”]; Smetana, 1988: 133 (Description, North America); Hansen, 1999: 314 (Catalogue, worldwide); Ryndevitch *et al.*, 2021: 481 (Species records, Far East Russia); Suzumura, 2020: 343–347 (Species record, Japan); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Dermestes lunatus: Marsham, 1802: 66.

Sphaeridium bipustulatum: Herbst, 1792 (misinterpret. of *Sphaeridium bipustulatum* Fabricius). – Syn.: Schönherr, 1806: 100.

Sphaeridium bimaculatum Ragusa, 1891: 136.

Redescription. Large, body length 6.5–8.0 mm, width 3.8–5.1 mm. Body shape oval, not strongly compressed dorsoventrally.

Coloration as in Figs. 4B, 21E, with some variation, head black, labrum black to dark brown; pronotum usually completely black, slightly lightened along lateral marginal beading anteriorly extending a variable distance posteriorly, not usually reaching posterior margin; elytra base color black, with two somewhat indistinct dark reddish humeral spots that do not have defined borders, also with dark yellow apical spots which are variable in size, small, almost indiscernible to covering apical 1/3, not reaching elytral suture, rarely contacting posterior margin, never extending anteriorly along lateral margins; epipleuron dark anteriorly, variably lightened posteriorly; pygidium dark brown throughout. Ventral base coloration black to dark brown, gula sometimes yellow, sometimes lightened on lateral areas of proventrite, posterior margin of metaventrital field between metacoxe and posterior margins of abdominal ventrites, Legs dark brown, sometimes lightened on trochanters, protibiae, and anterior part of meso- and metatibiae (Fig. 21F) Mentum and submentum black, gula black or yellow; maxillary palpi dark brown, yellow on apical half of terminal segment.

Dorsal surface of head with dense, uniform punctures separated by about their own diameter or slightly less, interstices without apparent microsculpture. Eyes of normal size, ventral interocular distance about 4.25x width of one eye, excised on anterior margin. Labrum exposed, anterior margin straight to slightly concave, with dense flat golden pubesence anteriorly, surface covered in dense transverse microrugae. Antennal club symmetrical, elongate, weakly compact (Fig. 22N).

Pronotum with base weakly bisinuate, not strongly bisinuate; lateral margins strongly rounded, almost angled, without row of small spines; marginal beading wide, flat, continuing around anterior margin, ending just beyond posterior angles; posterior angles forming an oblique angle (as in Fig. 23B), lacking emargination. Surface covered in dense uniform punctures consistent with those on head; interspaces without apparent microsculpture.

Scutellum wide, triangular, a little longer than 2x width, sides straight to slightly rounded (Fig. 24P); surface covered in dense punctures consistent with those on surrounding elytra, head, and pronotum, interspaces without apparent microsculpture. Elytra ovoid, sides rounded, apices only slightly rounded separately, only apex of pygidium exposed in dorsal view; sutural interval raised posteriorly, surface flat, continuous with marginal beading which is very narrow posteriorly, slightly widened anteriorly. Surface covered in dense uniform punctures consistent with those on head and pronotum, interspaces with superficial granulate microsculpture posteriorly, entirely with reticulate and sometimes radiating microrugae; striae indistinct, sometimes barely discernable as longitudinal microrugae and few, sparse larger punctures irregularly arranged, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (as in Fig. 3Ca).

Pygidium not to barely visible dorsally, flat to weakly convex, divided by median suture which is distinct to apex, apex rounded.

Mentum as in Fig. 58A, anterior margin straight to weakly and evenly concave, not carinate but beaded, weakly depressed behind; lateral margins gently curved, surface with uniform coarse setous punctures, interspaces with dense granulate microsculpture. Gula not distinctly narrow or wide, sides parallel to slightly wider posteriorly.

Proventral process as in Fig. 58B–C convex, without distinct median longitudinal ridge, bearing a large spine produced from ventral surface very near posterior apex and many large spines which become more numerous and less stout anteriorly, laterally with dense long pubesence.

Mesoventral process as in Fig. 58E–G, anterior protrusion elongate fusiform, about 3x as long as wide, anterior apex gently sloped, posterior apex protruding below posterior lip; with about 38 long strong spines on ventral and lateral surfaces, posterior apex usually with two spines; with sparse indistinct pubesence only posterolateral to protrusion; posterior lip short, about 1/5–1/4 length of protrusion, not distinctly separated from lateral areas of metaventrite by posterolateral corners of protrusion, not produced at a different level, surface flat to weakly convex medially, surface without pubesence.

Midmetaventral disc raised as in Fig. 58H, flat, about as long as wide, median furrow continuing to transverse furrows which are not impressed, only discenable medially or sometimes not discernable at all, straight laterally, not meeting at an angle, area around intersection weakly impressed; surface anterior to transverse furrows with fine uniform punctures, interspaces and area posterior to transverse furrows with dense microrugae. Posterior margin between metacoxae curved to weakly angled, with a row of long golden hairs produced along posterior surface.

Apex of fifth abdominal ventrite rounded, almost straight medially, without emargination, area medially near apex bare, with row of close setous punctures along margin.

Procoxae with strong spines interspersed with abundant long, fine pubesence, which is dense dorsoventrally (Fig. 58B), with long dentiform process at interior posterior apex; trochanters with uniform row of spines along ventral margin continuing along margin of femora (Fig. 58D). Male protarsus strongly modified, with tarsomeres 1–4 shortened and widened and tarsomere 5 longer than all other segments combined, much wider than other segments, with apical outer margin strongly angled, with weak emargination just above apex of ventral margin which forms a small, short angle. Each hind tibia with 1–3 small strong spines on ventral surface but most commonly with 2 spines on each.

Male genitalia as in Fig. 59, ratio of median lobe: tegmen = 1.1; ventral surface of median lobe straight, dorsal surface weakly curved apically in lateral view (Fig. 59D). Median lobe with sides parallel from base to about apical 1/14 at which they curve and meet at and oblique angle, forming a short apical protrusion; corona at about apical 1/10; posterior margin of ventral opening located near tip, very wide, truncate (Fig. 59B). Paramera narrow, dorsal surface slightly wider than ventral, apices pointed, internal margin with short dense pubesence. Acessory sclerite (9th ventrite) relatively long, about 1/3 length of aedeagus, apex pointed, median ridge strong, along almost full length of sclerite, arms about 4/5ths length of paramera (Fig. 59A).

Distribution. Europe: Andorra, Armenia, Austria, Azerbaijan, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Georgia, Germany, Great Britain, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Poland, Romania, Serbia, Slovenia, Spain, Sweden, Switzerland, Ukraine. Russia: Altai, Crimea, Irkutsk, Karachay-Cherkessia, Karelia, Khakassia, Kuril Islands (Kunashir), Leningrad, Moscow, Omsk, Saratov, St. Petersburg. Asia: Cyprus, Iran, Israel, Japan, Jordan, Kazakhstan, Mongolia, Syria, Tajikistan, Tunisia, Turkey, Uzbekistan. North America: Canada (Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Saskatchewan), U.S.A. (Alabama, Arizona, California, Colorado, Connecticut, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, South Dakota, Tennessee, Texas, Utah, Virginia, Washington, Wisconsin, Wyoming). Map: Fig. 61.

Remarks. Similar in appearance to and often living together in the same dung pats with *Sphaeridium scarabaeoides* but can be differentiated by the following characters: the elytral apical spot is not extended anteriorly along the lateral margins (extended at least half length along lateral margins in *S. scarabaeoides* though indistinct in some specimens); ventral surface of femora dark throughout though sometimes slightly reddish at extreme apices (yellow with a dark spot at center of each femora or at least lightened at base and apex in *S. scarabaeoides*); median lobe of aedeagus is parallel until just before tip which forms an oblique angle (gradually tapered to apex, with sides gently curved and tip acute in *S. scarabaeoides*).

Specimens examined. **Asia. Japan:** Hokkaido, Ebetsu, Ishikari, Yonemura Farm, 2.VIII.2020 cow dung, H. Yamamoto, A. Suzumura leg. (3♂♂, 9♀♀, 2 exs.); Tsukisamu, 15.VII.1991/A. Tanaka Coll., SEHU Japan, 2005 (1♂, 3♀♀); same label except 6.VIII.1991 (2♀♀); Rishiri, Kutsugata, Shinminato, 19.VII.1990, M. Satô leg. (1♂, 1♀); Nopporo, Ebetsu, 10.V.1987, M. Ôhara (1♀). **Russia:** [SK-02-MO-001] Sakhalin, Sokol Field Station, 8km S of Dolinsk, 30.VII.2002, 47˚14.570'N, 142˚46'540'E, M. Ôhara; dead chicken trap (1♂); [SK-02-MO-006] Sakhalin, Ca, 15km ENE of Sokol Town, the pass near g.Bychek, 31.VII.2002: M. Ôhara, 47˚18.149'N, 142˚55.039'E (1♀); [SK-02-MO-026] Sakhalin, Pervomayskoye, from cow dung, 49˚57.495'N 143˚15.991'E, 10.VIII.2002, M. Ôhara (1♂). **Europe. France:** [FR-06-MO-004] Haute-Corse (2B), Between Barchetta and Ponte Nuovo, 42˚30'29.1 "N 09˚19'37.5E, 23.V.2006, M. Ôhara (2♂♂); [FR-06-MO-007] (sweeping), Corse-du-Sud (2A), Ajaccio, alt. 167m, 41˚56'01.6"N 08˚40'59.0E, 24.V.2006, M. Ôhara (4♂♂, 2♀♀); [FR-06-MO-023] (from cow dung), Aveyron (12), St. Léons, alt. 750m, nr. Millau, 44˚13'08.3 "N 02˚58'57.1E, 30.V.2006, M. Ôhara (1♀); Lobes Gers, VI.1958, Monguillon leg. [EUMJ] (1♀). **Germany:** Schnellenberg, 4.III.1952, Plath jr./Nakane coll. SEHU Japan, 1999 (1♀). **Italy:** Rome, 17.IV.1977/A. Tanaka coll. SEHU Japan, 2005 (2♂♂). **Poland:** Runwald, Olszynek, 29.VIII.2004, M. Ôhara (2♂♂, 2♀♀). **Slovakia:** CSSR, Chlmec, okr. Humenne, lgt. V. Tyr (1♀). **Uzbekistan:** USSR, Chamzabad 1400m, 4.V.1975 [EUMJ] (1♂).

Sphaeridium scarabaeoides Linnaeus, 1758

(Figs. 1–2, 3A, Ca, 4A, 5A, 7–10, 11A–C, 12–14, 16–17, 21G–H, 22M, 24O, 25O, 60, 62)

Dermestes scarabaeoides Linnaeus, 1758: 356. – Europe [“Europa”].

Sphaeridium scarabaeoides: Fabricius, 1775: 66; Hansen, 1999: 315 (Catalogue, worldwide); Berge Henegowen, 1987: 3 (Key); Navarrete-Heredia, 2009: 212 (Species record, Mexico); Sazhnev *et al.*, 2021: 272 (Species record, Far East Russia); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Hister testudinarius Degeer, 1774: 345 (replacement name for *Dermestes scarabaeoides* Linnaeus, 1758).

Dermestes quadrimaculatum Schrank, 1781: 25. – Austria, Vienna. – Syn.: Rossi, 1790.

Dermestes tricolor Fourcroy, 1785: 24. – France, Paris [“…Parisiensis”]. – Syn.: Olivier, 1790: (no.15) 4; Ganglbauer, 1904: 271.

Dermestes quadrimaculatus Marsham, 1802: 66 (primary homonym of *Dermestes quadrimaculatu*s Schrank, 1781 and secondary homonym of *Sphaeridum quadrimaculatum* Herbst, 1783). – Britain [“Britannia”]. – Syn.: Sainte-Claire Deville, 1919: 233.

Sphaeridium crenatum Palisot de Beauvois, 1817: 158. – U.S.A. [“États-Unis d’Amérique”]. – Syn.: LeConte, 1861: 47.

Sphaeridium pictum Ménétriés, 1832: 172. – Azerbaijan, Lenkoran. – Syn: Smetana, 1978: 35).

Sphaeridium pictum Faldermann, 1835: 235 (as p. “285”). – Syn.: Smetana 1978: 35.

Sphaeridium quadrimaculatum Küster, 1845: no.23. – Italy, Sardegna, Cagliari. – Syn.: Ganglbauer, 1904: 271.

Redescription. Medium to large, body length 5.5–8.5 mm, width 3.7–5.0 mm. Body shape oval, not compressed dorsoventrally.

Coloration as in Figs. 4A, 21G, with some variation; head black, labrum black; pronotum base color black, variably lightened along lateral margins, without narrow marginal stripe though weakly testaceous on beading, with narrow marginal stripe from anterior angle to posterior angle, or variably shortened and/or interrupted; elytral base color black, with two distinct reddish humeral spots and variable fulvous apical spot covering apical about 1/4–1/5 which is extends anteriorly along lateral margins to about 1/2 length, often darkened at or near apex, elytral suture dark, black to testaceous; epipleuron dark anteriorly becoming fulvous or light testaceous posteriorly, lateral margin narrowly fulvous along length. Pygidium black to light brown. Ventral base color black; mentum and submentum black, gula lightened at least basally, dark testaceous, maxillary palps testaceous, sometimes lightened on apical 1/3 of terminal segment, antennal segments testaceous, club dark brown; lateral margins of pronotum with narrow fulvous stripe, metaventrital field sometimes testaceous posterior to transverse sutures, narrowly testaceous to fulvous on posterior margins of abdominal segments; legs fulvous to testaceous with a darkened spot at center of each femora (Figs. 5B, 21H).

Dorsal surface of head with dense, uniform punctures separated by less than their own diameter except alround smooth epicranial sutures, interstices without apparent microsculpture. Eyes of normal size, exceised on anterior margin. Labrum usually exposed, anterior margin straight medially, with very dense row of golden pubesence along anterior margin, surface with 2–3 rows of setous punctures on anterior half exposed half, basally with dense tranverse microrugae. Antennal club symmetrical, compact (Fig. 22M).

Pronotum with posterior margin weakly bisinuate; lateral margins strongly curved to roundly angled, with uniform row of very small spines; marginal beading narrow, flat, continuing around anterior margin and posterior angles, continuing narrowly some distance along basal margin; posterior angles forming a distinctly oblique rounded angle, lacking emargination (as in Fig. 23B). Surface covered in dense uniform deep punctures, consistent with those on head, interspaces shining, without discernable microsculpture.

Scutellum about 2.5x as long as wide, sides straight; surface covered in dense punctures consistent to those on surrounding elytra, interspaces without apparent microsculpture (Fig. 24O). Elytra ovoid, sides weakly rounded, apices rounded separately; sutural interval raised posteriorly but flat throughout, continuous with marginal beading which is narrow posteriorly, widened anteriorly, continuing around humeral angles to scutellum. Surface covered in dense uniform punctures slightly smaller and denser than those on pronotum, interspaces anteriorly with only radiating microrugae, posteriorly with denser and more numerous microrugae; striae indistinct, interspaces flat. Posterolateral margins inside beading slightly swollen in female (Fig. 3Ca).

Tip of pygidium visible dorsally; flat to weakly convex, median suture indistinct throughout, apex rounded.

Mentum as in Fig. 60A, anterior margin weakly carinate medially, gently curved, very slightly bisinuate, lateral margins curved, surface concave anteromedially, surface with coarse setiferous punctures separated by 1–2x their diameter, interspaces with dense granulate microsculpture. Gula not distinctly narrow or wide, sides parallel to slightly wider posteriorly.

Proventrital process as in Figs. 60B–C, convex, forming a large spine at posterior apex, bearing numerous strong spines medially, with long dense golden setae laterally.

Mesoventrital process as in Figs. 11C, 60E–G, anterior protrusion elongate-fusiform, about 4x as long as wide, anterior apex sloping, ventral and lateral surfaces with numerous long strong spines interspersed with sparse long setae, posterior apex protruding below posterior lip; posterior lip about 1/4 or less length of protrusion, continuous with surrounding mesoventrite, not distinctly separated by posterolateral corners of process, often angled ventrally, protruding below median anterior apex of metaventrite, surface concave where it contacts anterior protrusion, slightly convex posteriorly, without pubesence.

Midmetaventrital disc raised as in Fig. 60H, convex, longer than wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow continuing to transverse furrows; transverse furrows, if discernable, only discernable centrally, straight laterally, meeting at an oblique angle; area around intersection weakly concave; surface anterior to median furrows covered in coarse punctures separated by 1–2x their diameter, with dense but shallow granulate microsculpture on lateral areas and posterior to transverse furrows. Posterior margin between metacoxae weakly rounded, with a row of long golden hairs produced along posterior surface.

Apex of fifth abdominal ventrite simply rounded, without emargination, posterior margin without fringe of hairs.

Procoxae with strong spines and sparse long, weak pubesence around ventral margin (Fig. 60B), with somewhat blunt dentiform process at internal posterior apex (Fig. 60D). Posterior margin of trochanters with uniform row of spines continuing along posterior margins of femora. Male protarsus modified as in Fig. 25O, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 distinctly longer than the other segments combined, S5 distinctly wider than S4, with apical outer margin strongly rounded to angled, bearing a strong setae at or near apex, ventral apical corner forming blunt apical process, with or without a small emargination just dorsal to it. Hind tibiae each with 1–3 strong spines on ventral surface but usually with 2 on both.

Male genitalia as in Fig. 14, ratio of median lobe:tegmen = 1.35; basal 1/2 straight, apical 1/2 weakly curved in lateral view (Fig. 14D). Median lobe with sides simple, weakly rounded, gently tapered to apex, with only a small weak protrusion at tip; corona located at about 1/7 length from tip (Fig. 14B); posterior margin of ventral opening located a bit anterior to corona, truncate, anterior margin weakly curved (Fig. 14C). Paramera narrow, pointed apically, dorsal and ventral surfaces similarly shaped, with fringe of short pubesence along inner length. Accessory sclerite (9th ventrite) long, about 1/3 length of aedeagus, apex pointed, median ridge distinct, arms subequal in length to paramera (Fig. 14A).

Distribution. **Europe:** Armenia, Austria, Azerbaijan, Azores, Belarus, Belgium, Bosnia Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Georgia, Germany, Great Britain, Hungary, Ireland, Italy, Latvia, Lithuania, Macedonia, Netherlands, Norway, Poland, Portugal, Romania, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine. **Russia:** Central Territory, East Siberia, Far East, Northern Territory, West Siberia. **Africa:** Tunisia, Democratic Republic of the Congo (introduced). **Asia:** China (Heilongjiang, Inner Mongolia, Liaoning, Shanxi), Iran, Israel, Japan, Kyrgyzstan, Kazakhstan, Mongolia, Tajikistan, Turkey, Uzbekistan. **North America** (introduced): Canada (Alberta, British Columbia, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Saskatchewan), U.S.A. (Arizona, California, Colorado, Connecticut, Delaware, District of Columbia, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, Nevada, New Hampsire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming). **Pacific:** Hawaii (introduced). **Central America** (introduced): Mexico. Also recorded to be introduced in the Australasian region. Map: Fig. 62.

Remarks. Similar in appearance to and often living together in the same dung pats with *Sphaeridium lunatum* but can be differentiated by the following characters: the elytral apical spot is extended anteriorly at least half length along the lateral margins (not extended along lateral margins in *S. scarabaeoides*); ventral surface of femora yellow with a dark spot at center of each femora or at least lightened at base and apex in *scarabaeoides* (dark throughout though sometimes slightly reddish at extreme apices); median lobe of aedeagus gradually tapered to apex, with sides gently curved and tip acute (parallel until just before tip which forms an oblique angle in *lunatum*).

Specimens examined. **Asia. China:** Inner Mongolia, San-Shi-Liu-Ling-Chang, Erlun County, 25–30.VI.2005 (2♂♂, 1♀); Boro Horo Shan, Jining Ining-H-Sien, 44˚06'SS, 81˚56'VD, Snizek leg. (1♂); Yablonia, East-Manchuria, VII.1940, A.S.Loukashiin leg. (1♀); Border of Jiangsu, Zhejiang, and Anhui, VI.2005 (1♀). **Japan: Hokkaido:** Rishiri, Kutsugata, Shinminato, 16.VIII.1990, M.Satô leg. (2♂♂, 7♀♀.); Rishiri, Misaki, 30.VIII.2019. R. Satô leg. (1♂); Okushiri Is., 10.VIII.1986, M.Munakata (1♂, 1♀); same data but 19.VII.1968 (1♂); same location but 28.VI.1956, K. Umeya leg. (4♂♂, 2♀♀); Okushiri Is., Kyushimayama, 6.VIII.1964, Y.Komiya leg. (1♀); Hakodate, 19.VI.1952, K.Homma (1♂, 2♀♀); Hakodate, Kawakaracho, 18.VI.1951, K.Homma (1♂); Suttu, S.Hokkaido, 27.V.1988 (loc.1), M.Ôhara and S.Kudo leg. (1♀); Hanazono-bokujo, Niseko, Kutchan, 19.VIII.1994, M.Ôhara (1♂, 1♀); Hagino, Shibecha, 26.VII.1998, Y.Nishijima (1♂, 2♀♀); Shiranuka, 25.VI.1985, M.Ôhara leg (1♂); Somai, Koshimizu, Kitami, 17.V.1948, K.Buei leg. (1 ex.); Kenebetsu, Nemuro, 9.VIII.1952, T. Kumata leg.//in cow dung (2♂♂, 1♀); same data but 2.VIII.1973 (1♂, 3♀♀); Shiretoko-rindo, Utoro, Shari, 5.VI.1992, M.Ôhara leg. (1♀); Sapporo, 7.V–9.VI.1975, M.Kiuchi leg. (20♂♂, 22♀♀, 1 ex.); Obihiro, 23.VI.1985, M.Ôhara leg. (6♂♂, 1♀); Satsunai, 8.VIII.1968, H.Torikura leg.//H.Takizawa coll., SEHU Japan, 2012 (1♂, 1 ex.); Shintoku//27.V.1975, M.Kiuchi leg. (2♂♂, 2♀♀); Tsukisappu, 25.VII.1954, K.Mori//Nakane coll., SEHU Japan, 1999 (1♀); Tsukisamu, 15.VII.1991//A.Tanaka coll., SEHU Japan, 2005 (2♀♀); Yuubari, Kagoshima-rindo, 11.VIII.1988//Nishijima coll., SEHU Japan, 2014 (1♀.); Ishikarimachi, Ishikari, 13.IX.1998, T.Fujisawa; Echanankeppu, Kamikawa-Cho, 13.V.1975, N.Yasuda leg.//Yasuda coll., SEHU Japan, 2020 (1♂); Shirakawa, Kamikawa, 24.V.1975, N.Yasuda leg.// Yasuda coll., SEHU Japan, 2020 (2♂♂); ToyÔhara, Kamikawa, 23.V.1975, N.Yasuda leg.// Yasuda coll., SEHU Japan, 2020 (2♂♂); **Aomori:** Shiriya-Shimokitaguni, 5.VIII.1958, A.Abe leg.//Nakane coll. SEHU Japan, 1999 (1♂); Nanatsutaki (Kodomari), 18.V.1975, A.Abe leg.//Nakane coll. SEHU Japan, 1999 (1♀); Towada, 7.VIII.1964, K.Masumoto leg.// Nakane coll. SEHU Japan, 1999 (1♀); **Iwate:** Kuriyagawa, 20.V.1974, H.Hayakawa leg. (1♀). **Russia:** [SK-20-MO-026] Sakhalin, Pervomayskoye, from cow dung, 49˚57.495'N 143˚15.991E, 10.VIII.2992, M.Ôhara leg. (4♀♀); Sakhalin, Maoka, 7.VIII.1938, H.Hasegawa leg.//Nakane coll. SEHU Japan, 1999 (3♂♂, 1♀, 1 ex.). **Europe. France:** [FR-06-MO-007] (sweeping), Corse-du-Sud, Ajaccio, alt. 167m, 41˚56'01.6"N 008˚40'59.0", 24.V.2006, M.Ôhara leg. (1♂); [FR-06-MO-023] (from cow dung), Aveyron, St. Leons, alt. 750m, nr. Millau, 44˚13'08.3"N 002˚58'57.1"E, 30.V.2006, M.Ôhara leg. (2♂♂, 4♀♀). **Poland:** Grunwald, Olszynek, 29.VIII.2004 (2♂♂, 1♀). **Switzerland:** Soleve, Geneva, 7.VIII.1965, A.Richter leg.//H.Takizawa coll., SEHU Japan, 2012 (1♂, 1♀, 1 ex.). **N. Africa:** "Triest", Matsumura// 28.VII.1902 (1♂). **North America. United states:** Milwaukee, Wisconsin, VI.1951, Silmar leg. (1♂, 1♀); Urbana, Illinois, 9.VIII.1980, A.Tanaka leg.//A.Tanaka coll, SEHU Japan, 2005 (1 ♂); Ecuador, El Batan, 27.VII.1982, A.Tanaka leg.//A.Tanaka coll. SEHU Japan, 2005 (6♂♂, 3♀♀).

S. seriatum Group

(Figs. 3Cb–c, 4E, 5B, 6A–C, 20, 22H–J, 24I–L, 25I–L, 63–74)

Species included: *Sphaeridium huijbregtsi, S. seriatum, S. severini, S. vitalisi*

Distribution. Asian

Diagnosis. This group can be differentiated from other Asian *Sphaeridium* by their large size (> 6 mm) and light ventral coloration. The proventite is convex and bears many strong spines and while the mesoventral protrusion is variable in width, it is always carinate to fusiform, without posterolateral angles extending to separate the posterior lip from the surrounding mesoventrite.

Sphaeridium huijbregtsi Berge Henegowen, 1986
(Figs. 4E, 5B, 20A–B, 24I, 25I, 63, 64, 71)

Sphaeridium huijbregtsi Berge Henegowen, 1986: 253–257. – Indonesia, Halmahera, Irian Jaya.

Description. Body size large, length 7.7–8.5 mm, width 4.3–4.7 mm. Body shape broadly oval, sides of elytra subparallel, weakly compressed dorsoventrally.

Coloration as in Figs. 4E, 20A, head black, labrum black to dark brown; pronotum black with yellow stripe along lateral margins, slightly wider anteriorly, ending before posterior margin; elytra base color black, margin narrowly yellow posteroapically, not connected to weak apical spot covering less than 1/5 surface of elytra; epipleuron irregularly yellow and light brown. Pygidium dark brown, fulvous along lateral edges of posterior margin.

Ventral side base color yellow; mentum and submentum fulvous, gula yellow, areas lateral to gula fulvous with a dark brown spot at center of each, maxillary palps and antennal segments fulvous to brown, antennal club dark brown; lightly darkened on central part of proventrite, strongly darkened on middle and lateral areas of metaventrite; each abdominal segment yellow with 5–6 dark brown spots not reaching the posterior margin; all femora fulvous with dark brown spots at center though spots on profemora may be lighter and not as distinct; trochanters dark fulvous; tibiae fulvous, spines testaceous; tarsi testaceous (Fig. 20B).

Dorsal surface of head with dense uniform punctures separated by less than their diameter, interstices without apparent microsculpture. Eyes normal size, ventral interocular distance 3.78x width of one eye, excised on anterior margin. Labrum exposed, anterior margin straight to weakly concave medially, with dense and flat golden pubesence anteriorly, surface covered in dense transverse microrugae with irregularly arranged setous punctures separated by about 2x their diameter on anterior half. Antennal club symmetrical, somewhat elongate.

Pronotum with very weakly bisinuate posterior margin; lateral margins strongly and evenly curved, with even row of small spines; marginal beading narrow, convex, continuing around anterior margin, ending at posterior angles; posterior corners forming a distinctly oblique angle, lacking emargination (Fig. 23B). Surface covered in dense uniform punctures separated by about their own diameter, though denser medially, interspaces without discernable microsculpture.

Scutellum rather wide, about 1.5x as long as wide, sides almost straight (Fig. 24I); surface covered in dense fine punctures, consistent with surrounding elytra, interspaces without apparent microsculpture. Elytra elongate ovoid, sides rounded but almost parallel anteriorly; sutural interval slightly raised posteriorly, weakly convex, continuous with marginal beading which is narrow posteriorly widening laterally and anteriorly, continuing around humeral angles to scutellum. Surface covered in dense punctures separated by about their own diameter, with reticulate and radiating microrugae, with irregular superficial granulate microsculpture on middle and posterior; striae not distinct, lacking larger strial punctures, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (Fig. 3Ca).

Pygidium not or only slightly visible dorsally, flat to weakly convex, divided by median suture which is distinct to apex, apex, angled, slightly emarginate medially.

Mentum as in Fig. 63A, anterior margin not strongly carinate, concave behind, lateral margins weakly curved, surface with superficial but coarse setiferous punctures, interspaces with dense transverse microrugae except sometimes along anterior margin. Gula not distinctly narrow or wide, sides parallel to slightly curved.

Proventral process as in Fig. 63B–C, weakly convex, almost flat medially, not carinate or tectiform, forming a small spine at posterior apex, and with about 23 spines evenly distributed, medially, laterally and anteriorly with weak golden pubesence.

Mesoventral process as in Fig. 63E–G, very narrow, almost carinate, with a single strong spine at posterior apex which is protruding posteriorly, ventral and lateral surfaces covered in 15–20 strong spines and lacking pubesence; posterior lip about 1/5 length of protrusion, not distinctly separated from surrounding mesoventrite but produced at a slightly lower level, surface flat, posterior apex angled, without pubesence on surface.

Midmetaventral disc raised as in Fig. 63H, flat medially, about longer than wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow ending at transverse furrows; transverse furrows barely impressed, often only discernable centrally, forming a sinuate line across, area around intersection only very weakly impressed; surface anterior to transverse furrows densely covered in punctures of varying size, glabrous at center, lateral areas and entire area posterior to transverse furrows with dense but superficial microrugae. Posterior margin between metacoxae weakly curved to almost angled, posterior surface lined with irregular strong yellow pubescence.

Apex of fifth abdominal ventrite simply rounded, without emargination, posterior margin without fringe of hairs, with row of short hairs along margin.

Procoxae with long strong spines interspersed with very few light hairs along ventral and lateral margins; with distinct large dentiform process at internal posterior apex (Fig. 63D). Posterior margin of trochanters with a very irregular row of long spines along anterior ventral margin, smaller spines also present out of row, row continuing along posterior margin of mesofemorae. Male protarsus modified as in Fig. 25I, with tarsomeres 1–4 shortened and widened and tarsomere 5 longer than segments 1–4 combined and distinctly wider than segment 4, with apical outer margin weakly oblique, weakly sinuate, ventral apical corner forming an acute but blunt angle, without pointed angular process. Hind tibiae usually with 3 or in rare cases, 4 moderately strong spines on ventral surface.

Male genitalia as in Fig. 64, ratio of median lobe:tegmen = 1.02; basal 4/5 weakly curved when viewed laterally, apical 1/5 strongly curved ventrally (Fig. 64C). Median lobe with sides straight, almost parallel, weakly narrowed from base to apical 1/10 at which they are rounded to apex which forms a small protrusion; corona located near tip, at about 1/10 length from tip (Fig. 64A); posterior margin of ventral opening extending very close to tip, rounded (Fig. 64B). Paramera very narrow, rounded apically, dorsal surface thin, membranous, with short pubesence along inner length near apices.

Distribution. Indonesia (Halmahera, Irian Jaya), Papua New Guinea (Eastern Highlands, Bismarck Is.). Map: Fig. 71 (Berge Henegowen 1968).

Remarks. This species is very similar to *S. seriatum* but differs in the following characters: granlulate microsculpture present on elytra (not present in *seriatum*), reticulate microrugae less dense than in *seriatum*, aedeagus curved in lateral view (straight in *seriatum*), sides of median lobe almost parallel, not weakly constricted near tips of paramera.

Specimens examined. **Paratypes: Indonesia**: Halmahera: RMNH / HH 400/ Moluccas: Halmahera/Akelamo, 8km NEE of alt. m 100/ 31–3.VII–VIII.1985/J. Huijbregts// ♀// H1400 3 VIII. 12.15–14.15// Museon Den Haag/ Sphaeridium huijbregtsi sp. n./ det. A.L. van Berge Henegouwen 1985// Paratype♀// Paratype// RMNH.INS.1480884 (1♀). Irian Jaya: Neth. Ind.-Amer.// New Guinea Exp./ Lower Mist. Camp/ 1500m 28.I.1939/ L. J. Toxopeus leg.// Sphaeridium sp. nov./ C.R. Smith det. 1984// Sphaeridium huijbregtsi/ sp. n. Paratype ♂ Van/ Berge Henegowen 1985// Paratype// RMNS.INS.1480880 (1♂).

Sphaeridium seriatum Orchymont, 1913
(Figs. 4E, 5B, 20E–F, 22H, 24J, 25J, 65, 66, 72)

Sphaeridium seriatum Orchymont, 1913: 12. – Indonesia, Sumatra, Palembang (cf. Orchymont, 1929); Hansen, 1999: 316 (Catalogue, worldwide).

Redescription. Medium to large, body length 6.0–8.7 mm, width 3.8–4.8 mm. Body shape elongate oval, not strongly compressed dorsoventrally.

Coloration as in Figs. 4E, 20E, head black, labrum black to dark testaceous; pronotum black to dark testaceous with wide yellow stripes along lateral margins, continuing around anterior angles, ending at posterior angles; elytra with little variation, base color black to dark testaceous, without reddish humeral spots, with wide yellow apical spot covering apical 1/3–1/2 and confluent with yellow marginal stripe which continues to humeral angles, sutural interval and marginal beading dark; epipleuron fulvous. Pygidium dark brown, yellow along posterior margin. Ventral side base color yellow; mentum fulvous, sometimes darkened on anterior half, submentum testaceous, gula fulvous, though anterior portion and borders variably darkened, lateral areas of head variably darkened, maxillary palpi fulvous to testaceous, antennal segments fulvous, club dark brown; darkened on middle of pronotum and middle and lateral areas of metaventrite; each abdominal segment dark brown with 4–5 fulvous spots not reaching the posterior margin, except on the fifth segment which is fulvous along the posterior margin; profemora dark brown on upper half, dark area wider at about basal 1/3, meso- and metafemora fulvous with dark spots at center of each femora, trochanters testaceous, tibiae and tarsi fulvous (Figs. 5B, 20F).

Dorsal surface of head with dense, uniform punctures separated by less than their diameter except on smooth epicranial sutures, interstices without apparent microsculpture. Eyes of normal size, excised on anterior margin. Labrum exposed, anterior margin straight to very slightly concave medially, with dense and flat golden pubescence anteriorly, surface covered in dense microrugae, with irregularly arranged setous punctures separated by about 2x their diameter on anterior half. Antennal club symmetrical, somewhat elongate (Fig. 22H).

Pronotum with very weakly bisinuate posterior margin; lateral margins strongly and evenly curved, with even row of small spines; marginal beading narrow, convex, continuing around anterior margin, ending at posterior angles; posterior corners forming a distinctly oblique angle, lacking emargination (as in Fig. 23B). Surface covered in dense uniform punctures separated by about their own diameter, though denser medially, interspaces without discernable microsculpture.

Scutellum rather wide, about 1.5x as long as wide, sides almost straight; surface covered in dense coarse punctures, less dense on surrounding elytra, interspaces without apparent microsculpture (Fig. 24J). Elytra elongate ovoid, sides rounded but almost parallel anteriorly; sutural interval slightly raised posteriorly, strongly convex, continuous with marginal beading which is very narrow posteriorly widened laterally and anteriorly, continuing around humeral angles to scutellum. Surface covered in dense punctures separated by about their own diameter, with reticulate and radiating microrugae, without granulate microsculpture; striae distinct, larger strial punctures not evenly aligned, without grooves, interspaces flat. Posterolateral margins not swollen, not modified in female (as in Fig. 3Ca).

Pygidium not or only slightly visible dorsally, flat to weakly convex, divided by median suture, which is distinct to apex, apex, angled, slightly emarginate medially.

Mentum as in Fig. 65A anterior margin not strongly carinate, strongly concave, lateral margins weakly curved, surface with uniform deep coarse setiferous punctures, interspaces with dense conspicuous transverse microrugae except sometimes along anterior margin. Gula not distinctly narrow or wide, sides parallel to slightly curved.

Proventral process as in Fig. 65B–C, weakly convex, almost flat medially, not carinate or tectiform, forming a large spine at posterior apex, and with about 23 spines evenly distributed medially, laterally and anteriorly with long golden pubesence.

Mesoventral process as in Fig. 65E–G, very narrow, almost carinate, with two strong spines at posterior apex which is protruding posteriorly, ventral and lateral surfaces covered in 15–20 strong spines and lacking pubesence; posterior lip about 1/4–1/5 length of protrusion, not distinctly separated from surrounding mesoventrite but produced at a slightly lower level, surface flat, posterior apex angled, without pubesence on surface.

Midmetaventral disc raised as in Fig. 65H, convex, about as long as wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow ending at transverse furrows; transverse furrows barely impressed, often only discernable centrally, forming an almost straight line across, area around intersection only very weakly impressed; surface anterior to transverse furrows densely covered in punctures of varying size, glabrous at center, lateral areas and entire area posterior to transverse furrows with dense but superficial microrugae. Posterior margin between metacoxae gently curved, lateral areas lined with fine setous puntures.

Apex of fifth abdominal ventrite simply rounded, without emargination, posterior margin without fringe of hairs.

Procoxae with strong spines interspersed with very few light hairs along ventral and lateral margins; with distinct large dentiform process at internal posterior apex (though rather thin and easily broken) (Fig. 65D). Posterior margin of trochanters with a very irregular row of long spines along anterior ventral margin, smaller spines also present out of row, row continuing along posterior margin of mesofemorae. Male protarsus modified as in Fig. 25J, with tarsomeres 1–4 shortened and widened and tarsomere 5 longer than segments 1–4 combined and distinctly wider than segment 4, with apical outer margin weakly oblique, weakly sinuate, ventral apical corner forming an acute but blunt angle, without pointed angular process. Hind tibiae with 1–3 moderately strong spines on ventral surface but usually with 2 on both.

Male genitalia as in Fig. 66, ratio of median lobe:tegmen = 1.13; mostly straight when viewed laterally though weakly bent at about 1/6 length from apex (Fig. 66D). Median lobe with sides of basal 5/6 weakly rounded, parallel from apical 1/6, then rounded to form apex with small tubercle from apical about 1/12; corona located near tip, at about apical 1/12 (Fig. 66B); posterior margin of ventral opening located at corona, anterior margin rounded (Fig. 66C). Paramera very narrow, pointed apically, dorsal surface distinctively wider than ventral, membranous with weak pubesence at apex. Acessory sclerite (9th ventrite) long, about 1/3 length of aedeagus, sides sinuate, apex constricted but rounded, median ridge wide, arms about 2/3 length of paramera (Fig. 66A).

Distribution. China (Fujian, Guandong, Hainan, Hong Kong, Hunan), India, Indonesia (Batu, Borneo, Java, Sumatra), **Japan (Amami-Ôshima) [new record]**, Nepal, Philippenes, Vietnam. Map: Fig. 72.

Remarks. This large species is somewhat rarely collected but quite widely distributed from India and Nepal, throughout southern China and Southeast Asia, as far east as Amami-Ôshima in southern Japan.

The specimen from the island of Amami-Ôshima differs slightly from other specimens examined in its lighter coloration and somewhat narrower median lobe of the aedeagus but is not distinctly different enough to justify designation as a separate species.

One set of examined specimens from Negros Island in the Philippines is recorded as having been collected from dead bivalves ["shell"] and fish. While *Sphaeridium* species are mainly known to inhabit dung, they are also known to opportunistically colonize animal carcasses (Heo *et al.* 2011). It is however possible that this species along with its closely related sister species, *S. huijbregtsi* are more inclined towards necrophilous lifestyles as *S. huijbregtsi* has so far only been collected from carrion-baited pitfall traps (Berge Henegowen 1986).

While extremely similar to *S. huijbregtsi*, *S. seriatum* can be differentiated from it by the following characters: The posterior apex of the mesoventral protrusion bears one spine in *S. seriatum* (two spines in *S. huijbregtsi*); the sides of the median lobe are weakly constricted near the apex of paramera (*S. huijbregtsi* lacks this constriction); aedeagus is straight on basal 4/5ths and angled at apical 1/5th in lateral view (in *S. huijbregtsi*, the basal 4/5ths is weakly curved with apical 1/5 strongly curved in the opposite direction).

Specimens examined. **India:** Darjeeling Distr., India, Bhakta B.//Pedong, 12.VII.1981. **Nepal:** Janakpur, Malipu – Suri Dhoban, alt. 1000–1100m, 10.VIII.1983, Ent. Inst. Hokk. Univ. (1♀). **Japan:** KOSHOKU/Amami Is./5.VIII.1960/K. Yamada (1♂). **Philippenes:** Negros Is., near sea shoreline, 3.XII.1997, collected from dead shell and fish/ *Sphaeridium seriatum* Orchymont, det. F.L. Jia 2003 (2♂♂, 2♀♀).

Sphaeridium severini Orchymont, 1929

(Figs. 3Cb, 4E, 6A–C, 20C–D, 22I, 24K, 25K, 67, 68, 73)

Sphaeridium severini Orchymont, 1919: 116. – India, Kerala, Mahe; Hansen, 1999: 316 (Catalogue, worldwide); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Sphaeridium reticulatum Orchymont, 1929: 410. – Shandong, region of Qingdao ["Kiautschau"]. **Syn. n.**

Redescription. Size medium to large (usually larger), body length 5.3–8.3 mm, body width 3.5–4.7 mm. Body shape widely oval to subquadrate, somewhat compressed dorsoventrally.

Coloration as in Figs. 4E, 20C, head black, labrum black to dark brown; pronotum black with wide yellow stripe along lateral margins which continues around anterior angle and is roundly widened before posterior angles; elytral coloration not widely variable, base color black to dark brown, lateral margins with yellow border narrow on anterior 1/2, joining yellow apical spot which covers posterior 1/3–1/2 of elytra, color of elytral suture consistent with surrounding area, without distinct reddish humeral spots; epipleuron yellow. Pygidium dark brown, with light yellow stripe along posterior margin which becomes wider laterally and sometimes at apex. Ventral base color yellow; mentum yellow, sometimes darkened at center, submentum yellow to orange, gula yellow, with two dark spots located lateral to gular sutures which are darkened, maxillary palps and antennal segments yellow, antennal club dark brown; darkened at center of metaventral field and metepimerons, and variably darkened on lateral areas of metaventrite, abdominal ventrites with 6 rows of spots, the spots not reaching posterior margin of each ventrite; femora yellow, each with a distinct dark spot at center, tibiae and tarsi yellow to dark reddish (Figs. 5B, 20D).

Dorsal surface of head with dense, uniform punctures separated by a little less than their own diameter or less, interstices without apparent microsculpture. Eyes a little large, particularly ventrally, ventral interocular distance 6x width of one eye, excised on anterior margin. Labrum exposed, anterior margin straight medially, curved laterally, with dense flat golden pubesence anteriorly, surface covered in very dense granulate microsculpture and transverse microrugae. Antennal club asymmentrical, lamellate, not compact (Fig. 22I).

Pronotum with posterior margin convex, not strongly bisinuate, lateral margins rounded anteriorly, becoming almost straight posteriorly, with a row of consistent small spines along posterior half of lateral margin (may be indistinct in some specimens); marginal beading wide, flat to weakly convex, continuing around anterior margin and posterior angles, ending a short distance along basal margin; posterior angles forming rounded oblique angles, lacking emargination (as in Fig. 23B). Surface covered in dense uniform puctures consistent with those on head, interspaces shining, without discernable microsculpture, or with very faint superficial coriaceous microrugae.

Scutellum about 2x as long as wide, sides weakly rounded; surface covered in dense punctures consistent with those on surrounding elytra except along margins which are smooth, interspaces without apparent microsculpture (Fig. 24K). Elytra subquadrate, sides weakly rounded, apices rounded separately; sutural interval raised posteriorly but flat throughtout, distinctly continuous around posterior margin, abruptly and strongly widened posterolaterally in females (Fig. 3Cb), only slightly widened anteriorly in males, continuing around humeral angles but not reaching scutellum. Surface covered in dense uniform punctures slightly more widely spaced than those on head and pronotum, separated by about their own diameter, interspaces with dense coriaceous and granulate microsculpture and distinct radiating microrugae; striae distinct, consisting of irregularly arranged larger punctures, without grooves, interspaces flat. Posterolateral margins not swollen inside marginal beading in female (as in Fig. 3Cb).

Pygidium partially visible dorsally; weakly tectiform, divided my median suture which is distinct to apex, apex rounded to obliquely angled.

Mentum as in Fig. 67A, anterior margin not carinate, straight to weakly concave, lateral margins gently curved, surface with uniform fine setiferous punctures, interspaces with dense transverse microrugae. Gula not distinctly narrow or wide though wider at base, sides weakly curved.

Proventral process as in Fig. 67B–C, tectiform, forming a large stout spine at posterior apex, and bearing 3–5 strong dark spines medially, with or without several smaller stout spines anteriolaterally, with long setae and pubesence on lateral and anterior areas.

Mesoventral process as in Fig. 67E–G; anterior protrusion fusiform, more than 2x longer than wide, anterior apex gently sloping, with numerous strong dark spines ventrally and sparse golden setae on ventral and lateral surfaces, posteriorly margin sloping, continuous with posterior lip which is narrow, about 1/8–1/10x length of anterior protrusion, weakly separated from surrounding mesoventrite by posterolateral corners of process, produced at a lower level, surface strongly convex, without pubesence, apex roundly pointed, sometimes weakly emarginate at tip.

Midmetaventral disc raised as in Fig. 67H, flat to weakly convex, wider than long, lateral margins not distinctly separated from surrounding lateral areas, median furrow continuing to transverse furrows which are impressed centrally, distinct laterally, forming a straight transverse line though sometimes curving centrally to meet at an oblique angle, area around intersection flat, not strongly impressed; surface covered in coarse setiferous punctures which are gradually sparser centrally, absent around intersection of furrows and posterior to transverse furrow, interspaces with very fine dense microrugae. Posterior margin between metacoxae angled, with distinct row of golden setae.

Apex of fifth abdominal ventrite simply rounded, without emargination, posterior margin without fringe of hairs.

Procoxae with strong spines interspersed with fine long pubesence (Fig. 67B), with long, sharp dentiform process at internal posterior apex (Fig. 67D). Posterior margin of trochanters with uniform row of long spines which continues along posterior margin of profemorae. Male protarsus strongly modified as in Fig. 25K, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 as long as previous segments combined, S5 distinctly wider than S4, with apical outer angled, forming a blunt denticle at ventral apical corner. Hind tibiae each with 1–3 strong spines on ventral surface, but most commonly each with 2 spines below.

Male genitalia as in Fig. 68, ratio of median lobe:tegmen = 1.16; straight in lateral view though apical 1/8 slightly angled posteriorly (Fig. 68D). Median lobe wide, with wides parallel until apical about 1/12 at which they are angled to meet at an almost right angle, with a small flat protrusion at tip; corona located at about 1/10 length from apex (Fig. 68B); posterior margin of ventral opening located just anterior to corona, rounded (Fig. 68C). Paramera narrow, pointed apically, dorsal and ventral sides similar in width, with short pubesence along inner margin. Accessory sclerite small, narrow, about 1/4 length of aedeagus, apex pointed, median ridge very strong, arms about 2/3 length of paramera (Fig. 68A).

Distribution. **Europe:** Turkey. **Asia:** Cambodia, China (East Tibet, Guandong, **Guangxi [new record]**, Hong Kong, Jiangxi, Sichuan, Shandong, Yunnan), India (Himachal Pradesh, Kerala, Tamil Nadu, Uttarakhand/Uttar Pradesh, West Bengal), Laos, Nepal, Indonesia (**Flores [new record]**, **Sulawesi [new record]**, Sumatra), Malaysia, Singapore, Taiwan, **Thailand [new record]**, Vietnam. Map: Fig. 73.

Remarks. There has been a significant amount of confusion around the identities of the species *S. reticulatum*, *S. severini*, and *S. vitalisi*, in part because the original description for *S. vitalisi* lacked male individuals. Upon close inspection of specimens from SEHU, EUMJ, and RMHN, I have determined that the male described in Orchymont's description of *S. reticulatum* was in fact *S. vitalisi* and *S. reticulatum* is a junior synonym of S. *severini*. In

Orchymont (1925), the male genitalia of *S. reticulatum* was illustrated as narrow and strongly tapered to a pointed tip (Fig. 70), however in all of the specimens I have examined, this shape is only seen in males that fit the characters described in *S. vitalisi*, wheras the median lobe in specimens with the characters described for *S. reticulatum* is wide with sides parallel to a blunt tip forming a right angle (Fig. 68). Once the identities of these two species were determined, it became apparent that *S. reticulatum* is in fact a junior synonym of *S. severini*. *S. severini* can be distinguished from *S. vitalisi* by the following characters: elytral striae are not distinct, never deeply grooved (striae are distinct and sometimes deeply grooved in *S. vitalisi*); the marginal beading of the elytra of the female is strongly widened posterolaterally (Fig. 3Cb) (the marginal beading is normal width throughout in females of *S. vitalisi* (Fig. 3Cc)); the posterolateral margin of the elytra inside the beading is not swollen in females (Fig. 3Cb) (swollen in females of *S. vitalisi* (Fig. 3Cc)); the apical margin of the outer side of the terminal segment of the male protarsus is sinuate and forms a small denticle ventrally (Fig. 25K) (the apical outer margin forms a straight obliquely directed line in *S. vitalisi* (Fig. 25L)); mesoventral tablet diamond-shaped, somewhat flattened (Fig. 67E–F) (carinate in *S. vitalisi* (Fig. 69E–F)); metaventral field is wider than long (Fig. 67H) (longer than wide in *S. vitalisi* (Fig.69H)).

Specimens examined. **China:** East Tibet, Jiaka, about 4000m, Zhuogong County, VIII.2005. He et al. leg. (2♂♂, 1♀); S-Guangxi, Ningming County, Shilang Mt., 1600m, X.2005, Yi et al. leg. (4♂♂, 1♀); Guangdong, Border with Fujian, Zaoyang vill. About 1300m, Jiaolin County, XII.2005, Jin et al. leg. (1♂, 4♀♀); Yunnan (near border Vietnam and Laos), Huang Lian Shan, 2600m, Laizhou IX.2005 (1♂); Mt. Liu-Zhao-Shan, Lang Huan Xiang, Lida town, Fu Ning county, Yunnan prov. 1–8.VII.2006, [MO-06-024], M. Ôhara leg. (1♂); Hong Kong: New Territories: Wu Kwai Sha, XI.1982, D. Dudgeon// Sphaeridium severini Orchymont, det. A.L. van Berge Henegowen 1989// RMNH.INS.14808855–14808857 (1♂, 2♀♀) [RMNH]; Fort de Kock (Sumatra) 920m, 1924, leg. E. Jacobson// Knisch det. 1925, Sphaeridium seriatum// Sphaeridium severini Orchymont, det. A.L. van Berge Henegowen 1989// RMNH.INS.1480888 (1♂) [RMNH]. **Indonesia:** South Sulawesi, Pangia near Bantimurung, Maros, 5.I.2006, T.Matsumoto leg. (2♀♀); Sulawesi Is. [SU-06-MO-050], 01˚15’08”N 124˚48’19”E, Desa Leilern, Kec. Sonder, Kab. Minhasa, Prop. Sulawesi Utara, 31.VIII.2006, M. Ôhara leg., collected from cow (Zebu) dung (2♂♂); Flores, 08˚39’64”S, 121˚19’49”E, Desa Lobolewa, Kec. Aesesa, Kab. Ngada, Flores, Prop. Nusa Tenggara Timur (NTT), 25.I.2003, M.Ôhara leg. (1♂). **Malaysia:** Sabah, Kinabaru Park, Head Quator, Liwagu Trail, 1500m, 29.X.1998 (1♀); Sabah, Kinabaru Park, Bukit Ular, 1850m, 26.X.1998, Y.Kikuta leg., dung trap (2♀♀). **Cambodia:** Siempang, Stoeng Treng province, 9–25.IV.2006// contributed by Dr. Masahiro Kon (1♀). **Thailand:** Phuping Palace, nr. Doi Suthep, North Thailand, 6.IX.1980, coll. N.Nishikawa (1♀).

Sphaeridium vitalisi Orchymont, 1925

(Figs. 3Cc, 4E, 5B, 20G–H, 22J, 24L, 25L, 69, 70, 74)

Sphaeridium vitalisi Orchymont, 1925: 153. – Laos ["Haut Mekong"], Nam Mat; Hansen, 1999: 316 (Catalogue, worldwide); Przewoźny, 2021: 37 (Catalogue, Palearctic).

Redescription. Medium to large, body length 6.3–8.0 mm, width 3.4–5.0 mm. Body shape oval, rather convex dorsoventrally.

Coloration as in Figs. 4E, 20G, head black, labrum black to dark testaceous; pronotum black with yellow stripes along lateral margins, slightly narrower medially, wider anteriorly and posteriorly, continuing a short distance around anterior angles, ending just before posterior angles; elytral coloration with little variation, base color black to dark testaceous, without reddish humeral spots, awith fulvous apical spot which covers apical about 1/3–1/2, confluent with fulvous lateral marginal stripe which usually reaches humeral angles but rarely, fades at about apical 1/2–2/3; epipleuron fulvous. Pygidium black, yellow along posterior margin and marginal suture. Ventral side base color fulvous; mentum fulvous with or without black or dark brown spot at center, submentum fulvous or testaceous, gula fulvous with lateral borders darkened, areas lateral to gula fulvous, each with a black spot at center, maxillary palps fulvous, first segment with longitudinal testaceous stripe dorsolaterally, second segment darkened dorsally and ventrally, and terminal segment testaceous on basal half, fulvous apically, antennal segments fulvous, club dark brown; mesoventrite darkened around mesoventrital process and along posterior margin; metaventrite with black spots at center of metaventrital field, with variable dark spots on lateral areas, metepiventrites each with black spot at center; abdominal ventrites 1–4 each with about six black spots and terminal ventrite with four black spots, posterior margins fulvous; legs each with a dark brown spot at center of femora (Figs. 5B, 20H).

Dorsal surface of head with dense coarse punctures separated by less than their diameter except around smooth epicranial sutures, interstices without apparent microsculpture. Eyes normal size, excised on anterior margin. Labrum exposed, anterior margin straight medially, with dense flat golden pubesence anteriorly, surface covered in dense superficial transvere microrugae and several rows of setous punctures anteriorly. Antennal club not compact, not symmetrical, weakly serrate (Fig. 22J).

Pronotum with weakly bisinuate posterior margin; lateral margins evenly curved, without row of small spines; marginal beading narrow, convex, continuing around anterior margin, ending at posterior angles, posterior angles forming oblique angles, lacking emargination (as in Fig. 23B). Surface covered in dense uniform punctures consistent with those on head, interspaces without discernable microsculpture.

Scutellum wide, about 1.5x as long as wide, sides straight to weakly rounded; surface covered in dense punctures consistent with those on surrounding elytra, interspaces without apparent microsculpture (Fig. 24L). Elytra ovoid, sides rounded, apices not rounded separately; sutural interval slightly raised posteriorly, surfac convex, continuous with marginal beading which disappears posterolaterally but is distinct laterally, around humeral angles, and along base to scutellum. Surface covered in dense uniform puctures which are finer than those on pronotum and head, separated by about 2x their diameter except on sutural interval and strial interval 1 on which they are much finer and denser, separated by about 1x their own diameter, interspaces with dense granulate microsculpture making elytra appear matte, as well as reticulate, longitudinal, and radiating microrugae, striae distinct, larger strial punctures rather evenly aligned and often distinctly grooved, interspaces flat or convex. Posterolateral margins distinctly swollen in female (Fig.3Cc).

Pygidium not visible to only slightly visible dorsally; convex, median suture only visible apically, apex rounded.

Mentum as in Fig. 69A, anterior margin rounded, not strongly carinate, lateral margins gently curved, surface with dense uniform coarse setiferous punctures, interspaces with conspicuous microrugae. Gula not distinctly narrow or wide, sides parallel to slightly curved.

Proventrital process as in Fig. 69B–C, convex, forming a small spine at posterior apex, and bearing three large strong spines posteriorly along median line, several smaller spines anterior to strong spines but not aligned along midline, and fine pubesence anteriorly and laterally.

Mesoventrital process as in Fig. 69E–G, anterior protrusion narrow fusiform, almost carinate, about 4–5x longer than wide, posterior apex with two spines, protruding under posterior lip, ventrally and laterally with numerous strong spines, anteriorly and laterally with sparse fine pubesence; posterior lip about 1/5 or less length of protrusion, not distinctly separated from surrounding mesoventrite by posterolateral corners of process, nor produced at a lower level, surface flat to concave, without pubesence.

Midmetaventrital disc raised as in Fig. 69H, rather flat medially, distinctly longer than wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow continuing to posterior margin though often very weak posterior to transverse furrows; transverse furrows often only discernable medially, straight laterally, curving to meet at an oblique angle, area around intersection not strongly impressed; surface anterior to transverse furrows covered in fine setous punctures which are denser anteriorly and laterally, interspaces with dense but fine microrugae. Posterior margin between metacoxae angled, with a few setae produced from posterior surface laterally.

Apex of fifth abdominal ventrite simply rounded but with one to many irregular emarginations medially in females, posterior margin without fringe of hairs.

Procoxae with strong spines interspersed with sparse fine pubesence, with long sharp dentiform process at internal posterior apex (Fig. 69D). Posterior margin of trochanters with a row of long yellow spines which continue along posterior margin of femora. Male protarsus modified as in Fig. 25L, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 as long as segments 1–4 combined, segment 5 slightly wider than segment 4, with apical outer margin oblique, ventral apical corner forming an acute angle. Hind tibiae each usually with 3 strong spines on ventral surface but may have 1 or 3 spines on one or both legs in rarer cases.

Male genitalia as in Fig. 70, ratio of median lobe:tegmen = 1.25; strongly curved ventrally when viewed laterally (Fig. 70D). Median lobe with sides weakly curved, widest point at about basal 1/3, gradually narrowed to apex which bears a small, indistinct protrusion at tip; corona located near apex at about apical 1/12 (Fig. 70B); posterior margin of ventral opening located at or just anterior to corona, anterior margin angulate (Fig. 70C). Paramera very narrow, rounded apically, dorsal surface very narrow, without distinctive fringe of pubesence along inner length. Acessory sclerite (9th ventrite) about 1/4 length of median lobe, apex rounded, lateral sides sinuate, median ridge robust, about 4/5 length of paramera (Fig. 70A).

Distribution. **China (Tibet, Guangxi, Guizhou, Sichuan, Yunnan) [new record]**, **India** (Rajasthan) **[new record], Indonesia [new record]**, Laos, **Nepal [new record]**, **Taiwan [new record]**, Vietnam. Map: Fig. 74.

Remarks. When originally described in 1925, Orchymont had lacked a male of the species and described it based only on female specimens collected from Laos. He later described the *species S. reticulatum*, which we now know to be synonymous with *S. severini*, based on both male and female specimens from India. However, upon examination of many sets of specimens from SEHU, EUMJ, and RMHN, the genitalia he illustrated for his description of "*S. reticulatum*" in fact fits *S. vitalisi*. Due to the confusion around these two species, many specimens had not been identified and the distribution of the species in many Asian countries had not been realized. Previously only known from Laos and Vietnam, from the specimens examined, this species has in fact been collected in China, India, Indonesia, Nepal and Taiwan.

Specimens examined. **India:** Rajasthan, Kandu 28.VI.1989//A.Tanaka coll., SEHU Japan, 2005 (1♀). **Nepal:** Bagmati, S.Takagi leg.//Ramche, 14.IX.1975 (1♀). **China:** East Tibet, Jiaka, about 4000m, Zhuogong County, VIII.2005, He et al. (3♂♂, 3♀♀); Tibet, Zuogong, 11.VII.2006//Contributed by Masahiro Kon, 2007 (1♂, 2♀♀); **Guizhou:** Mt. Bao-Shang-San (alt. 1687m), XingYi city, South Guizhou province, 11–21.VII.2006//Contributed by Masahiro Kon, 2007 (5♂♂, 6♀♀); Guizhou, Gaolingshan, 1700m, Tianzhu, East Guizhou, IX.2005, Ton et al leg. (2♂♂); **Guangxi:** S. Guangxi, Ningming County, Shilang Mt., 1600m, X.2005, Yi et al leg. (1♂, 1♀); **Sichuan:** Sichuan, Baoxing env., cca 50km NNW of Yaan, 30˚22'N 102˚50'E, M.Tryzna et O. Safranek leg. (7♂♂, 5♀♀); **Yunnan:** (near border Vietnam and Laos), Huang Lian Shan, 2600m, Laizhou IX.2005 (1♂, 1♀); Yunnan, Labashan, Wei-Shi County, 8–19.VIII.2005 (1♂, 2♀♀). **Taiwan:** Wushe, Nantou County//30.X.1976, M.Kiuchi leg. (1♂). **Vietnam:** Cat Cat, Sapa City, 4.V.2009, Y.Kusui leg. (1♂). **Myanmar-Laos border:** 2005 (2♂♂, 2♀♀). **Indonesia:** [JA-05-MO-058], 06˚32'22"S, 107˚03'66"E, West Java, Ds. Sukkaresmi, 400m alt., Kec. Sukamakmur, Kab. Jonggol, 27.XI.2005, M.Ôhara leg., collected from cow dung (Bali sapi in cowshed) (1♂, 1♀); [SB-00-MO-035], 08˚35'31"S, 117˚16'38"E, Desa Batudulang, Kecamatan Batulanteh, Kabupaten Sumbawa Besar, Propinsi Nusa Tenggara Barat (NTB), 10.XI.2000, M.Ôhara leg. (1♂).

S. sundense Group

Species included: *Sphaeridium sundense*

Distribution. Indonesia

Diagnosis. While superficially similar to members of the *bipustulatum* and *quinquemaculatum* groups, this species differs from the *bipustulatum* group in its southern distribution and lack of thin lateral margins on the median lobe of the male genitalia. It differs from the *quinquemaculatum* group in the shape of the mesoventral protrusion which is distinctly longer than wide and lacks pubesence on the posterior lip.

Sphaeridium sundense Suzumura, van Berge Henegowen, and Budi, 2022
(Figs. 4H, 19G–H, 22G, 24H, 25H, 75–78, 79A, 80A, C, E)

Sphaeridium sundense Suzumura, van Berge Henegowen, and Budi, 2022: 85–94.

Description. Small, body length 3.0−5.0 mm, body width 2.0−3.0 mm. Body shape oval to slightly subquadrate, moderately compressed dorsoventrally.

Coloration not widely variable, usually as in Figs. 4H, 19G–H, 75, 79A, head black, sometimes with a small indistinct reddish spot at middle behind level of eyes, labrum reddish, pronotum black with wide yellow stripe along lateral margins (Figs. 75A–C, 79A), continuing around anterior and posterior angles but not contacting posterior margin; elytra black to reddish in more freshly emerged adults, lateral margins with yellow border beginning slightly posterior to base, widening before midlength, continuing around posterior tip and ending abruptly at about 1/4–1/3 the length of elytral suture, border of this stripe indistinct posteriorly; lacking reddish humeral spots; epipleuron fulvous. Pygidium dark brown on anterior 1/2–1/4, yellow posteriorly. Ventral base color dark brown except narrow yellow stripe on gula, lateral portions of pronotum, and posterior margins of ventrites (Fig. 75B); legs yellow with brown spots at centers of femora. Mentum piceous-testaceous, maxillary palps yellow, antennae yellow with dark brown club.

Dorsal surface of head with dense, uniform punctures separated by less than their diameter except around smooth epicranial sutures, interstices with shallow microsculpture. Eyes of normal size, excised on anterior margin. Labrum exposed, anterior margin straight medially, with dense, flat, golden pubesence anteriorly, surface covered in dense transverse microrugae. Mentum *ca.* 0.6x as long as wide, slightly bisinuate on anterior margin, lateral margins gently curved, surface with deep, coarse setiferous punctures, interspaces with dense, conspicuous microrugae (Fig. 76A); gula parallel-sided or slightly wider posteriorly, of normal width, not distinctly wide or narrow. Antennal club symmetrical, compact (Fig. 22G).

Pronotum with bisinuate posterior margin; lateral margins evenly curved, with irregular row of small blunt spines along posterior 2/3 (Fig. 76B); marginal beading wide, flat, continued along anterior margin, ending at posterior margin; posterolateral corners forming an oblique angle. Surface covered in dense punctures separated by less than their diameter, slightly larger than those on head, interspaces with dense, granulate microsculpture (Figs. 76B, F). Proventral process convex, weakly tectiform posteriorly between coxae, forming a large spine at posterior apex, and bearing 2−4 strong spines along longitudinal median line, the anterior of which is flanked by several weaker spines, golden setae, and sparse pubesence (Fig. 76C).

Scutellum about twice as long as wide, sides almost parallel-sided anteriorly, gently curved posteriorly (Fig. 75A); surface densely punctured, consistent with surrounding punctation on elytra, interspaces without discernable microsculpture.

Elytra ovoid, sides strongly rounded, apices rounded separately; sutural interval slightly raised, surface flat, continuous with marginal beading which is distinct along lateral margins and around posterior apices (Figs. 75C, D). Surface covered in dense, uniform punctures separated by less than their diameter, interspaces with distinct granulate microsculpture and sparse microrugae throughout; striae distinct, though larger strial punctures not evenly aligned, without grooves, interspaces flat (Fig. 75A). Mesoventral process as in Figs. 76D, 80C, E, anterior protrusion triangular, distinctly longer than wide, with a distinctive symmetrical pattern of long, strong spines: four rows of strong spines of increasing size numbering 3-6-4-2 from anterior to posterior. Posterior lip slightly convex, slightly shorter than protrusion, separated from lateral areas of mesoventrite by posterolateral angles of protrusion, distinctly raised above level of metaventrite, lacking pubesence on surface (Figs. 76D).

Metaventrite with metaventral field slightly raised as in Fig. 76E, convex, longer than wide, lateral margins not distinctly separated from surrounding lateral areas, median furrow weakly continuing posterior to transverse furrows which are only distinct centrally, curved laterally, meeting at an oblique angle; posterior margin between metacoxae gently curved, emarginate medially; surface covered in deep uniform punctures, separated by about 2× their diameter, interspaces with dense microrugae (Fig. 76G), central area posterior to transverse furrow with fewer punctures but microrugae strong throughout.

Procoxae with strong spines and sparse short indistinct setae, lacking long golden pubesence interspersed among the spines, with dentiform process at internal posterior apex. Posterior margin of trochanters with a row of spines continuing along posterior margin of femora. Male protarsus modified, with tarsomeres 1–4 shortened and slightly widened and tarsomere 5 almost as long as segments 1–4 combined, tarsomere 5 a little wider than tarsomere 4, with apical outer margin straight to slightly curved, slightly longer along ventral margin, without pointed angular process. Hind tibia with one small, moderately strong spine on ventral surface (Fig. 75B).

Pygidium weakly tectiform, apex obtusely pointed; abdominal ventrite 5 with apex evenly rounded, surface bare, without fringe of short setae.

Abdominal apex simply rounded, without emargination.

Male genitalia as in Figs. 77. Ratio of median lobe:tegmen = 1.73. Median lobe with sides parallel on basal half, slightly constricted at about apical 1/3–1/4, slightly widened before tip, with truncate apical process (Fig. 77B); corona located at about apical 1/8; posterior margin of ventral opening located just anterior to corona, apical margin sinuate, emarginate. Parameres about half the length of median lobe, rather wide on ventral side, with rounded tips. Acessory sclerite (9th ventrite) about half the length of the lateral struts, apex roundly pointed, median ridge short (Fig. 77A).

Etymology. The specific epithet "*sundense*" is an adjective taken from the geographical name Sundaland, the former landmass that fell apart into the many islands including what is now called the Lesser Sundas.

Distribution. Indonesia: Sumatra, Java, Bali, Lombok, Sumbawa, Sumba, Flores, Timor, Wetar, Kei. Map: Fig. 74.

Remarks. While there are several small (> 8 mm in length) species of *Sphaeridium* recorded from the Indonesian archipelago, *S. sundense* can be easily differentiated from most of the others by the following characters: ventral coloration dark, base color black to dark brown, never yellow (as in *S. flavomaculatum* and *S. huijbregtsi*); posterior angles of pronotum without emargination (as in *S. dimidiatum* and the larger species *S. discolor*); and with distinct elytral striae (lacking in *S. flavomaculatum* and *S. huijbregtsi*).

Perhaps the most morphologically similar species to *S. sundense* is *S. quinquemaculatum*, particularly in size and often coloration. *Sphaeridium sundense* can, however, be easily separated from the former by the structure of the mesoventral process, of which the anterior protrusion is distinctly longer than wide, bears a unique pattern of strong spines on the ventral surface, and the posterior lip lacks pubescence (Figs. 76D, 80C). In *S.*

quinquemaculatum, the anterior protrusion is about as wide as long and the posterior lip is sparsely but distinctly pubescent (Fig. 5D). Additionally, the procoxa of *S. sundense* lack the abundant long yellowish pubescence interspersed among the strong spines as is seen in *S. quinquemaculatum* (Fig. 80B). *Sphaeridium quinquemaculatum* shows remarkable variation in color pattern, and some specimens are rather dark and quite similar to *S. sundense*. Differences in the extent of yellow on the lateral margins of the pronotum, however, are highly constant, with *S. quinquemaculatum* having a yellow border which does not continue around anterior and posterior angles, whereas the yellow border of *S. sundense* does continue around the angles and reaches some distance inward from both anterior and posterior margins.

Arno van Berge Henegowen recorded it from Sumatra, Bali, Wetar, and Kei based on material in museum collections. This indicates that as far as we know, the new species reaches eastwards to what is known as Lydekker's Line.

Specimens examined. **Type Material. Holotype.** "[SM-03-MO-012]/ 09°40′17″S 120°21′43″E/ [Sumba: Indonesia]/Desa Watumbaka,/Kecamatan Pandawai,/Kabupaten Sumba Timur,/Propinsi Nusa Tenggara/Timur (NTT), 28.Jan.2003,/M.Ôhara and S. Hartini" (1♂). **Paratypes. Kei:** (= "Insel Key"), Coll. Régimbart (4♂♂, MNHN); (= "Kai Isl"), (1♂, ZMHB). **Wetar:** (= "Wetter Insel"), IV.1901, *S.quinquemaculatum* d'Orchymont det. (15♂♂, 9♀♀, ZMHB; 2♂♂, 2♀♀, ALBH; 1♂, RBINS); 19.VI.1917, coll. Corporaal, *S.quinquemaculatum* d'Orchymont det. (1♂, RBINS); 1927, coll. C.H.Moore, *S.quinque-maculatum* J.Balfour-Browne det. (4♂♂, 3♀♀, NHMUK); Coll. Régimbart (1♂, MNHN). **Timor:** [TI-03-MO-002] Desa Penfui, Kecamatan central Kupang, Propinsi Nusa Tenggara Timur (NTT), 10°10′01″S 123°39′49″E, 23.I.2003, coll. M.Ôhara (2♂♂, 2♀♀, SEHU); [TI-03-MO-003] Desa Baumata (Fenonisa), Kecamatan central Kupang, Propinsi Nusa Tenggara Timur (NTT), 10°11′49″S 123°40′20″E, 23.I.2003, coll. M.Ôhara (1♀, SEHU); [TI-03-MO-025] Desa Camplong Il, Kecamatan Fatuleu, Kabupaten Kupang, Propinsi Nusa Tenggara Timur (NTT), 10°00′58″S 123°59′02″E, 1.II.2003, coll. M.Ôhara (2♂♂, SEHU); [TI-03-MO-027] Desa Boentuka, alt. 100m, Kecamatan Batuputih, Kabupaten Timor Tengah Selaten, Propinsi Nusa Tenggara Timur (NTT), 10°57′34″S 123°09′01″E, 1.II.2003, coll. M.Ôhara (1♂, 1♀, SEHU); [TI-03-MO-029] Desa Oekabiti, Kecamatan Amarasi, Kabupaten Kupang, Propinsi Nusa Tenggara Timur (NTT), 10°10′30″S 123°49′46″E, 2.II.2003, coll. M.Ôhara (1♂, SEHU). **Flores:** [FL-03-MO-006] Desa Baramari, Kecamatan, Nanguala, Kabupaten Ende, Flores, Propinsi Nusa, Tenggara Timur (NTT), 08°47′88″S 121°33′58″E, 25.II.2003, coll. M.Ôhara (1♂, 2♀♀, SEHU); [FL-03-MO-009] Desa Labolewa, Kecamatan Aesesa, Kabupaten Ngada, Flores, Propinsi Nusa Tenggara Timur (NTT), 08°39′64″S 121°19′49″E, 25.I.2003, coll. M.Ôhara (1♀, SEHU); Woloare, Desa Roworena ca 5 km N of Ende, sea level, 09.IV.1986, coll. A.L.van Berge Henegouwen and S.Pariwono 147 (4♂♂, 4♀♀, ALBH) from kerbau dung by hand in cultivated area (2♂♂, CNCI); Sikka 5 km W of Lela near junction with Ende road, sea level, 19.IV.1986, A.L.van Berge Henegouwen and S.Pariwono 157 (66♂♂, 58♀♀, ALBH), from fresh kerbau dung by hand (2♂♂, 4♀♀, CNCI). **Sumba:** [SM-03-MO-012] Desa Watumbaka, Kecamatan Pandawai, Kabupaten Sumba Timur, Propinsi Nusa Tanggara Timur (NTT), 09°40′17″S 120°21′43″E, 28.I.2003, coll. M.Ôhara and S. Hartini (1♂, SEHU); [SM-03- MO-013] Desa Lupah Watumbaka, Kecamatan Pandawai, Kabupaten Sumba timur, Propinsi Nusa Tenggara Timur (NTT), 09°38′75″S 120°24′14″E, 29.I.2003, coll. M.Ôhara (FIT trap) (3♂♂, 2♀♀, SEHU); [SM-03-MO-014] Desa Watuhadang, Kecamatan Umalulu, Kabupaten Sumba timur, Propinsi Nusa Tenggara Timur (NTT), 09°56′16″S 120°38′50″E, 29.I.2003, coll. M.Ôhara (3♂♂, 2♀♀, SEHU); [SM-03-MO-021] Desa Makaminggit, Kecamatan Nggaha Ori Ango, Kabupaten Sumba timur, Propinsi Nusa Tenggara Timur (NTT), 09°42′53″S 120°01′76″E, 30.I.2003, coll. M.Ôhara (1♀, SEHU). **Sumbawa: [**SB-00-MO-034], Desa Tatebal, Kecamatan Ropang, Kabupaten Sumbawa Besar, Propinsi Nusa Tenggara Barat (NTB), 08°48′50″S 117°19′45″E, 9.XI.2000, coll. M.Ôhara (2♂♂, 1♀, SEHU); [SB-00-MO-037], ca. 5 m. Desa Sukajaya, Kecamatan Plampang, Kabupaten Sumbawa Besar, Propinsi Nusa Tenggara Barat (NTB), 08°45′48″S 117°50′15″E, 11.XI. 2000, coll. M.Ôhara (1♂, 1♀, SEHU); [SB-00-MO-039], Desa Tolonggeru, Kecamatan Bolo, Kabupaten Bima, Propinsi Nusa Tenggara Barat (NTB), 08°29′48″S 118°32′43″E, 11.XI.2000, coll. M.Ôhara (1♀, SEHU); Desa Belo 21 km S of Bima, sea level, 02.IV.1986, coll. A.L.van Berge Henegouwen and S.Pariwono (13♂♂, 11♀♀, ALBH); Lape ca 35 km E of Sumbawa Besar, 200 m, 29.III.1986, coll. A.L.van Berge Henegouwen and S.Pariwono (16♂♂, 15♀♀, ALBH). **Lombok:** [LO-00-MO-026], alt. 55m. Desa Betek, Kecamatan Pamenang, Propinsi Nusa Tenggara Barat (NTB), 08°26′40″S 116°05′07″E, 6.XI.2000, coll. M.Ôhara (1♂, SEHU). **Bali:** Banyuwedang, 2.VII.1976, coll. van Zon, (1♂, 3♀♀, RMNH); Lalanglingah (= Lalang Linggah) near Lalian Beach, 08°30′04″S, 114°58′13″ E, hill side near beach, from Bos sondaicus dung, coll. R.T.A.Schouten (6♂♂, 5♀♀, ALBH). **Java:** [JA-05-MO-58] West Java: Ds. Sukaresmi, 400m alt., Kec. Sukamakmur, Kab. Jonggol, 27.XI.2005, 06°32′22″S 107°03′66″E, coll. M.Ôhara leg., collected from cow dung (Bali sapi in cowshed) (2♂♂, SEHU). Kota Batoe, coll. v.de Poll, (5♂♂, 6♀♀, ALBH; USNM); Java, *S.quinquemaculatum* d'Orchymont det. (1♂, RBINS); Java, coll. Horsfield, (1♂, NMHUK); Slawi Tegal, 1909 coll. Valck Lucassen (1♂, RBINS); Baluran Nature Reserve near Bekol, 16.VI.1976, coll. van Zon, Bos javanicus dung, (2♂♂, 1♀, RMNH). [MZB.COLE.125.878] Banten: Ujung Kulon, Cidaon, XII.1958, coll. A.M.R. Wegner (1♀, MZB); [MZB.COLE.125.613] Central Java: Cilacap, V.1935, coll. Drescher (1♂, MZB). **Sumatra:** Balige, 10.III.1891, coll. Modigliani, *S.quinquemaculatum* d'Orchymont det. (1♀, RBINS); 10.1890, Balige, X.1890, coll. Modigliani (1♂, ZMUC); Fort de Cock (Bukitinggi) 1925, coll. Jacobson, from cow dung, *S.quinquemaculatum* d'Orchymont det. (1♀, RBINS); Medan, Tjinta Radja (= "Tjintaradja"), 19.VI.1917, coll. Corporaal, *S.quinquemaculatum* d'Orchymont det. (1♂, RBINS); Padang, 1890, coll. Modigliani, (1♂, ZMUC); Padang Pandjang, 1896, coll. Kannegieter, *S.quinquemaculatum* d'Orchymont det. (2♀♀, RBINS); Padang Pandjang, 800m, 1.VI.1896, coll. Kannegieter, *S.quinquemaculatum* var noire d'Or- chymont det. (1♂, ZMAN); Tandjong Morawa/ Serdang, coll. Hagen (1♀, RMNH).

Discussion

Studies on coprophilous beetles are rather common due to their importance in agricultural processes including decomposition of livestock dung which contributes to the enhancement of soil fertility and also often reduce populations of pest diptera resulting in lowered prevalence of livestock disease (Wassmer 2014). For many of these studies, species diversity and richness are assessed (Przewoźny and Bajerlein 2010, Beynon *et al.* 2012, Mroczyński and Komosiński 2014, Wassmer 2014, Anto and Vinod 2017) so good diagnostic literature for proper identification is necessary, particularly with the terrestrial hydrophilids which often occur together with both distant and closely related species.

From this review of the *Sphaeridium* species occurring in Europe and Asia, it is clear that while the genus is rather well known in the European subregion (Berge Henegowen and Foster 2019), it has been poorly understood in Asia. Without good keys including more than a few species, specimens have been commonly misidentified, leading to gaps and errors in distribution data (Jia and Ôhara 2004). By comprehensively reviewing large sets of specimens from collecting in Japanese museums (SEHU and EUMJ) and comparing to specimens from European and North American museums and collections (ALBH, CNCI, MNHN, MUDH, NHMUK, NMPC, RBINS, RMNH, USNM, ZMHB, and ZMUC) examined by Arno van Berge Henegowen, the identities of many of the species of *Sphaeridium* could be more clearly understood.

Main taxonomic revisions

The tribe Sphaeridiini is morphologically quite distinct, even from its sister group, the Megasternini, and many of its unique characters vary between species. This includes color, relative size, and shape of the aedeagus, which have been previously well documented but the shapes of the proventrite, male protarsus, and particularly the shape of the mesoventral protrusion have shown to be highly useful in species-level identification.

Of particular interest, *Sphaeridium quinquemaculatum* which was originally thought to be a single species is in fact three closely related species, with *S. quinquemaculatum* distributed in India, throughout southeast Asia to the Ryukyu archipelago in Japan and *S.* sp.1 occupying mainland China. It is unclear whether *S. quinquemaculatum* occurs anywhere in mainland China but from the specimens examined, the two species only seem to cooccur in the area around Northern Laos. Additionally, one more species that appears similar to *S.*

quinquemaculatum was found in Pedong, in northeastern India. While externally similar, all three species distinctly differ in the shape of the male genitalia.

Complications around the identities of the species *S. vitalisi* and *S. reticulatum*, two large species occurring in southeast Asia were also resolved through detailed comparison of specimen sets. Both were originally described by Orchymont in 1925 and 1929 respectively but he lacked male specimens when he described *S. vitalisi*. His description of *S. reticulatum* had both male and female but when compared to my specimen sets, the aedeagus of the male originally described as *S. reticulatum* matched my specimens of *S. vitalisi* which coincided in both dorsal sculpture but also in the shape of the median lobe which is very thin and almost carinate in *S. vitalisi* (Fig. 69E–F) and much wider and less defined laterally in *S. reticulatum* (Fig. 67E–F). Once the aedeagus was properly understood for *S. reticulatum*, it then became clear from comparison with specimens borrowed from BMNH that it is also in identical to and thus a junior synonym of *S. severini*.

Species groups

From on their morphology and to a lesser degree, geographic distribution, many of the species of *Sphaeridium* can be easily grouped together. The general body size and ventral coloration in combination with the shape of the mesoventral tablet is especially helpful in differentiating many of the groups.

Of the northern species, most of which also occur widely in Europe, the smaller species (*S. bipustulatum*, *S. densepunctatum*, *S. marginatum*, and *S. substriatum*) can be grouped into the *bipustulatum* species group and the larger species (*S. lunatum* and *S. scarabaeoides*) can be grouped into the *scarabaeoides* species group. Both of these groups can also be defined by the shapes of their mesoventral processes which is elongate triangular in the *bipustulatum* group and fusiform-teardrop shaped in the *scarabaeoides* group.

S. quinquemaculatum, *S.* sp 1, and *S.* sp. 2. form the *quinquemaculatum* species group and are all very similar morphologically and likely very closely related. All three species are very small in size and their mesoventral protrusion forms an equilateral triangle with the posterior lip finely pubescent. *S.* sp. 2 can be separated from the other two species by the lack of an anterior apical tubercle on the anterior protrusion as well as by the distinctive genitalia which bear lateral protrusions on the median lobe before the apex (Fig. 50B, C). The other two species are much more closely related and while *S.* sp.1 is larger on average and has more consistent dorsal coloration (Fig. 19E), they can only be reliably differentiated through dissection of the male genitalia of which the apex of the median lobe is gradually tapered as in Fig. 52 in *S. quinquemaculatum* and more abruptly narrowed to an almost right angle as in fig. 54 in *S.* sp.1.

The *seriatum* group comprises most of the large-sized, ventrally light species occurring in the Oriental subregion of Asia. This species group was previously mentioned in Fikáĉek and Kopráĉek's (2015) description of *S. daemonicum*, they mentioned this group as containing *S. seriatum*, *S. severini* (as *S. reticulatum* and *S. severini*), *S. vitalisi* "and probably also *S. kolleri* but from images of *S. kolleri* provided by Arno van Berge Henegowen of a dissected male specimen with the genitalia, the paramera are not apically narrow as was mentioned as a character of the group (fig. 46C). This species however has many other similarities with the other members, so I am maintaining its position within the group. *S. daemonicum* however differs in both its size which is much smaller (< 6 mm) and lacks the checkerboard pattern of dark spots on the abdominal ventrites so I am placing it in a separate group as was suggested in Fikáĉek and Kopráĉek (2015).

Chapter III:

Revision of the beach dwelling *Cercyon* Leach (Coleoptera: Hydrophilidae) of Pacific Shorelines

Introduction

Cercyon Leach is a genus of terrestrial hydrophilid beetles in the subfamily Sphaeridiinae comprised of over 260 species worldwide (Hansen 1999; Short and Fikáĉek 2011). Commonly inhabiting dung and decaying plant material, they include several halobiont species that specialize on seaweed wrack in beach habitats. Adults and larvae of these shore-dwelling species can be found from early spring through fall, often with two or more species living together in the same pile of wrack (Smetana 1978; Ôhara 2008; Inari *et al*. 2018). They are fully winged and are known to colonize piles quite readily and often in large numbers (Olabarria *et al.* 2007; Chatzimanolis and Caterino 2008), but, unlike many sandy beach-dwelling tenebrionids and carabids, they seem to be largely concentrated to wrack piles and are not often found on or in open sand (Chang 1976). Though constrained to narrow beach habitats, these beetles have nevertheless been shown to be highly mobile, and in a study by Chatzimanoli and Caterino (2008), high levels of genetic connectivity were found between geographically separated populations of *C. fimbriatus* on Californian coasts, which also suggests that these beetles can move quite easily along coastlines.

Until recently, not much attention has been paid to the ecology of terrestrial beach organisms inhabiting the zone above the intertidal, so much is still unknown about these beetles' natural history, including information on their overwintering and feeding habits (Inari *et al.* 2018; Kobayashi 2009; Kobayashi and Ôhara 2017). Recently, some work on wrack ecology has mentioned members of the genus, as they are among the more abundant beetle species represented in wrack habitats (Behbehani and Crocker 1982, Olabarria *et al.* 2007), but most of these studies only looked at general habits and population levels and did not address specifics of their taxonomy or life histories.

While the taxonomy of this group in the Pacific Northwest was studied by Hatch (1965) and later Smetana (1978, 1988) and by Sharp (1873, 1884), Shatrovskiy (1992), Ôhara and Jia (2006) and Ryndevich (1995, 2011) in the Far East, the group has not previously been examined in a global context. Worldwide, fourteen species of shore dwelling *Cercyon* have been described so far, of which ten species are endemic to the North Pacific from Japan through Southern California. On the West Coast of North America, four species, *C. fimbriatus* Mannerheim, *C. luniger* Mannerheim, *C. spathifer* Smetana, and *C. tolfino* Hatch were previously known, while six species, *C. algarum* Sharp, *C. aptus* Sharp, *C. dux* Sharp, *C. numerous* Shatrovskiy, *C. symbion* Shatrovskiy, and *C. setulosus* Sharp are known from the Far East, including Japan, Russia, and South Korea (Shatrovskiy, 1992; Ôhara and Jia, 2006). Two species are known from Atlantic shorelines and include *C. littoralis* Gyllenhal, which can be found on both North American and European beaches, and *C. depressus* Stephens, which is endemic to European shorelines with scattered records from North America (Smetana 1978). In the Southern Hemisphere, two species, *C. maritimus* Knisch and *C. aphodioides* Orchymont, are endemic to coasts of South Africa. Additionally, another genus, which is endemic to coasts of Southern Australia and New Zealand, *Cercyodes* Broun, is also known to inhabit beach wrack (Hansen 1990), although molecular data shows that it belongs to a separate lineage within the sphaeridiines (Short and Fikáĉek 2013).

In this review, I am treating the nine species of beach dwelling *Cercyon* which occur on Pacific coasts of both North America and the Far East. Redescriptions are provided for all of the species occurring in North America as well as for *C. algarum* which was not treated in the 2008 review of terrestrial hydrophilids of the Kuril Archipelago by Ôhara and Jia. Habitus photographs are provided for all species and scanning electron photographs and illustrations of the male genitalia are provided for all redescribed species.

Due in part to the close similarities of two of the treated species, *Cercyon numerosus* and *C. symbion*, I also treating additional characters that were not treated in Ôhara and Jia (2008) and my review of the North American species for the species occurring in the Far East. The use of the metafurca to differentiate between members of the *C. dux* species group was outlined in Ryndevich (2001) so am including and elaborating on the use of this character. Additionally, I am including characters of the female genitalia. While some studies have included detailed descriptions of the female genitalia of the Hydrophilidae including works on *Hydrochara* (Nasserzadeh *et al*. 2005), *Psalitrus* (Bameul, 1992), and *Kanala* (Fikáček 2010), this character has yet to be described in the littoral species of the genus *Cercyon*. In this work, the morphology of the spermatheca, spermathecal glands, ducts, bursa and coxites of six Japanese species are discussed and illustrated.

Materials and Methods

Individuals were collected using the following methods: 1) Beach wrack was shaken in a sifter of 0.2–1.0 cm mesh size depending on the substrate over a light-colored tray, from which individuals were collected (Fig. 84A–C); 2) wrack was submerged in a bucket of water, and individuals were collected as they floated to the surface; and 3) wrack samples were collected by pushing a 15 cm diameter PVC cylinder through the wrack and a couple of centimeters into the sediment, which was then inverted into a plastic bag, returned to the laboratory in a cooler, and placed in a freezer and the specimens later picked out in the lab. Specimens were collected from 56 sites in the Kenai Peninsula and Aleutian Islands, Alaska (seven sites), Vancouver Island, British Columbia (26 sites), and northern Washington (18 sites).

Examined specimens from Hokkaido came from a total of 90 localities, most were visited by members of the Laboratory of Systematic Entomology of Hokkaido University and colleagues, but two were visited by Mr. S. Hiruta, and four localities were taken from the label data of specimens housed museum collection. Names of districts ("-shichô") representing old names for the subregions of Hokkaido are used for convenience. Collecting sites are divided into four categories based on the landscape of beaches (Fig. 85): sandy (SA), shingle (SH), cobble beaches (CO) and rocky shore (RO). Generic names of seaweeds and seagrasses composing the wrack piles sampled are also provided. Specimen codes read as follows: Locality abbreviation – last two digits of year – collector's initials – site number / beach profile. Collectors: AS – Alyssa Lee Suzumura; MO – Masahiro Ôhara; SH – S. Hiruta; YS – Yoshihiro Sawada. Beach profiles: SA – sandy beach; SH – shingle beach; CO – cobble beach; RO – Rocky shore. The suffix "-shichô" refers to the subprefectures or districts of Hokkaido.

Specimens were preserved in 70–90% ethanol and later point mounted and identified in the laboratory using a stereomicroscope. When mounting specimens, mandibles were opened to show the presence or absence of maxillary discs, present only in males, to facilitate sex determination. Identification was based on external morphology and structure of genitalia using the keys in Smetana (1988) and Ôhara and Jia (2006) and comparison with museum specimens.

Terminology for female genitalia follows Bameul (1992), Nasserzadeh *et al*. (2005) and Fikáček (2010) and for metendosternites, we are following Fikáček (2010). Maximum and minimum body length was measured by adding the median length of head, pronotum, elytra, and pygidium (if exposed beyond elytra) which were measured separately to account for differences in body posture of specimens. Maximum and minimum body width was measured across the widest part of the elytra.

Dissections were performed by relaxing specimens in boiled water for about 15 minutes before removing genitalia from the body either through a slit made between abdominal tergites or by removing the terminal two to four segments of the abdomen. Genitalia were then placed in 10% KOH solution for 20–30 minutes at 60˚C before muscle was removed in 70% ethanol and then dyed in lactic acid with 1–2 drops of acid fuchsine for three hours at 60˚C. They were then dehydrated in acetic salicylate (methyl salicylate 1: acetic acid 1) for 15 minutes at 60˚C, followed by xylene for about two minutes at room temperature before examination in α-terpineol under a dissecting microscope (Nikon SMZ645, Nikon SMZ800). α-terpineol was chosen because it has a relatively low refractive index and material can be preserved in it for an extended amount of time. Genitalia were preserved in Canada balsam resin on a small circle of glass glued to cardboard and attached to the specimen. Ratios were determined by measuring pictures taken using a compound microscope (Nikon Eclipse E800, Nikon Digital Sight DS-Fi1) and calculated as an average of the length of the inner margin of the parameres divided by the length of the phallobase. Habitus photos were taken with a Nikon Digital Sight DS-Fi1 on a Nikon SMZ745T stereomicroscope, SEM photos were taken with a JSM-6510 scanning electron microscope, and all photos were edited using Adobe Photoshop CS6.

In addition to collected material, specimens and distribution data from the following collections were examined:

BBM	Beaty Biodiversity Museum, University of British Columbia, Vancouver, British Columbia, Canada (K. Needham)
EUMJ	Ehime University Museum, Matsuyama
LUOMUS	Finnish Museum of Natural History, Helsinki, Finland (J. Mattila)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (B. D. Farrell)
NAK	Collection of Dr. Takehiko Nakane preserved in SEHU
OSAC	Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA (C. Marshall)

SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California, USA (M. Caterino)
SEHU	Laboratory of Systematic Entomology, Hokkaido University Museum, Hokkaido University, Sapporo, Hokkaido, Japan (M. Ôhara)

Specimens from SEHU, OSAC (Suzumura 2019), and two type specimens from MCZ were examined. Specimens of four additional species of Japanese marine *Cercyon* from SEHU were also examined in addition to the five North American species treated in this paper. These include *C. algarum* Sharp, *C. aptus* Sharp, *C. numerous* Shatrovskiy, and *C. symbion* Shatrovskiy. Specimens from BBM were not used, but the collection was checked for unidentified or potentially mislabeled specimens. Collecting records from the SBMCZ (Caterino 2009) were considered in determining distribution ranges.

Systematics

Genus *Cercyon* Leach, 1817

Diagnosis. Body variously oval, rather flat to strongly convex; pronotum and elytra forming a continuous curve in lateral view. Dorsal surface glabrous, with punctation and sometimes with microsculpture or indistinct pubescence; pronotum without longitudinal grooves or pit-like impressions except often with two lateroposterior depressions; color ranging from pale yellow to black. Ventral surface covered in dense, short pubescence except raised surfaces of meso- and metaventrites. Antennae nine-segmented, terminal three segments forming compact club; bases visible dorsally, not hidden by lateral margin of head. Clypeus not separated from frons by a distinct suture, often truncate, extending anterior to eyes when viewed dorsally; mentum of various shape, anterior margin subtruncate or emarginate, often impressed anteromedially. Maxillary palpi shorter than antennae, with second segment swollen apically, length of apical segment equal to or slightly longer than penultimate; maxilla of males bearing adhesion discs, though may be indistinct in smaller species. Elytra with distinct epipleura, at least in basal half. Middle portion of prosternum elevated to form a tectiform longitudinal keel, not differentiated laterally from antennal excavations. Median portion of mesoventrite elevated to form a median keel or plate; contacting metaventrite at a single point or separated from it by a narrow gap. Outer margin of profemora rounded; tarsi 5-5-5 with first segment always longer than second.

Male genitalia of trilobed type, as in Figs. 89 and 96. Female genitalia as in Figs. 102–104.

Notes on Identification: Along with members of the Staphylinidae, *Cercyon* is one of the more common beach-dwelling beetle taxa. As it is the only beach-dwelling hydrophilid genus in most regions excluding Australia and New Zealand, it can be easily differentiated from other beach beetles by its evenly oval habitus, uninterrupted outline between pronotum and elytra, presence of a mesoventral tablet, maxillary adhesion discs, and clubbed antennae.

Key to Beach-dwelling *Cercyon* of the Pacific

1. Size large, body length over 3mm. Elytra densely punctate, 2nd interspace with more than eight rows of punctures (Cercyon dux group).

…2

- Size smaller, body length usually less than 3 mm. Elytra more sparsely punctate, 2nd interspace with less than six rows of punctures

…4

2. Elytra without apparent microsculpture. Mesoventral tablet forming a narrow triangle, with anterior apex slightly depressed (Figs. 90E–F, 100G). Males with mentum covered in a dense patch of oily felt-like hairs (Fig. 90C). Male genitalia as in Fig. 96D–F. North America and Far East.

Cercyon dux Sharp, 1873

- Elytra with rugous microsculpture. Mesoventral tablet fusiform (Figs. 90C–D). Males without a dense patch of felt-like hairs, at most with sparse, long hairs. Far East.

…3

3. Elytra piceous to fulvous. Scutellum usually longer than wide (Fig. 100A). Mesoventral tablet fusiform, anterior half usually not constricted to apex (Fig. 100C). Anterior margin of metafurca strongly projecting forward at ends of furcal arms (Fig. 101D). Median lobe of male genitalia rather long (see Ôhara and Jia, 2006).

Cercyon numerosus Shatrovskiy, 1989

- Elytra piceous, except for lateral and posterior margins. Scutellum usually wider than long (Fig. 100B) Mesoventral tablet fusiform, anterior half constricted to apex (Fig. 100D). Anterior margin of metafurca not strongly projecting forward at ends of furcal arms (Fig. 101E). Median lobe of male genitalia rather short (see Ôhara and Jia 2006).

Cercyon symbion Shatrovskiy, 1989

4. Size very small, body length under 2.5 mm. Head and lateral portions of pronotum covered in dense granulate microsculpture. Posterior portion of elytra with sparse indistinct pubescence. Male genitalia as in Fig. 96M–O.

Cercyon setulosus Sharp, 1884

- Size bigger, body length usually over 2.5 mm. Head and pronotum without apparent microsculpture. Elytra without pubescence.

…5

5. Elytral striae rather superficial; elytral intervals flat; mesoventral tablet long and narrow, almost carinate (Figs. 92E–F, 95E–F). North America.

…6

- Elytral striae more deeply impressed, intervals convex; mesoventral tablet fusiform.

…7

6. Pronotum piceous, elytra uniformly piceous to testaceous or fulvous (Fig. 82G), sometimes with darkened crescentic spot in apical 1/3; small area behind apical angles of pronotum with microsculpture (Fig. 92D); apices of parameres widened, as in Fig. 96J.

Cercyon luniger Mannerheim, 1853

- Pronotum and elytra piceous to testaceous, irregularly lightened at margins (Fig. 82A); pronotum completely without microsculpture (Fig. 95D); apices of parameres narrow, as in Fig. 96A.

Cercyon whuljensis Suzumura, 2020

7. Elytral striae deeply impressed, particularly at base where first two seemingly connected (Fig. 91A, D); male genitalia as in Fig. 96G–I. North America.

Cercyon fimbriatus Mannerheim, 1852

- Elytral striae variable, first two striae not seemingly connected at base. Far East.

…8

8. Interspaces of elytral striae posteriorly alternating convex and flat. Mesoventral tablet forming a narrow pentagon (Fig. 100F).

Cercyon aptus Sharp, 1873

- Interspaces of elytral striae posteriorly all evenly convex. Mesoventral tablet fusiform (Fig. 100E).

Cercyon algarum Sharp, 1873

Cercyon (*Cercyon*) *algarum* Sharp, 1873
(Figs. 81F–G; 87–89; 97A; 100E; 101A; 102A)

Cercyon algarum Sharp, 1873, 65 [Type locality: Japan: Kyushu (Nagasaki: Amakusa)];
Satô, 1989, 242 [Hokkaido, Honshu, Izu Islands (Hachijô-jima); Kyushu];
Shatrovskiy, 1989, 281.
Cercyon (*Cyceron*) *algarum*: Shatrovskiy, 1992, 366 [Kunashir].
Cercyon (*Cercyon*) *algarum*: Hansen, 1999, 275.

Redescription. Body size small to medium (length 2.0–3.0 mm, width 1.0–1.4 mm), shape oval, outline interrupted between pronotum and elytra, convex; shiny with dense punctation (Figs. 81F–G; 7A, C); with sparse rugose microsculpture on elytra.

Head piceous, pronotum testaceous though often blackened on middle, elytra testaceous though sometimes darkened along anterior margin of elytra. Ventrally piceous to testaceous, sometimes lightened at apices of femorae, with light pubesence; mouthparts and antennae testaceous to fulvous. Head covered in deep, coarse punctures except narrow area around epicranial sutures, separated by less than their own diameter, without microsculpture; clypeus roundly truncate with marginal striae (Fig. 87D). Eyes small, separated by about 9x their width dorsally. Mentum trapezoidal (length: width index = 0.49), anterior margin straight to emarginate, not carinate though may be slightly depressed behind; surface with granulate microsculpture which is dense anteriomedially but becoming more superficial posteriorly and with sparse, indistinct setae on latero-posterior areas. Length of maxillary palpi about half width of head; 2nd palpomere swollen apically, about 2.6x as long as wide; apical palpomere fusiform, slightly longer than penultimate. Male with adhesion discs on maxillae, diameter about 1/3 width of mentum. Antennae about 0.75x width of head; pedicel about 1/4 length of scape; club compact, about 2x as long as wide.

Pronotum widest at base, lateral margins evenly rounded; surface with dense, coarse and deeply impressed punctures separated by a little less than their own diameter, without distinct microsculpture (Fig. 87F).

Elytra with sides regularly curved, widest at about 2/5 length from anterior; with ten deeply impressed striae though more superficial at center, becoming more deeply impressed laterally and dorsally (Fig. 87A, C, F). Intervals flat in middle but increasingly convex posteriorly and laterally; with small, finely setous punctures, separated by about 1–2x their own diameter; surface shiny, with sparsely reticulate rugous microsculpure (Fig. 87F). Scutellum longer than wide.

Prosternum strongly tectiform, particularly anteriorly, and carinate medially; with well-defined grooves for reception of antennal club; pubescent though not reaching lateral margin. Mesoventral tablet fusiform, though variable in shape (length:width index = 2.4), surface flat, shiny, densely punctate (Figs. 88C; 100E). Metaventrite with raised pentagonal plate, convex, shiny, and densely and regularly punctate, punctures separated by little more than their own diameter; projecting anteriorly between mesocoxae and contacting mesosternal tablet at a single point; lateral portions densely pubescent, without punctures or femoral lines (Fig. 88C).

Profemur with sparse superficial punctures separated by about 2–5x their diameter; meso- and metafemora with deeper setous punctures separated by about 1–2x their diameter; metafemora with fine, indistinct, rugous microsculpture.

Metafurca as in Fig. 101A, about as long as wide, anterior margin of furcal arms not prominently projecting forward before apex, forming a rounded hump at most. Lateral extensions spatulate, oriented ventrally.

Aedaegus as in Fig. 89, rather wide; median lobe rounded and with short dense setae from about apical third, opening at about 1/4 from apex; parameres short and wide, sides almost parallel and tips truncate (genital ratio = 0.73). Female genitalia as in Fig. 102A, canal of fecundation joining into spermathecal duct at about 2/3 length of bursa, lateral projections of laterotergites narrow, median sclerite narrow anteroposteriorly, lateral halves joined narrowly at middle of posterior margin. Each ovary with 3 developed ovarioles.

Distribution. Japan (Hokkaido, Honshu, Shikoku, Kyushu, Ryukyus), Korea, Russian Fed. Map: Fig. 97A.

Specimens examined. **Hokkaido.** [Sôya-shichô] HK-09-MO-051/SI: Higashiura (45˚25'09"N 142˚02'02"E), Wakkanai, 23.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Laminaria*, *Sargassum*) and eelgrass (*Zostera*) (12 exs.); Rishiri Is., Oiso Oshidomari, (45.225829˚N, 141.151498˚E), 25.VIII.2020, A. Suzumura leg., kelp wrack (19 exs.); Rebun Is., Cape Sukkotan, (45.46370˚N, 141.96340˚E), 28.VIII.2020, A. Suzumura leg., kelp wrack (1 ex.). [Abashiri-shichô] HK-18-AS-028: Hinode-misaki (44.528838˚N 143.063675˚E) Omu, Monbetsu, 26.VI.2018, A. Suzumura leg., under seaweed (kelps) (1 ex.). [Nemuro-shichô] HK-09-MO-097/CO: Shôji riv. (44˚07'09"N 145˚15'12"E), Rausu, 13.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) (2 exs.); HK-09-MO-100/SI: Notsuke (43˚36'26"N 145˚17'08"E), Shibetsu, 14.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) and eel grass (*Zostera*) (4 exs.); HK-99-MO-003: Ochiishi-kaigan (Sotohama) (43˚10'37"N 145˚29'58"E), Nemuro, 13.VI.1999, M. Ôhara leg., under seaweeds and eel grass (*Zostera*) (1 ex.); HK-99-MO-004: Tomoshiri (43˚19'05"N 145˚40'36"E), Nemuro, 13.VI.1999, M. Ôhara leg., under seaweeds and eel grass (*Zostera*) (2 exs.); HK-99-MO-006: Goyoumai (43˚21'47"N 145˚47'43"E), Nemuro, 14.VI.1999, M. Ôhara leg., under seaweeds (1 ex.); HK-99-MO-007/CO: Nosappu-misaki (43˚23'05"N 145˚48'55"E), Nemuro, 2.VI.1992, M. Ôhara, S.I. Uéno and A. Saito leg., under seaweed, 14.VI.1999, M. Ôhara leg. (1 ex.); HK-99-MO-008: ToyoSatô (43˚23'00"N 145˚43'05"E), Nemuro, 14.VI.1999, M. Ôhara leg., under seaweeds (1 ex.). [Kushiro-shichô] HK-08-MO-032/SA, SH: Horomanbetsu (43˚59'17"N 144˚53'18"E), Akkeshi, 13.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (3 exs.). [Tokachi-shichô] HK-09-MO-007/CO: Oshirabetsu (42˚07'40"N 143˚19'03"E), Hiroo, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (7 exs.); HK-18-AS-021: Sakakimachi (43.132777˚N 145.122882˚E) Hamanaka, Akkeshi, 18.VI.2018, A. Suzumura leg., under seaweed (3 exs.). [Hidaka-shichô] HK-09-MO-006/SA: Nishi-shoya (42˚02'17"N 143˚17'31"E), Erimo, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (1 ex.); HK-09-MO-004/SH: Shiogama tunnel (42˚07'55"N 142˚53'44"E), Samani, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (27 exs.). [Iburi-shichô] HK-09-MO-080/CO: Arutori-misaki (42˚30'03"N 141˚13'44"E), 12.VIII.2009, M. Ôhara, N. Kobayashi AND H. Yamamoto leg., under seaweeds (*Laminaira*) and eel grass (*Zostera*) (1 ex.); HK-09-MO-081/CO: Chikyû-misaki (42˚18'18"N 140˚59'18"E), Muroran, 12.VIII.2009, M. Ôhara, N. Kobayashi AND H. Yamamoto leg., under seaweeds (*Laminaira*) (6 exs.); HK-09-MO-090/SA: Nishikioka (42˚35'20"N 141˚27'09"E), Tomakomai, 27.VIII.2009, M. Ôhara leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (10 exs.). [Oshima-shichô] Shiriuchi, 8.VII.1976, T. Kumata (1 ex.); HK-95-MO-0DD/CO: Tachimachi-misaki (41˚44'43"N 140˚43'19"E), Hakodate, 8.IX.1995, M. and K. Homma leg., under seaweeds (1♀, 2 exs.); Hakodate, 15.VII.1952, K. Homma (1 ex.); Osatsube, 11.VIII.1952, K. Homma (2 exs.); HK-09-MO-077/SA: Kun'nui (42˚26'10"N 140˚19'29"E), Oshamambe, 12.VIII.2009, K. Homma, N. Kobayashi, H. Yamamoto AND P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (1 ex.); HK-09-MO-076/CO: Uchiura (42˚14'28"N 140˚18'08"E), Yakumo, 12.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) (12 exs.); HK-09-MO-042/CO: Esan-misaki (41˚48'42"N

141˚10'59"E), Esan, 15.VII.2009, M. Ôhara leg., under seaweeds (*Laminaria*) (1 ex.); HK-09-MO-031/CO: Yafurai (41˚47'14"N 140˚37'12"E), Dateno, Hokuto, 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum, Laminalia*) (29 exs.); HK-09-MO-032/SA: Kikonai (41˚40'33"N 140˚26'22"E), 12.VII.2009, M. Ôhara leg., under seaweeds (*Laminalia*) and eel grass (*Zostera*) (2 exs.); HK-09-MO-033/SI: Shiragami-misaki (42˚23'52"N 140˚11'56"E), Matsumae, 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum*) (3 exs.); HK-09-MO-034/CO: Tatehama to Futatsuiwa (42˚27'04"N 140˚02'20"E), Matsumae, 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum, Laminalia*) (10 exs.). [Hiyama-shichô] HK-09-MO-037/SA: Tatenomisaki (41˚58'40"N 140˚07'53"E), Otobe, 14.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (14 exs.); HK-09-MO-074/SI: Setana-kaigan (42˚29'01"N 139˚50'52"E), Setana, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (1 ex.); HK-09-MO-075/SA, SI: Udomari (42˚21'48"N 139˚48'08"E), Kitahiyama, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto AND P. Węgrzynowicz leg., under seaweeds (*Laminaria, Sargassum*) (2 exs.). [Shiribeshi-shichô] HK-09-MO-089/SA: Shioya (43˚12'54"N 140˚55'16"E), Otaru, 22.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Sargassum*, *Ulva*) (2 exs.); HK-09-MO-086/CO: Shimamui (43˚22'24"N 140˚28'38"E), Shakotan, 22.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Sargassum*, *Laminalia*) (2 exs.); HK-96-MO-0EE/CO: Kamui-misaki (43˚19'79"N 140˚22'05"E), Shakotan, 5.X.1996, M. Ôhara and M. Maegata leg., under seaweeds (*Laminaria*, *Sargassum*) (1♀, 1 ex.); HK-09-MO-069/CO: same locality as preceding, except date and collectors, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg (8 exs.); HK-09-MO-072/SA, CO: Nr. Benkei-misaki (42˚48'42"N 140˚10'41"E), Suttsu, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (6 exs.); HK-09-MO-073/SA: Enoshima-kaigan (42˚41'15"N 140˚01'41"E), Shimamaki, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) and eel grass (*Zostera marina*) (11 exs.). [Ishikari-shichô] HK-03-MO-013/SA: same data as preceding except date and collectors as follows: 6.VII.2003, M. Ôhara, F.L. Jia and A. Armen leg. (1 ex.); HK-09-MO-085/CO: Gunbetsu (43˚37'25"N 141˚21'51"E), Hamamasu, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminalia*) (12 exs.). [Rumoi-shichô] HK-09-MO-084/CO: Nobusha (43˚52'47"N 141˚35'11"E), Mashike, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminalia*, *Sargassum*) (13 exs); HK-09-MO-083/SA: Onishika (44˚03'14"N 141˚39'14"E), Obira, Rumoi, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Sargassum*) (5 exs.).

Cercyon (*Cercyon*) *aptus* Sharp**,** 1873
(Figs. 8A–E; 97B; 100F; 101B; 102B; 104–105)

Cercyon aptus Sharp, 1873, 65 [Type locality: Japan: Honshu, Kyushu]; Satô, 1989, 242 [Shikoku]; KILS, 1999, 177 [Hokkaido].
Cercyon (*Cercyon*) *aptus*: Ôhara and Jia, 2006, 131 [redescription].

Diagnosis. Body size small to medium (length 2.5–3.0 mm, width 1.5–1.9 mm). Head black, pronotum variously testaceous to piceous, elytra fulvous or testaceous-piceous with light-colored lateral and posterior margins. Dorsal surface with relatively sparse punctation, with rugous microsculpture on elytra. Eltral striae deeply and distinctly punctate, intervals alternating convex and flat on posterior portion. Mesoventral tablet narrow pentagonal with sides almost parallel in posterior half but tapering to a point in anterior half (Fig. 100F). Maxillary adhesion discs about 1/3 width of mentum. Metafurca as in Fig. 101B, distinctly longer than wide, anterior margin of furcal arms prominently projecting forward before apex. Lateral extension teardrop-shaped, oriented ventrally. Female genitalia as in Fig. 102B, canal of fecundation joining into spermathecal duct at about 4/5 length of bursa, lateral projections of laterotergites narrow, lateral halves of median sclerite broadly joined but posterior margin emarginate. Each ovary with three developed ovarioles (Fig. 104C).

Distribution. Palearctic: Japan (Hokkaido, Honshu, Shikoku, Kyushu), Korea, Russian Fed. (Far East). Map: Fig. 97B.

Specimens examined. **Hokkaido.** [Sôya-shichô] HK-09-MO-049: Sarobetsu (45˚10'25"N 141˚34'46"E), Toyotomi, 22.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (18 exs.); HK-09-MO-050/SA: Koetoi (45˚24'15"N 141˚46'52"E), Wakkanai, 23.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (4 exs.); HK-09-MO-052/SA: Tombetsu (45˚06'13"N 142˚25'42"E), Hamatombetsu, 23.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) and eel grass (*Zostera*) (1 ex.); Rishiri Is., Oiso Oshidomari, (45.225829˚N, 141.151498˚E), 25.VIII.2020, A. Suzumura leg., kelp wrack (1 ex.); Rebun Is., Cape Sukkotan, (45.46370˚N, 141.96340˚E), 28.VIII.2020, A. Suzumura leg., kelp wrack (1 ex.). [Abashiri-shichô] HK-09-MO-055/SA: Higashi-hama

(44˚07'05"N 144˚06'46"E), Tokoro, 23.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) (4 exs.). [Nemuro-shichô] HK-09-MO-098: Azabu (43˚57'59"N 145˚08'46"E), Rausu, 13.IX.2009, M. Ôhara, H. Yamamoto AND M. Furuta leg., under seaweeds (*Sarugassum*) (2 exs.); HK-09-MO-100/SI: Notsuke (43˚36'26"N 145˚17'08"E), Shibetsu, 14.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) and eel grass (*Zostera*) (1 ex.); HK-99-MO-003: Ochiishi-kaigan (Sotohama) (43˚10'37"N 145˚29'58"E), Nemuro, 13.VI.1999, M. Ôhara leg., under seaweeds and eel grass (*Zostera*) (35 exs.). [Kushiro-shichô] HK-08-MO-023: On'betsu (42˚54'45"N 143˚59'19"E), 11.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds and eel grass (*Zostera*) (3 exs.); HK-08-MO-024: Konbumori (42˚57'01"N 144˚32'13"E), Kushiro, 11.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds and eel grass (*Zostera*) (2 exs.); HK-09-SH-001/SA: Mataitoki (42˚56'27"N 144˚29'42"E), Kushiro, 7.IX.2009, S. Hiruta leg., under seaweed (53 exs.); HK-08-MO-030: Sakaki-machi (43˚07'32"N 145˚07'01"E), Hamanaka, 13.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (5 exs.); HK-08-MO-031: Esahito (43˚10'23"N 145˚17'44"E), Hamanaka, 13.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Laminaria, Sargassum*) and eel grass (*Zostera*) (3 exs.); HK-08-MO-032/SA,SH: Horomanbetsu (43˚59'17"N 144˚53'18"E), Akkeshi, 13.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (3 exs.). [Tokachi-shichô] HK-09-MO-058/SA: Atsunai (42˚47'23"N 143˚47'50"E), Urahoro, 26.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (10 exs.). [Hidaka-shichô] HK-09-MO-005: Hyakunin-hama (41˚57'29"N 143˚14'36"E), Erimo, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (18 exs.); HK-09-MO-003/SA: Mitsuishi-onsen (42˚13'07"N 142˚37'58"E), Shin-hidaka, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (10 exs.); HK-09-MO-002/SA: Irifune-chô (42˚19'32"N 142˚22'11"E), Shizunai, 4.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (6 exs.); HK-09-MO-001/SA: Midori-machi (42˚28'29"N 142˚04'27"E), Hidaka-monbetsu, 4.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (9 exs.). [Iburi-shichô] HK-09-MO-080/CO: Arutori-misaki (42˚30'03"N 141˚13'44"E), 12.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminaira*) and eel grass (*Zostera*) (2 exs.); HK-09-MO-092: Ayoro cape (42˚27'11"N 141˚12'21"E), Noboribetsu, 27.VIII.2009, M. Ôhara, under seaweeds (*Sargassum, Laminaria*) and eel grass (*Zostera*) (2 exs.); HK-09-MO-091: Kojôhama (42˚28'07"N 140˚46'52"E), Noboribetsu, 27.VIII.2009, M. Ôhara, under seaweeds (*Sargassum, Laminaria*) (2 exs.). [Oshima-shichô]

HK-09-MO-078/SA: Shizukari (42˚34'44"N 140˚27'23"E), Oshamambe, 12.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (20 exs.); HK-09-MO-077/SA: Kun'nui (42˚26'10"N 140˚19'29"E), Oshamambe, 12.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (30 exs.); HK-09-MO-040: Kakarima (42˚07'23"N 140˚38'50"E), Sawara, Mori, 15.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum*) (3 exs.); HK-09-MO-043/SA: Ishizaki (41˚44'59"N 140˚53'35"E), Hakodate, 15.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum*, Konbu, Wakame) (3 exs.); HK-09-MO-030: Shitaikan, Hakodate (41˚45'53"N 140˚49'12"E), 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum, Laminalia*) (10 exs.). [Hiyama-shichô] HK-09-MO-075/SA,SI: Udomari (42˚21'48"N 139˚48'08"E), Kitahiyama, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria, Sargassum*) (1 ex.). [Shiribeshi-shichô] HK-05-MO-008: Zenibako (43˚08'1739"N 141˚09'43"E), Otaru, 16.VII.2005, M. Ôhara, under seaweeds (4 exs.); Zenibako, Otaru, 5.VII.1979, T. Fujisawa (113 exs.); HK-09-MO-087: Bikuni (43˚17'44"N 140˚36'47"E), Furubira, 22.VIII.2009, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Sargassum*) (2 exs.); HK-09-MO-089: Shioya (43˚12'54"N 140˚55'16"E), Otaru, 22.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Sargassum*, *Ulva*) (3 exs.); HK-09-MO-071/SA: Iwanai-ôhama (42˚59'55"N 140˚31'26"E), Kyôwa, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (7 exs.). [Ishikari-shichô] HK-03-MO-013: Kotan (43˚21'18"N 141˚25'37"E), Hamamasu, Ishikari, 6.VII.2003, M. Ôhara, F.L. Jia and A. Armen leg. (15 exs). [Rumoi-shichô] HK-09-MO-046/SA: Chikubetsu (44˚25'09"N 141˚44'22"E0), Haboro, 22.VII.2009, M. Ôhara and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) (1 ex.); HK-09-MO-083: Onishika (44˚03'14"N 141˚39'14"E), Obira, Rumoi, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Sargassum*) (17 exs.); HK-09-MO-082: Rumoi (43˚57'47"N 141˚38'31"E), 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Ulva*) (30 exs.); HK-18-AS-016: Zenibako (43.144958˚N 141.165762˚E) Otaru, 5.VI.2018, A. Suzumura leg., under seaweed (sargassum) (4 exs).

Cercyon (*Cercyon*) *dux* Sharp, 1873

(Figs. 81M–N, 82C–D, 83B, 90, 96D–F, 98A, C, 99, 100G, 101C, 102C)

Cercyon dux Sharp, 1873, 65 [Type locality: Japan: Kyushu (Nagasaki: Amakusa)]; Satô, 1981, 213 [Hokkaido, Honshu, Shikoku, Kyushu]; 1989, 243 [Kyushu: Okin-no-shima].
Cercyon (*Cyceron*) *dux*: Shatrovskiy, 1992, 366.
Cercyon (*Cercyon*) *dux*: Hansen, 1999, 278.

Redesription. Body size large (length 3.5–5.0 mm, width 2.1–2.8 mm), shape oval, outline slightly interrupted between pronotum and elytra, convex; shiny with dense punctation (Figs. 81A–E; 82C–D; 90A); elytra without apparent microsculpture. Color variable, head piceous, pronotum testaceous to piceous though often lighter along lateral margins, elytra 1) piecous-testaceous, irregularly fulvous along lateral and posterior margins, rarely slightly lightened along striae or 2) fully fulvous or testaceous, striae and elytral suture sometimes darkened. Ventrally piceous to testaceous, covered in white pubescence.

Head covered in dense punctures, separated by less than their own diameter, except narrow area around epicranial sutures, without microsculpture; clypeus roundly truncate with marginal striae (Fig. 90B). Eyes big, separated by about 6x their width dorsally. Mentum roundly trapezoidal (length:width index = 0.56), anterior margin emarginate, sometimes deeply depressed behind margin, evenly covered with dense patch of oily felt-like hair in males (Fig 90C); surface with setous punctures separated by about 1–2x their diameter, interspaces with granulate microsculpture in females. Maxillary palpi about half width of head; 2nd palpomere swollen apically, about 2.5x as long as wide; apical palpomere fusiform, about as long as penultimate, sparsely covered in flat setae. Male with adhesion discs on maxillae, diameter about 1/2 width of mentum. Antennae length a little less than width of head; pedicel about 0.3x length of scape; club compact, about 1.7x as long as wide.

Pronotum widest at about anterior 1/3, lateral margins strongly and evenly rounded; surface with very dense and deeply impressed punctures separated by a little less than their own diameter, without distinct microsculpture.

Elytra with sides regularly curved, widest at about 1/2 length; with nine deeply impressed striae and 10th striae darkened but not impressed, (Figs. 82C; 90A). Intervals flat basally but becoming increasingly convex towards apex; with dense punctures separated by less than their own diameter; surface shiny, with no apparent microsculpture (Fig. 90D). Scutellum a little longer than wide.

Prosternum tectiform, carinate medially, with well-defined grooves for reception of antennal club; pubescent though not reaching lateral margin. Mesoventral tablet shape variable but narrow, triangular, widest posterior and narrowed anteriorly (length:width index = 6.6), surface flat, shiny, densely punctate (Figs. 90E–F; 100G) anterior tip depressed. Metaventrite with raised pentagonal plate, convex, shiny, and densely punctate exept often, for two narrow anterio-posterior lines at center; projecting anteriorly between mesocoxae and almost contacting posterior margin of mesoventral tablet; lateral portions densely pubescent, without punctures or femoral lines (Fig. 90E).

Profemur with sparse punctures separated by about 3x their own diameter; meso- and metafemur with dense punctures separated by about 2x their diameter; mesofemur with dense granulate microsculpture and metafemur with fine, indistinct, granulate microsculpture.

Metafurca as in Fig. 101C, about as long as wide, anterior margin of furcal arms moderately projecting forward before apex. Lateral extension teardrop-shaped, oriented anterolaterally.

Female genitalia as in Fig. 102C, canal of fecundation joining into spermathecal duct at about short, about 1/3–1/2 length of bursa, lateral projections of laterotergites wide, rounded, anterior margin of median sclerite slightly emarginate at middle. Each ovary with 8 developed ovarioles.

Aedaegus as in Fig. 96D–F, median lobe wide, with opening at about 1/3 from apex, rounded and with dense hairs from opening to tip; parameres wide, diagonally weakly tapered to diagonally truncate apices (genital ratio = 0.92).

Distribution. Palearctic: Japan (Hokkaido, Honshu, Shikoku, Kyushu, Ryukyus), Korea, Russian Federation (Far East); Nearctic: British Columbia, northern Washington State. Map: Fig. 98A, C.

Remarks. Easily distinguished from other littoral *Cercyon* by its large size, lack of dorsal microsculpture, and presence of an oily, felt-like patch of hair covering the mentum in males. This is the first Nearctic record of this species, and it has only been collected from a few localities in the Strait of Georgia region of the Salish Sea (Fig. 98C). Only individuals of the second, darker coloration have been found in North American populations. The absence of records of this distinctively large species in the region prior to 2014 suggests a recent introduction. One possibility is that it may have been directly introduced from Asia via debris generated by the 2011 Tohoku Earthquake Tsunami Disaster, though more physiological and phylogenetic studies are needed to better support or refute this hypothesis.

Specimens examined. **North America. Canada, British Columbia.** Vancouver Isle: Cowichan Bay, near Dancan, 48.740556°N, 123.941667°W, M. Ôhara, 28.VI.2014, BC14MO-012 (1 ex.); Connox Bay, Royston, 49.64917°N, 125.94417°W, M. Ôhara, 2.VII.2014, BC14MO-027 (1♂, 4♀♀); Arbutus Grove Provincial Park, Nanoose Bay, 49.26194°N, 124.18889°W, M. Ôhara, 3.VII.2014, BC14MO-030 (3♂♂, genitalia illustrated); Qualicum Beach, Nanaimo, 49.35664°N, 124.48334°W, M. Ôhara, 4.VIII.2016, BC16MO-032 (17♂♂, 6♀♀); Qualicum Beach, Nanaimo, 49.86327°N, 125.11438°W, M. Ôhara, 5.VIII.2016, BC16MO-033 (1♀); Campbell River, 50.00677°N, 125.23288°W, M. Ôhara, 7.VIII.2016, BC16MO-040 (7♂♂, 6♀♀). **USA, Washington.** Neptune Beach, Lummi Reservation, Ferndale, 48.79467°N, 122.71103°W, B. Oxborrow, 25.X.2016, WA16AS-015 (4♂♂); Derelict Conveyor, Ferndale, Whatcom Co., 48.855832°N, 122.72963°W, A. Suzumura, 26.VIII.2018, WA18AS-015 (3♂♂, 3♀♀); Libbey Beach Park, Coupeville, Whidbey Island, 48.232156°N, 122.701029°W, A. Suzumura, 7.IX.2019 (3♂♂). **Japan. Hokkaido.** “Tachimachi-misaki/ Hakodate, Hokkaido/ Japan, 8.IX.1995/ M. Ôhara [under seaweed]” (1♂: SEHU0000027966); “Tachimachi-misaki/Hakodate, Hokkaido/ Japan, 8.IX.1995/M. Ôhara [under seaweed]” (1♂: SEHU0000027860); “Hokkaido: JAPAN/ Aikage, Teuri-to,/Off Haboro/ TE-08-MO-007/44°25’07”N, 141°19’16”E/ 15.VI.2008, M. Ôhara/ Under sea weed” (2♂♂: SEHU0000027838, SEHU0000027839); “Hokkaido: JAPAN/ TomiSatô, Okushiri-to/ Off Setana/OK-08-MO-015/42°04’18”N, 139°28’17”E/12.VII.2008, M. Ôhara/ under sea weed” (2♂♂: SEHU0000027901, SEHU0000027900); “Tokachi: Hokkaido: Japan/Oshirabetsu, Hiroo/HK-09-MO-007/cobble beach/ 42°07’40”N, 143°19’03”E/ 5.VI.2009, M. Ôhara/ Under seaweed” (1♂: SEHU0000028026); “Nemuro: Hokkaido: JAPAN/ Shoji riv., Rausu,/44°07’09”N, 145°15’12”E/13.IX.2009, M. Ôhara,/H. Yamamoto and M. Furuta/under seaweeds (Laminaria)/[HK-09-MO097/CO]” (1♂: SEHU0000027994); Motoineppu, Oumu, Monbetsu, 44.624293°N, 142.931578°E, A. Suzumura leg., 26.VI.2018, HK18AS-027 (3♂♂). Honshu. “Japan: Shimane/Izumo-shi Takicho Kumura/Tamura beach/5.X.2008/T. Hayama leg.” (1♂: SEHU0000028111). Hokkaido. [Sôya-shichô] Rishiri Is., Oiso Oshidomari, (45.225829˚N, 141.151498˚E), 25.VIII.2020, A. Suzumura leg., kelp wrack (9 exs.); Rebun Is., Cape Sukkotan, (45.46370˚N, 141.96340˚E), 28.VIII.2020, A. Suzumura leg., kelp wrack (6 exs.). [Nemuro-shichô] HK-09-MO-097/CO: Shôji riv. (44˚07'09"N 145˚15'12"E), Rausu, 13.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) (5♂♂, 7♀♀); HK-09-MO-098/SA: Azabu (43˚57'59"N 145˚08'46"E), Rausu, 13.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Sarugassum*) (1♂, 2♀♀); HK-09-MO-100/SI: Notsuke (43˚36'26"N 145˚17'08"E), Shibetsu, 14.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) and eel grass (*Zostera*) (1♀); HK-99-MO-004: Tomoshiri (43˚19'05"N 145˚40'36"E), Nemuro, 13.VI.1999, M. Ôhara leg., under seaweeds and eel grass (*Zostera*) (1♂, 2♀♀); HK-99-MO-007/CO: Same data except for the date and collector of HK-99-MO-001: 14.VI.1999, M. Ôhara leg. (1♂). [Abashiri-shichô] Otamoi, Shari, 10.IX.1994, Y. Yamakawa (1♂). [Kushiro-shichô] HK-08-MO-024/SA: same locality, except date, collector and habitat: 11.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds and eel grass (*Zostera*) (2 exs.); HK-09-SH-001/SA : Konbumori (42˚57'01"N 144˚32'13"E), Kushiro, 20.VI.1985, M. Ôhara leg., under seaweeds (3♀♀); HK-08-MO-032/SA, SH: Horomanbetsu (43˚59'17"N 144˚53'18"E), Akkeshi, 13.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (3 exs.); HK-18-AS-027: Otoineppu-misaki, Omu, Monbetsu (44.624236˚N 142.931885˚E), 26.VI.2018, A. Suzumura leg., under seaweed (kelps) (3 exs.); HK-18-AS-028: Hinode-misaki (44.528838˚N 143.063675˚E) Omu, Monbetsu, 26.VI.2018, A. Suzumura leg., under seaweed (kelps) (3 exs.). [Tokachi-shichô] HK-09-MO-007/CO: Oshirabetsu (42˚07'40"N 143˚19'03"E), Hiroo, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (3♂♂, 2♀♀). [Hidaka-shichô] HK-09-MO-001/SA: Midori-machi (42˚28'29"N 142˚04'27"E), Hidaka-monbetsu, 4.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (1♂); HK-09-MO-004/SH: Shiogama tunnel (42˚07'55"N 142˚53'44"E), Samani, 5.VI.2009, M. and M. Ôhara and P. Węgrzynowicz leg., under seaweeds (6♂♂, 1♀). [Iburi-shichô] HK-97-MO-0CC/CO: Toyoura (nr. Okishi tunnel) (42˚35'12"N 140˚38'49"E), 15.IX.1997, M. Ôhara leg., under seeweed (2 exs.); HK-09-MO-081/CO: Chikyû-misaki (42˚18'18"N 140˚59'18"E), Muroran, 12.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminaira)* (3♂♂, 4♀♀, 9 exs.); HK-09-MO-090/SA: Nishikioka (42˚35'20"N 141˚27'09"E), Tomakomai, 27.VIII.2009, M. Ôhara leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (1♂). [Oshima-shichô] HK-09-MO-031/CO: Yafurai (41˚47'14"N 140˚37'12"E), Dateno, Hokuto, 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum, Laminalia*) (1♂); HK-09-MO-032/SA: Kikonai (41˚40'33"N 140˚26'22"E), 12.VII.2009, M. Ôhara leg., under seaweeds (*Laminalia*) and eel grass (*Zostera*) (5♂♂, 3♀♀); HK-09-MO-033/SA: Shiragami-misaki (42˚23'52"N 140˚11'56"E), Matsumae, 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum*) (1♀); HK-09-MO-034/CO: Tatehama to Futatsuiwa (42˚27'04"N 140˚02'20"E), Matsumae, 12.VII.2009, M. Ôhara leg., under seaweeds (*Sargassum, Laminalia*) (2♂♂); HK-09-MO-042/CO: Esan-misaki (41˚48'42"N 141˚10'59"E), Esan, 15.VII.2009, M. Ôhara leg., under seaweeds (*Laminaria*) (1♂, 1♀); Hakodate, 23.VII.1952, K. Homma (8 exs.); HK-95-MO-0DD/CO: Tachimachi-misaki

(41˚44'43"N 140˚43'19"E), Hakodate, 8.IX.1995, M. and M. Ôhara leg., under seaweeds (1♀, 26 exs.); Hakodate, 23.VII.1952, K. Homma (2 exs.); Hakodate (2 exs., 17.VII.1954; 8 exs., 19.VII.1954), T. Nakane; Hakodate, 19.VII.1954, K. Sawada (1 ex.); HK-09-MO-076/CO: Uchiura (42˚14'28"N 140˚18'08"E), Yakumo, 12.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) (2♂♂); Shiriuchi, 8.VII.1976, T. Kumata (1 ex.). [Hiyama-shichô] HK-09-MO-074/SI: Setana-kaigan (42˚29'01"N 139˚50'52"E), Setana, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (1♂); HK-09-MO-075/SA, SI: Udomari (42˚21'48"N 139˚48'08"E), Kitahiyama, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria, Sargassum*) (1♂). [Shiribeshi-shichô] HK-96-MO-0EE: Kamui-misaki (43˚19'79"N 140˚22'05"E), Shakotan, 5.X.1996, M. Ôhara and M. Maegata leg., under seaweeds (*Laminaria*, *Sargassum*) (1♀); HK-03-MO-012/CO: Kusanai (43˚19'47"N 140˚22'00"E), Kamui-misaki, Shakotan, 24.V.2003, M. Ôhara and F. L. Jia leg., under seaweeds (*Sargassum*) (1 ex.); Asari, Otaru, 10.VI.1978, 8.VIII.1978, T. Fujisawa (2♀♀, 4 exs.); HK-05-MO-008/SA: Zenibako (43˚08'1739"N 141˚09'43"E), Otaru, 16.VII.2005, M. Ôhara, under seaweeds (4♂♂, 5♀♀); HK-09-MO-069/CO: same locality as preceding, except date and collectors, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg. (3♂♂, 3♀♀, 4 exs.); HK-09-MO-072/SA, CO: Nr. Benkei-misaki (42˚48'42"N 140˚10'41"E), Suttsu, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (4 exs.); HK-09-MO-073/SA: Enoshima-kaigan (42˚41'15"N 140˚01'41"E), Shimamaki, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) and eel grass (*Zostera marina*) (10 exs.); HK-09-MO-087/CO: Bikuni (43˚17'44"N 140˚36'47"E), Furubira, 22.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Sargassum*) (2♂♂). [Ishikari-shichô] HK-03-MO-013/SA: Bikuni (43˚17'44"N 140˚36'47"E), Furubira, 6.VII.2003, M. Ôhara, F.L. Jia and A. Armen leg., under seaweeds (*Sargassum*) (5♂♂, 3♀♀); HK-09-MO-085/CO: Gunbetsu (43˚37'25"N 141˚21'51"E), Hamamasu, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminalia*) (1♂, 2♀♀). [Rumoi-shichô] HK-09-MO-082/SA: Rumoi (43˚57'47"N 141˚38'31"E), 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Ulva*) (2♀♀); HK-09-MO-084/CO: Nobusha (43˚52'47"N 141˚35'11"E), Mashike, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminalia*, *Sargassum*) (3♂♂). **Ryukyu Islands.** "Onna, Onna-son/ Okinawa-ken, Japan/ 26°29'34"N, 127°50'34"E/ [seashore], 25.VII.2015/ Takuma Yoshida leg."

Cercyon (Cercyon) fimbriatus Mannerheim, 1852

(Figs. 82E–F; 83C; 91; 96G–I; 98B)

Cercyon fimbriatum Mannerheim, 1852: 344 [USA, Alaska, Mt. Edgecumbe]; Smetana, 1978, 105.

Cercyon (*Cyceron*) *fimbriatus*: Shatrovskiy, 1992: 326

Cercyon (*Cercyon*) *fimbriatus*: Horn, 1890: 293.

Redescription. Body size small to medium (2.8–3.5 mm, width: 1.6–2.1 mm), shape oval, convex though dorsoventrally compressed (Figs. 82E–F; 91A), body outline interrupted between pronotum and elytra; glabrous with dense punctuation. Surface shiny on head and pronotum, elytra matte, color patterns (Fig. 82E–F) as follows: 1) piceous with lateral margins and apex of elytra paler, fulvous, 2) head and disc of pronotum piceous, lateral margins of pronotum paler, fulvous, elytra yellow to light brown, opaque, often with dark crecentic spot on apical 1/3, scutellum and elytral suture darkened. Ventrally piceous with white pubescence; femora fulvous to piceous; maxillary palpi and antennal club testaceous; scape, pedicel, and flagellum testaceous to fulvous.

Head covered with punctures separated by about 2x their diameter except a narrow space around epicranial sutures; clypeus truncate, anterior margin emarginate, with marginal stria (Fig. 91B). Eyes separated by about 10x their width dorsally. Mentum trapezoidal, convex, widened to apical 2/5 and narrowed anteriorly, anterior margin truncate, carinate, depressed behind; with sparse punctures separated by about 3–5x their diameter, denser posteriorly; interspaces filled with dense, rugose microsculpture (length:width index = 0.44). Maxillary palpi about 0.6x width of head, second segment swollen apically, about 2x as long as wide, last fusiform, slightly longer than penultimate. Male with adhesion disks on maxillae, their diameter a little over 1/3 width of mentum. Antenna about 0.70x width of head; pedicel about 0.27x as long as scape; club compact, about 2x as long as wide.

Pronotum widest at base, lateral margins evenly rounded; surface covered with dense punctures separated by a little more than their diameter; without microsculpture.

Elytra with sides regularly curved, widest at about half length; with nine deeply impressed striae, first two curved towards each other, often seemingly joined at base (Fig. 91D).

Prosternum weakly tectiform, almost flat except for median carina, with well-defined grooves for reception of antennal club; pubescent, not reaching lateral margin. Mesoventral tablet variably shaped, fusiform, widest at about half length, acute anteriorly, rounded posteriorly (length:width index = 3.3–4.7) (Fig. 91E–F); surface flat, shiny, densely punctate. Metaventrite with raised pentagonal plate, convex, projecting anteriorly between mesocoxa and almost contacting posterior margin of mesoventral plate; shiny, densely punctate, punctures separated by about their diameter; lateral portions densely pubescent, lacking punctures or femoral lines.

Femora punctate, punctures separated by about 2x their diameter; interspaces with dense granulate microsculpture. Tibiae with dense granulate microsculpture.

Aedeagus as in Fig. 96G–I; median lobe with apical 1/5, tapered to a truncate apex, bearing short hairs; parameres apically rounded with a membranous protrusion on inner apical margin (genital ratio = 0.71).

Distribution. Pacific Coast of North America, Alaska through Mexico. Map: Fig. 98B.

Remarks. The most common species of beach dwelling *Cercyon* in the region, it can be easily distinguished by the deeply impressed, often connecting bases of the first and second striae (Fig. 91D). Body size and coloration is highly variable within this species.

Specimens examined. Paratype: “Sitkha // MCZ-ENT00007932” (1 ex.). **Canada, British Columbia.** Vancouver Isle: Alberthead Regional Park, Metchosin, 48.39583°N, 123.48833°W, M. Ôhara, 26.VI.2014, BC14MO-005 (1♂); French Beach, Juan de Fuca, 48.39583°N, 123.94528°W, M. Ôhara, 26.VI.2014, BC14MO-006 (1 ex.); Otter Point, Sooke, 48.39667°N, 123.86694°W, M. Ôhara, 26.VI.2014, BC14MO-007 (2 exs.); Wickaninnish Beach, Ucluelet, 49.01611°N, 125.67417°W, M. Ôhara, 29.VI.2014, BC14MO-015 (9 exs.); Halifmoo Bay, Ucluelet, 48.94444°N, 125.61278°W, M. Ôhara, 30.VI.2014, BC14MO-017a (3 exs.); Florencia Bay, Ucluelet, 49.98111°N, 125.61111°W, M. Ôhara, 30.VI.2014, BC14MO-018 (4 exs.); Long Beach, Ucluelet, 49.07028°N, 125.75583°W, M. Ôhara, 30.VI.2014, BC14MO-019 (1 ex.); Esowista, Long Beach, Ucluelet, 49.06861°N, 125.78417°W, M. Ôhara, 30.VI.2014, BC14MO-020 (3 exs.); Little Beach, Ucluelet, 48.93389°N, 125.54056°W, M. Ôhara, 1.VII.2014, BC14MO-023a (2♂♂); Terrace Beach, Ucluelet, 48.92861°N, 125.54722°W, M. Ôhara, 1.VII.2014, Terrace Beach, BC14MO-024 (3 exs.); Arbutus Grove Provincial Park, Nanoose Bay, 49.26194°N, 124.18889°W, M. Ôhara, 3.VII.2014, BC14MO-030 (6 exs.); Qualicum Beach, Nanaimo, 49.35664°N, 124.48334°W, M. Ôhara and N. Kobayashi, 4.VIII.2016, BC16MO-032 (1 ex.); Qualicum Beach, Nanaimo, 49.86327°N, 125.11438°W, M. Ôhara and N. Kobayashi, 5.VIII.2016, BC16MO-033 (2♂♂); Fort Rupert, near Port Hadley, 50.69515°N, 127.41035°W, M. Ôhara and N. Kobayashi, 6.VIII.2016, BC16MO-036 (1 ex.); Sayward, 50.39783°N, 125.96224°W, M. Ôhara and N. Kobayashi, 7.VIII.2016, BC16MO-039 (1 ex.); Perimeter Park, Metchosin, Colwood, 48.47530°N, 123.47365°W, M. Ôhara, 8.VIII.2016, BC16MO-044 (3 exs.). **USA, Alaska.** Unalaska, Amaknak Island, 53.88491°N, 166.55671°W, M. Ôhara, 12-13.VIII.2015, UN15MO-019 (5 exs.); Land End, Homer, Kenai Peninsula, 59.600849°N, 151.412078°W, M. Ôhara, 17.VIII.2015, AL15MO-022 (28 exs.); Anchor Point, Homer, Kenai, Alaska, 59.77291°N, 151.87000°W, M. Ôhara, 18.VIII.2015, AL15MO-023 (21 exs.); Nash Road, Seward Peninsula, 60.08330°N, 149.35199°W, M. Ôhara, 19.VIII.2015, AL15MO-029 (55 exs.). **Washington.** Roosevelt Ocean Beach Access, Copalis Crossing, 47.17639°N, 124.19694°W, M. Ôhara, 21.VI.2013, WA13MO-039 (1 ex.); Glenwood Creek, Snohomish Co., 47.959751°N, 122.248971°W, A. Suzumura, 6.VI.2016, WA16AS-006 (1 ex.); Neptune Beach, Lummi Reservation, Ferndale, 48.79467°N, 122.71103°W, B. Oxborrow, 25.X.2016, WA16AS-015 (8 exs.); Howarth Park, Snohomish Co., 47.96440°N, 122.24050°W, A. Suzumura, 5.VI.2017, WA17AS-001 (2 exs); Meadowdale, Snohomish Co., 47.85948°N, 122.33526°W, A. Suzumura, 9.VI.2017, WA17AS-004 (7♂♂); North of Battery Van Horne, Whidbey Island, 48.16159°N, 122.68286°W, A. Suzumura, 24.VI.2017, WA17AS-005 (2♂♂); Port Williams County Park, Sequim, Clallam Co., 48.097421°N, 123.046779°W, A. Suzumura, 14.VIII.2018, WA18AS-004 (1 ex.); Dungeness Landing County Park, Sequim, Clallam Co., 48.151984°N, 123.143518°W, A. Suzumura, 21.VIII.2018, WA18AS-005 (1 ex.); Cline Spit County Park, Sequim, Clallam Co., 48.151984°N, 123.152187°W, A. Suzumura, 21.VIII.2018, WA18AS-006 (1 ex.); Port Angeles waterfront, Clallam Co., 48.119615°N, 123.428617°W, A. Suzumura, 21.VIII.2018, WA18AS-007 (1 ex.); Chito Beach Resort, Sekiu, Clallam Co., 48.305656°N, 124.428559°W, A. Suzumura, 2018.VIII.22, WA18AS-009 (1 ex.); unnamed beach, Sekiu, Clallam Co., 48.345279°N, 124.172070°W, A. Suzumura, 22.VIII.2018, WA18AS-010 (1♂); Hobuck Beach, Neah Bay, Makah Reservation, 48.336265°N, 124.663221°W, A. Suzumura, 22.VIII.2018, WA18AS-011 (1 ex.); Clallem Bay Spit, Clallam Bay, Clallam Co., 48.255792°N, 124.26017°W, A. Suzumura, 23.VIII.2018, WA18AS-013 (1 ex.); Washington Park Boat Landing, Anacortes, Skagit Co., 48.500156°N, 122.693686°W, A. Suzumura, 26.VIII.2018, WA18AS-016 (1 ex.); Libbey Beach Park, Coupeville, Whidbey Island, 48.232156°N, 122.701029°W, A. Suzumura, 26.VIII.2018, WA18AS-017 (1♂). **Oregon.** OSAC_00000206873; OSAC_00000206879; OSAC_00000206882; OSAC_00000206894.

Cercyon (*Cercyon*) *luniger* Mannerheim, 1853

(Fig. 82G–H; 83D; 92; 93; 96J–L; 98B)

Cercyon lunigerum Mannerheim 1853: 168 [type locality: Kodiak, AK].

Heteryon luniger: Winters 1944: 94.

Cercyon (*Cercyon*) *spathifer* Smetana 1978: 149 [San Pedro, CA].

Cercyon (*Cyceron*) *luniger*: Smetana 1988: 161; Shatrovskiy 1992: 362.

Cercyon (*Cyceron*) *spathifer*: Smetana 1978: 150; Shatrovskiy 1992: 362.

Redescription. Body size medium (3.1–3.9 mm, width: 1.8–2.1 mm), shape oval, convex though dorsoventrally compressed (Figs. 82G–H; 92A); body outline continuous between pronotum and elytra. Surface shiny anteriorly, though becoming matte, rugose on posterior 1/2 of elytra.

Head, pronotum, and scutellum piceous with lateral margins of pronotum often paler, testaceous; elytra fulvous-testaceous, often with crecentic oblique spot in apical third (Fig. 82G–H). Ventrally piceous with pale pubescence, legs and maxillary palpi testaceous to fulvous. Head covered with dense punctures separated by a little more than their diameter except a narrow space around epicranial suture; interspaces with dense, granulate microsculpture except along median line and posterolaterally to epicranial sutures; clypeus anteriorly truncate with marginal stria, anterior corners rounded (Fig. 92B). Eyes separated by about 9x their width dorsally. Mentum trapezoidal to almost rectangular (length:width index = 0.52), anterior margin carinate, depressed behind; surface with even, dense granulate microsculpture and long hairs around lateral and posterior margins. Maxillary palpi a little longer than 1/2 width of head; second segment swollen apically, a little over 2x as long as wide; last segment fusiform, slightly longer than penultimate. Male with adhesion disk on maxilla, diameter about 1/4 width of mentum (Fig. 92C). Antenna about 0.90x width of head; pedicel about 1/5 length of scape; club compact, about 2x as long as wide.

Pronotum widest at base, lateral margins evenly rounded; surface covered with dense punctures separated by a little more than their diameter; without microsculpture except a small area behind anterolateral corners (Fig. 92D).

Elytra with sides regularly curved; widest at about half length; with ten relatively superficial striae, becoming less impressed posteriorly and laterally; 10th stria almost completely unimpressed, only marked by dark pigmentation. Intervals flat with dense punctures separated by 1–2x their diameter; interspaces with sparse rugose microsculpture and dense granulate microsculpture.

Prosternum weakly tectiform, with a weak or incomplete carina medially; with grooves for reception of antennal club; pubescent though not reaching lateral margin. Mesoventral tablet extremely narrow, almost linear (length:width index > 10.0), surface flat, shiny, with fine punctures (Fig. 92E–F). Metaventrite with raised pentagonal plate, convex, projecting anteriorly between mesocoxae and almost contacting posterior margin of mesoventral plate; shiny, sparsely punctate, punctures separated 2–5x their diameter; lateral portions densely pubescent, lacking punctures or femoral lines (Fig. 2E).

Femora with punctures separated by about 2–3x their diameter, interspaces with dense to indistinct granulate microsculpture. Tibiae apically rounded, with dense granulate microsculpture.

Aedaegus as in Fig. 96J–L, median lobe roundly narrowed to apex; with short, indistinct hairs; parameres extremely wide, apical 2/5 almost triangular in shape, apical margin flat (genital ratio = 0.71).

Distribution. Pacific Coast of North America, Alaska through Mexico. Map: Fig. 98B.

Remarks. Similar to *Cercyon whuljensis* and often found living with it (Smetana, 1978) but differs in the shape of the male parameres, the presence of a small area of microsculpture on the apical angles of the pronotum, and lighter elytral coloration. Due to the close external similarities, specimens of *C. whuljensis* in OSAC had previously been identified by Hatch (OSAC_0000186121 – OSAC_0000186126) and described within *C. luniger* in Smetana (1988), but examination of genitalia has revealed that what had previously been considered interspecies variation in coloration and microsculpture, in fact, corresponds to two different species (Suzumura, 2019). The genitalia illustrated as belonging to *C. spathifer* in Smetana (1978) correspond to this species, while genitalia illustrated as belonging to *C. luniger* in Smetana (1988) correspond to *C. whuljensis*.

Specimens examined. Lectotype: "Kadjak//Holmberg// Cercyon/ lunigerum/ Mannerheim//Cercyon luniger/ Mannh./ Smetana des 1974/ LECTOTYPE// Mus. Zool. H:fors/

Spec. typ. No 2379/ Cercyon lu-/ nigerum/ Mannh.// Mus.Zool. Helsinki/ Loan No./ CA 32// Photographed/ 2019/ Pekka Malinen// http://id.luomus.fi// GAC. 28090/ UNITED STATES Alaska/ Kodiak/ 57.47 N, 152.48 W/ Holmberg leg.” (LUOMUS). Paralectotype: “Type 7930 // C. lunigerum / Kadjak. Mann. // MCZ-ENT00007930” (MCZ). **Canada, British Columbia.** Vancouver Isle. Alberthead Regional Park, Metchosin, 48.39583°N, 123.48833°W, M. Ôhara, 26.VI.2014, BC14MO-005 (1 ex.); Otter Point, Sooke, 48.39667°N, 123.86694°W, M. Ôhara, 26.VI.2014, BC14MO-007 (1♂); Whiffin Spit Beach, Sooke, 48.35694°N, 123.86694°W, M. Ôhara, 27.VI.2014, BC14MO-008 (1♂); Sombrio Beach, Juan de Fuca, 48.4981°N, 124.30000°W, M. Ôhara, 27.VI.214, BC14MO-010 (2♂♂); Nanaimo, Nanaimo, 49.17583°N, 123.94165°W, M. Ôhara, 28.VI.2014, BC14MO-013 (1 ex.); Little Beach, Ucluelet, 48.93389°N, 125.54056°W, M. Ôhara, 1.VII.2014, BC14MO-023a (1♂); Big Beach, Ucluelet, 48.93500°N, 125.55250°W, M. Ôhara, 1.VII.2014, BC14MO-025 (6♂♂, 1♀); Connox Bay, Royston, 49.64917°N, 125.94417°W, M. Ôhara, 2.VII.2014, BC16MO-027 (1 ex.); Sayward, 50.39783°N, 125.96224°W, M. Ôhara and N. Kobayashi, 7.VIII.2016, BC16MO-039 (1 ex.). **USA, Washington.** “Bowser, B.C./VI.8: -55/W. J. Brown// C.luniger/ det. M. Hatch” OSAC_000184564, OSAC_000184565; just North of Battery Van Horne, Whidbey Island, 48.16159°N, 122.68286°W, A. Suzumura, 24.VI.2017, WA17AS-005 (3♂♂, 1♀); Whisky Creek Beach, Port Angeles, Clallam Co., 48.15557°N, 123.780673°W, A. Suzumura, 22.VIII.2018, WA18AS-008 (13 exs.); unnamed beach, Sekiu, Clallam Co., 48.345279°N, 124.172070°W, A. Suzumura, 2018.VIII.22, WA18AS-010 (4 exs.).

Cercyon (*Cercyon*) *numerosus* Shatrovskiy, 1989
(Figs. 81I–J; 97C; 100A, C; 101D; 103A)

Cercyon numerosus Shatrovskiy, 1989: 281; KILS, 1999, 177 [Hokkaido].
Cercyon (*Cercyon*) *numerosus*: Ôhara and Jia, 2006, 134 [redescription].

Diagnosis. Body size large (length 3.1–3.8 mm, width 2.0–2.5 mm). Coloration various, head and pronotum black, elytra fulvous to piceous with lightened lateral and dorsal margins. Dorsal surface densely punctured, with rugous microsculpture on elytra. Scutellum usually distinctly longer than wide (Fig. 100A). Mesoventral tablet fusiform, usually diamond shaped, tapering more sharply anteriorly and with posterior apex rounded (Fig. 100C). Maxillary adhesion discs about 1/4 width of mentum. Surface of mentum posterior to impression of anterior transverse sulcus concave medially to flat throughout, often with long, golden pubescence in male specimens. Metafurca as in Fig. 101D, about as long as wide, anterior margins of furcal arms prominently projecting forward before apex, lateral extension narrow, oriented anterolaterally. Female genitalia as in Fig. 103A, canal of fecundation joining into spermathecal duct at about 1/2–2/3 length of bursa, lateral projections of laterotergites narrow, middle of anterior margin of median sclerite deeply emarginate. Each ovary with five developed ovarioles.

Distribution. Palearctic: Japan (Hokkaido, Honshu, Kyushu), Korea, Russian Federation. Map: Fig. 97C.

Specimens examined. **Hokkaido.** [Sôya-shichô] Rishiri Is., Oiso Oshidomari, (45.225829˚N, 141.151498˚E), 25.VIII.2020, A. Suzumura leg., kelp wrack (9 exs.); Rebun Is., Cape Sukkotan, (45.46370˚N, 141.96340˚E), 28.VIII.2020, A. Suzumura leg., kelp wrack (2 exs.). [Abashiri- shichô] HK-18-AS-027: Motoineppu-misaki (44.624236˚N 142.931885˚E) Omu, Monbetsu, 26.VI.2018, A. Suzumura leg., under seaweed (kelps) (3 exs.). HK-18-AS-028: Hinode-misaki (44.528838˚N 143.063675˚E) Omu, Monbetsu, 26.VI.2018, A. Suzumura leg., under seaweed (kelps) (2 exs.) [Nemuro-shichô] HK-09-MO-100/SI: Notsuke (43˚36'26"N 145˚17'08"E), Shibetsu, 14.IX.2009, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) and eel grass (*Zostera*) (6♂♂). [Rumoi-shichô] HK-09-MO-084/CO: Nobusha (43˚52'47"N 141˚35'11"E), Mashike, 18.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminalia*, *Sargassum*) (6♂♂). [Kushiro-shichô] HK-09-SH-001/SH: Konbumori (42˚57'01"N 144˚32'13"E), Kushiro, 20.VI.1985, M. ÔHARA leg., under seaweeds (9♂♂); HK-08-MO-024/SA: Konbumori (42˚57'01"N 144˚32'13"E), Kushiro, 11.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds and eel grass (*Zostera*) (3 exs.); HK-09-SH-001/SA: Mataitoki (42˚56'27"N 144˚29'42"E), Kushiro, 7.IX.2009, S. Hiruta leg., under seaweed (10♂♂); HK-08-MO-030/SA: Sakaki-machi (43˚07'32"N 145˚07'01"E), Hamanaka, 13.VIII.2008, M. Ôhara, N. Inari and H. Yamamoto leg., under seaweeds (*Sargassum*) and eel grass (*Zostera*) (1 ex.). [Shiribeshi-shichô] HK-09-MO-070/SI, CO: Sakazuki-onsen (43˚06'45"N 140˚27'01"E), Tomari, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Ulva*) and eel grass (*Zostera marina*) (1♂); HK-09-MO-072/SA: Nr. Benkei-misaki (42˚48'42"N 140˚10'41"E), Suttsu, 11.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Sargassum*) (2♂♂). [Iburi-shichô] HK-97-MO-0CC/CO: Toyoura (nr. Okishi tunnel) (42°35'12"N 140°38'49"E), 15.IX.1997, M. Ôhara leg., under seeweed (3♂♂); HK-97-MO-0BB/SA: Usu beach (43°30'05"N 140°46'53"E), Date, 15.IX.1997, M. Ôhara leg., under seeweed (2♂♂); HK-09-MO-080/CO: Arutori-misaki (42°30'03"N 141°13'44"E), 12.VIII.2009, M. Ôhara, N. Kobayashi and H. Yamamoto leg., under seaweeds (*Laminaira*) and eel grass (*Zostera*) (1♂). [Oshima-shichô] HK-96-MO-0GG/CO: Matsumae (41°25'38"N 140°06'29"E), 4.V.1996, M. Ôhara leg., under seaweeds (1♂); HK-09-MO-076/CO: Uchiura (42°14'28"N 140°18'08"E), Yakumo, 12.VIII.2009, M. Ôhara, N. Kobayashi, H. Yamamoto and P. Węgrzynowicz leg., under seaweeds (*Laminaria*) (2♂♂).

Cercyon (*Cercyon*) *setulosus* Sharp, 1884

(Figs. 81H; 82I–J; 83E; 94; 96M–O; 98A; 100H; 101F; 103C)

Cercyon setulosus Sharp 1884: 48; Kuwayama 1967: 134 [Japan, Kuril Isles.: Kunashir].

Cercyon (*Cercyon*) *tolfino* Hatch 1965: 41; Smetana 1978: 150, synonymized by Shatrovskiy 1992: 367 [British Columbia, Washington].

Cercyon (*Cyrceon*) *setulosus*: Shatrovskiy 1992: 367 [Southern Kurils].

Cercyon (*Cercyon*) *setulosus*: Hansen 1999: 289; Shatrovskiy 1989: 281 [Southern Kurils]; Ôhara and Jia 2006: 2 [Kurils].

Redescription. Body size small (2.0–2.8 mm, width: 1.0–1.4 mm), shape oblong, convex though dorsoventrally compressed (Figs. 82I–J; 94A); surface matte, predominately covered with microsculpture. Body outline interrupted between pronotum and elytra, piceous, lateral margins of pronotum and elytra, apical portion of elytra, and elytral suture often paler (Fig. 82I, J). Ventrally piceous with pale pubescence, legs and maxillary palpi testaceous. Eyes separated by about 10x their width.

Head covered with fine punctures, separated by a little more than their diameter except around epicranial sutures, interspace with dense granulate microsculpture; clypeus anteriorly truncate with marginal striae, anterior corners rounded (Fig. 94B). Mentum trapezoidal, anterior margin emarginate and carinate, sparsely punctate with interspaces filled with microsculpture consisting of short, horizontal wrinkles (length:width index = 2.44). Maxillary palpi a little less than 0.5x width of head, second segment swollen apically, last segment fusiform and a little longer than penultimate. Male with small, indistinct adhesion disk on maxillae, their diameter about 1/4 width of mentum (Fig. 94C). Antenna about 0.70x width of head, pedicel about 1/4 length of scape, club compact, about 2x as long as wide.

Pronotum widest at base, about 2x as wide as long, lateral margins evenly rounded, surface covered with dense punctures separated by a little more than their diameter, interspaces with granulate microsculpture (Fig. 94D), densest laterally and reduced towards center.

Elytra with sides regularly curved, widest at about middle, with 10 deeply impressed striae, sometimes transversely indented parallel to margin; intervals flat, with fine punctures separated by 2–3x their diameter, interspaces with fine microrugae and sparse, indistinct decumbent pubescence laterally from 6th stria and in posterior 1/3 (Fig. 94G).

Prosternum tectiform, carinate medially, with well-defined grooves for reception of antennal club, pubescent. Mesoventral plate fusiform though variably shaped, widest at about middle, acute and often constricted anteriorly (length:width index = 2.0–3.0) (Fig. 94E–F), surface flat, shiny, sparsely punctate. Metaventrite with raised pentagonal plate, convex, shiny and irregularly punctate, projecting anteriorly between mesocoxae and contacting mesoventral tablet at a single point, lateral portions densely pubescent, lacking punctures or femoral lines (Fig. 94E).

Femora with punctures separated by about 3x their diameter, interspaces with dense granulate microsculpture. Tibiae with indistinct granulate microsculpture.

Metafurca as in Fig. 101F, wider than long, anterior margins of furcal arms not prominently projecting forward before apex, smoothly rounded, lateral extensions teardrop-shaped, oriented ventrolaterally.

Female genitalia as in Fig. 103C, canal of fecundation before joining into spermathecal duct very short, only about 1/5 length of bursa, lateral projections of laterotergites wider, triangular, median sclerite very weak, not pigmented. Each ovary with two developed ovarioles.

Aedaegus as in Fig. 96M–O; median lobe evenly tapered to a point with long, sparse hairs on apical 1/4; parameres apically narrowed and diagonally truncate at tips (genital ratio = 0.92).

Distribution. Palearctic: Kuril Islands, Japan, Russia Federation; Nearctic: Alaska through Washington. Map: Fig. 98A.

Remarks. A very small and flat species characterized by the presence of dense microsculpture on most of dorsal surface. *Cercyon tolfino* was previously placed in junior synonymy with *C. setulosus* by Shatrovskiy (1992), though the revision was either overlooked or not accepted as the two names have continued to be used. I am basing my understanding of this species on specimens examined by Shatrovskiy. This confirmed synonymy gives it a trans-Pacific distribution, ranging along the coastlines of the Northern Pacific Rim from northern Japan to Washington State.

Specimens examined. Paratype: "Bowser, B.C./VI.8 -55/W. J. Brown// PARATYPE/Cercyon (s. str)/tolfino Hatch/1960//OSAC_0000063017-0000063021" (5 exs.). **Canada, British Columbia.** Vancouver Isle.: Alberthead Regional Park, Metchosin, 48.39583°N, 123.48833°W, M. Ôhara, 26.VI.2014, BC14MO-005 (1 ex.); French Beach, Juan de Fuca, 48.39583°N, 123.94528°W, M. Ôhara, 26.VI.2014, BC14MO-006 (3 exs.); Otter Point, Sooke, 48.39667°N, 123.86694°W, M. Ôhara, 26.VI.2014, BC14MO-007 (2♂♂, 2♀♀); Whiffin Spit Beach, Sooke, 48.35694°N, 123.86694°W, M. Ôhara, 27.VI.2014, BC14MO-008 (3♂♂); Sombrio Beach, Juan de Fuca, 48.4981°N, 124.30000°W, M. Ôhara, 27.VI.2014, BC14MO-010 (9 exs.); Brown's Beach, Ucluelet, 49.93750°N, 125.55778°W, M. Ôhara, 29.VI.2014, BC14MO-016a (2 exs.); Florencia Bay, Ucluelet, 49.98111°N, 125.61111°W, M. Ôhara, 30.VI.32014, BC14MO-018 (1 ex.); Chesterman Beach, Tolfino, 49.12250°N, 125.89694°W, M. Ôhara, 30.VI.2014, BC14MO-022 (1 ex.); Little Beach, Ucluelet, 48.93389°N, 125.54056°W, M. Ôhara, 1.VII.2014, BC14MO-023a (1♂, 13 exs.); Terrace Beach, Ucluelet, 48.92861°N, 125.54722°W, M. Ôhara, 1.VII.2014, BC14MO-024 (20 exs.); Big Beach, Ucluelet, 48.93500°N, 125.55250°W, M. Ôhara, 1.VII.2014, BC14MO-025 (2 exs.); Connox Bay, Royston, 49.64917°N, 125.94417°W, M. Ôhara, 2.VII.2014, BC14MO-027 (7 exs.); Arbutus Grove Provincial Park, Nanoose Bay, 49.26194°N, 124.18889°W, M. Ôhara, 3.VII.2014, BC14MO-030 (4♂♂); Transfer Beach Park, Ladysmith, 49.26194°N, 124.18889°W, M. Ôhara, 3.VII.2014, BC14MO-031 (32 exs.); Qualicum Beach, Nanaimo, 49.35664°N, 124.48334°W, M. Ôhara and N. Kobayashi, 4.VIII.2016, BC16MO-032 (8♂♂, 2♀♀, 69 ex.); Fort Rupert, near Port Hadley, 50.69515°N, 127.41035°W, M. Ôhara and N. Kobayashi, 6.VIII.2016, BC16MO-036 (7♂♂); Sayward, 50.39783°N, 125.96224°W, M. Ôhara and N. Kobayashi, 7.VIII.2016, BC16MO-039 (1 ex.); Campbell River, 50.00677°N, 125.23288°W, M. Ôhara, 7.VIII.2016, BC16MO-040 (7♂♂); Otter Point, Muir Creek Beach, Sooke, 48.37970°N, 123.86755°W, M. Ôhara and N. Kobayashi, 2016.VIII.8, BC16MO-042 (5♂♂); Whiffin Spit, Sooke, 48.37970°N, 123.86755°W, M. Ôhara and N. Kobayashi, 8.VIII.2016, BC16MO-043 (2 exs.); "Bowser, BC/VI.8 -55/W.J. Brown". **USA, Alaska.** Whitter, Kenai Peninsula, 60.78064°N, 148.71776°W, M. Ôhara, 17.VIII.2015, AL15MO-021 (7 ex.); Land End, Homer, Kenai Peninsula, 59.600849°N, 151.412078°W, M. Ôhara, 17.VIII.2015, AL15MO-022 (19 ex.); Lowel Point, Seward, Kenai Peninsula, 60.07127°N, 149.43613°W, M. Ôhara, 19.VIII.2015, AL15MO-028 (4 exs.). **Washington.** Snohomish Co: Glenwood Creek, Snohomish Co., 47.959751°N, 122.248971°W, A. Suzumura, 6.VI.2016, WA16AS-006 (3♂♂, 2♀♀, 1 ex.); Chito Beach Resort, Sekiu, Clallam Co., 48.305656°N, 124.428559°W, A. Suzumura, 22.VIII.2018, WA18AS-009 (1 ex.); unnamed beach, Sekiu, Clallam Co., 48.345279°N, 124.172070°W, A. Suzumura, 22.VIII.2018, WA18AS-010 (1 ex.); Derelict Conveyor, Ferndale, Whatcom Co., 48.855832°N, 122.729630°W, A. Suzumura, 26.VIII.2018, WA18AS-015 (1 ex.); Libbey Beach Park, Coupeville, Whidbey Island, 48.232156°N, 122.701029°W, A. Suzumura, 26.VIII.2018, WA18AS-017 (1 ex.). **Japan, Hokkaido.** "Daikoku-jima: Akkeshi: Hokkaido/ 42°57'39"N, 144°52'11"E/ 12.VII.2005, M. Ôhara", DA05MO-005 (2♂♂: SEHU0000029423, SEHU0000029424) ; "Hokkaido: Japan/ Yagishiri-to/ Off Haboro/ 44°26'02"N141°25'41"E/ 16.VI.2008, M. Ôhara/ Under sea weed" YA08MO-010 (1♂: SEHU0000028193); "Oshima: Hokkaido: Japan/ Osatsube, Minami-kayabe/ 41°53'37"N, 141°00'42"E/ 15.VII.2009, M. Ôhara/under seaweeds (*Laminaria* sp.)" HK09MO-041/SI (1♂: SEHU0000029596); "Soya: Hokkaido: JAPAN/ Higashiura, Wakkanai/ 45°25'09"N142°02'02"E/ 23.VII.2008, M. Ôhara/ under seaweeds (*Laminaria*) and eel grass (*Zostera*)" HK09MO-051/SI (1♂: SEHU0000029538; 2♀♀: SEHU0000029539, SEHU0000029540); Nosappu, Nemuro, 43.3855492°N, 145.81350176°E, A. Suzumura, 2018.VI.17, HK18AS-017 (2♂♂, 3♀♀).

Cercyon (*Cercyon*) *symbion* Shatrovskiy, 1989
(Figs. 81K–L; 97D; 100B; D; 101E; 103B)

Cercyon symbion Shatrovskiy, 1989: 281; KILS, 1999: 177 [Hokkaido].
Cercyon (*Cercyon*) *symbion*: Ôhara and Jia, 2006: 140 [redescription].

Diagnosis. Size large (length 3.2–3.6 mm, width 2.0–2.4 mm). Coloration consistently piceous with lightened lateral and posterior margins. Dorsal surface densely punctured with rugous microsculpture on elytra. Scutellum usually about as wide as long (Fig. 100B). Mesoventral tablet fusiform, as in *C. numerosus* but generally with margins of anterior half concave, more strongly constricted as in Fig. 100D. Maxillary adhesion discs large, almost 1/2 width of mentum. Surface of mentum posterior to impression of anterior transverse sulcus flat, without long golden pubescence. Metafurca as in Fig. 101E, about as long as wide, anterior margin of furcal arms barely to not projecting forward before apex, lateral projections oval, oriented ventrally. Female genitalia as in Fig. 103B, canal of fecundation longer, joining into spermathecal duct at about 2/3–3/4 length of bursa, lateral projections of laterotergites wider, triangular, middle of anterior margin of median sclerite deeply emarginate. Each ovary with five developed ovarioles.

Distribution. Japan (Eastern Hokkaido), Russian Federation (Far East). Map: Fig. 97D.

Specimens examined. **Japan, Hokkaido.** [Abashiri-shichô] Misaki, Shirekoto, 10 to 17.VII.1965, T. Kumata and I. Miyagi (1♂). [Nemuro-shichô] HK-09-MO-100/SI: Notsuke (43˚36'26"N 145˚17'08"E), Shibetsu, M. Ôhara, H. Yamamoto and M. Furuta leg., under seaweeds (*Laminaria*) and eel grass (*Zostera*) (7 exs.); (2♂♂). [Kushiro-shichô] HK-85-MO-001/SH: Konbumori (42˚57'01"N 144˚32'13"E), Kushiro, 20.VI.1985, M. Ôhara leg., under seaweeds (1♂).

Cercyon (*Cercyon*) *whuljensis* Suzumura
(Figs. 82A–B; 83A; 86; 95; 96A–C; 98C)

Cercyon whuljensis Suzumura 2020: 477.
Cercyon luniger: Smetana 1978: 150 (partim.).

Description. Body size medium (length: 2.1–4.2 mm, width: 1.7–2.9 mm), shape oval, convex though dorsoventrally compressed (Figs. 82A–B; 95A), body outline continuous between pronotum and elytra. Surface shiny anteriorly, becoming matte, rugose on posterior 1/2 of elytra; head piceous; pronotum and elytra irregularly piceous to testaceous with lateral and posterior margins pale, variegated; base of elytra often with pale spots, elytral suture often dark. Ventrally piceous with white pubescence; femora testaceous or fulvous.

Head covered in dense punctures separated by a little more than their diameter except a narrow space around epicranial suture; interspaces with dense, granulate microsculpture except along median line and posterolateral to epicranial sutures, clypeus anteriorly truncate with marginal stria, anterior margins rounded (Fig. 95B). Eyes separated by about 9x their width dorsally. Mentum trapezoidal (length:width index = 0.46); anterior margin carinate; surface slightly convex; covered in even, dense granulate microsculpture and hairs on posterior

1/2 and around to anterolateral margins. Maxillary palpi a little longer than 1/2 width of head; second segment swollen apically, about 2x as long as wide; last segment fusiform, a little longer than penultimate. Male with adhesion disks on maxillae, diameter a little over 1/5 width of mentum (Fig. 95C). Antenna about 0.85x width of head; pedicel about 1/5 length of scape; club compact, about 2x as long as wide.

Pronotum widest at base, lateral margins evenly rounded; surface covered in dense punctures separated by about their diameter; with very sparse, minute microsculpture only visible at high magnification (Fig. 95A, D).

Elytra with sides regularly curved, widest at about the middle; with 10 relatively superficial striae, becoming less impressed posteriorly and laterally. Intervals flat, with dense punctures separated by about their diameter, interspaces with dense granulate microsculpture and sparse microrugae, though absent on anteromedial disk of elytra.

Prosternum weakly tectiform, with or without complete carina medially, with grooves for reception of antennal club, pubescent, not reaching lateral margin. Mesoventral tablet extremely narrow, almost linear (length:width index = 7.3–13.0); surface flat, shiny, with fine punctures (Fig. 95E–F). Metaventrite with raised pentagonal plate, convex, shiny, punctate, punctures separated by about 2–3x their diameter, interspaces in anteromedial area sometimes with weak granulate microsculpture, projecting anteriorly between mesocoxae and contacting mesoventral tablet at a single point; lateral portions densely pubescent, lacking punctures or femoral lines (Fig. 95E).

Femora punctate, punctures separated by 2–3x their diameter; interspaces with indistinct to dense granulate microsculpture. Tibia with dense granulate microsculpture.

Aedeagus as in Fig. 96A–C; median lobe roundly narrowed to apex, apical 1/3 with short dense hairs, parameres narrow (genital ratio = 1.01).

Distribution. British Columbia and Washington State. Map: Fig. 98C.

Etymology. "Whulj" from the Lushootseed language means "salt water" and is the original name for the Salish Sea, a complex network of waterways extending from southwestern British Columbia through northwestern Washington State and the type locality for this species.

Remarks. Similar to *C. luniger* and often found living with it (Smetana 1978) but differs in the shape of the male parameres, absence of a small area of microsculpture on the apical angles of pronotum, and darker, more mottled coloration. Due to close external similarities, several specimens of *C. whuljensis* had previously been identified by M. H. Hatch (OSAC_00000186121-00000186126) as *C. luniger*, but examination of the lectotype (GAC. 28090) and one paralectotype (MCZ-ENT00007930) specimen of *C. luniger* have revealed that they are in fact a previously undescribed species. The genitalia illustrated as belonging to *C. luniger* in Smetana (1988) corresponds to this species, while that of *C. spathifer* in Smetana (1978) corresponds to the true *C. luniger*.

Type material. Holotype ♂. **Canada, British Columbia.** Big Beach, Ucluelet, 48.93500N, 125.55250W, M. Ôhara, 1.VII.2014, BC14MO-025, pinned, with genitalia preserved in Canada balsam, deposited in BBM. Paratypes. Canada, British Columbia, Vancouver Isle: Otter Point, Sooke, 48.39667N, 123.86694W, M. Ôhara, 26.VI.2014, BC14MO-007 (1 ex.); Sombrio Beach, Juan de Fuca, 48.49810N, 124.30000W, M. Ôhara, 27.VI.2014, BC14MO-010 (2♂♂); Little Beach, Ucluelet, 48.93389N, 125.54056W, M. Ôhara, 1.VII.2014, BC14MO-023a (1♂); Big Beach, Ucluelet, 8.93500N, 125.55250W, M. Ôhara, 1.VII.2014, BC14MO-025 (5♂♂, 2♀♀); "Bowser, B.C./VI.8: -55/W. J. Brown// C. luniger Mannerheim/ Det. M. Hatch" OSAC_0000186121 – OSAC_186126 (4♂♂, 1 ex.); USA, Washington. Whisky Creek Beach, Port Angeles, Clallam Co., 48.15557N, 123.780673W, A. Suzumura, 22.VIII.2018, WA18AS-008 (9♂♂, 9♀♀); Chito Beach Resort, Sekiu, Clallam Co., 48.305656N, 124.428559W, A. Suzumura, 22.VIII.2018, WA18AS-009 (6 ex.); unnamed beach, Sekiu, Clallam Co, 48.345279N, 124.17207W, A. Suzumura, 22.VIII.2018, WA18AS-010 (4♂♂, 1♀); Hobuck Beach, Neah Bay, Makah Reservation, 48.336265N, 124.663221W, A. Suzumura, 22.VIII.2018, WA18AS-011 (1 ex.); Derelict Conveyor, Ferndale, Whatcom Co., 48.855832N, 122.72963W, A. Suzumura, 28.VIII.2018, WA18AS-015 (1♂, 1♀).

Holotype deposited in BBM along with 6 paratypes (BC14MO-007, 1 specimen; BC14MO-010, 1 specimen; BC14MO-023a, 1 specimen; BC14MO-025, 3 specimens). 6 paratypes will be deposited in MCZ (WA18AS-008, 6 specimens) and 5 in OSAC (OSAC_0000186121 – OSAC_0000186126, 5 specimens). The remaining paratypes will be deposited in SEHU (BC14MO-010, 1 specimen; BC14MO-25, 3 specimens, WA18AS-008, 12 specimens; WA18AS-010, 5 specimens; WA18AS-011, 1 specimen; WA18AS-015, 2 specimens).

Discussion

Though members of the beach dwelling *Cercyon* can be found continuously from the southern islands of Japan through the Kuril Islands, Kamchatka, Aleutian Islands, Alaska, down to southern California, previous treatments of the group have divided species between the Nearctic and Palearctic. By comparing all species from the Pacific region, it is apparent that this group cannot be so easily divided by geography. The existence of two trans-Pacific species suggests a greater degree of connectivity between coastal regions of either side of the Pacific Ocean and that a concept of the North Pacific as a bioregion in itself should be considered when studying organisms within these distributions. In fact, many other groups of beach-dwelling insects including but not limited to *Phaleromela* Reitter 1916 and *Phaleria* Laterille 1802 (Tenebrionidae), *Aegialites* Mannerheim 1853 (Salpingidae), and the closely related monotypic genera Hadropinus Sharp 1889 and *Thinopinus* LeConte 1852 (Staphylinidae) (Chatzimanolis *et al.* 2021) which indicates a rather high degree of interconnectedness across the region.

The genus *Cercyon* is recognized to be polyphyletic and is in need of revision (Short and Fikáĉek 2013, Arriaga-Varela and Fikáĉek 2021), and phylogenetic determination based on morphological characters has shown to be unreliable at the species level. In a recent phylogenetic study of the Megasternini by Arriaga-Varela and Fikáĉek (2021), *Cercyon* appeared in 16 different positions in their tree. One beach dwelling species, *C. fimbriatus* appears as a sister group to a clade including Oriental *Cercyon* species along with members of the genus *Paracercyon* which might suggest an Asian origin for at least some of the beach *Cercyon* occurring on the Pacific Coast of North America. Lineages within the Hydrophilidae are known to shift habitats multiple times (Bloom *et al*. 2014) and the existence of the Australasian genus *Cercyodes* Broun, 1886 shows that adaptation to the beach environment has happened at least twice within the Sphaeridiinae so whether or not the species treated in this work comprise a monophyletic group is not known with certainty. The *Cercyodes* are quite distinct from the other beach-dwelling megasternines which are joined by several characters including their rather flat body shape, extensive dorsal microsculpture, and lack of femoral lines however and the combination of morphological and ecological similarities may provide strong evidence for grouping the beach dwelling *Cercyon*.

Structure of metafurca. Ryndevich (2001) outlined the use of the metafurca as a diagnostic character that is useful in differentiating female specimens of the *Cercyon dux* species group including *C. numerosus* and *C. symbion* which cannot be reliably differentiated without dissection. In our analysis we also found consistent differences in the shape of the anterior margin of the furcal arms. In particular, this part protrudes strongly in the species *C. algarum*, *C. dux*, and *C. numerosus* (Figs. 101A, C, D) but only weakly *in C. aptus*, *C. symbion*, and *C. setulosus* (Figs. 101B, E, F). Additionally, the shape and orientation of the lateral extensions of the furcal arms are consistently different between species. We did not, however find strong or consistent differences in the stalk width as Ryndevich had described so we did not include this character in our diagnoses.

Structure of the female genitalia. The morphology of the female genitalia is relatively similar between species but some differences exist in the shape of the lateral projections of the laterotergites, the shape of the median sclerite, and the length of canal of fecundation of the bursa. The spermatheca and spermathecal glands, however, do not vary significantly in shape or size between species.

The overall internal structure of the female genitalia appears to be consistent with other hydrophilid beetles with a pair of ovaries, each composed of several ovarioles converging into lateral oviducts which join to form a common oviduct that attaches to the ventral side of the bursa copulatrix just anterior to the sclerotized segments (Fig. 104B–C). Two types of colleterial glands are present which is also typical of the Hydrophilidae. Oviduct colleterial glands arise from either lateral oviduct while ovariole colleterial glands are formed from one or more egg tubes of either ovary (Hinton, 1981). These glands produce secretions which are used to attach silk egg sacs to substrates, (in this case seaweed wrack) (Fig. 105). Through our dissections, we also found that the number of developed ovarioles varies between species with the smallest species, *C. setulosus* carrying four eggs at a time to the largest, *C. dux* carrying sixteen. The differences in number of eggs between species seems largely size-dependent but not much is yet known about the life histories and reproductive cycles of these species.

The area we found the most consistent differences between species in is what Nasserzadeh *et al.*, (2005) describe as "four fine tube-like structures" leading to the spermathecal duct. These tubes run along the dorsal wall of the bursa starting on either side of the vaginal opening near the entry of the common oviduct (Imms, 1964) and join some distance up the bursa where they form the spermathecal duct. In the specimens we observed, these tubes surround an area of membrane that differs from the surrounding membrane of the bursa in texture and is often more darkly pigmented. This area, which Imms (1964) refers to as the "canal of fecundation", also seems to be connected to the vaginal opening medially and when stained with acetic acid fuscine, this membrane and connecting internal mass stained more readily. Nasserzadeh et al., (2005) also noted that in *Oodes helopioides*, the "tubes" seem to be composed of a different tissue structure than the surrounding bursa copulatrix but from both studies, it is clear that more detailed histological studies are needed to understand the soft structures of the female genitalia of hydrophilid beetles.

For the purposes of this study, we found that the length and shape of this structure differs between species with that of *Cercyon setulosus* being rather small and round (Fig. 103C) and that of *C. aptus* extending across almost the entire length of the bursa copulatrix (Fig. 102B). While not enough is known about this structure to draw any conclusions about the reasons for these differences, it does not seems to have a strong relationship to the size of the male genitalia.

Taxonomy. In addition to the biogeographic implications of this work, it was also necessary for us to address concerns of a more taxonomic nature in both confirming the synonymy of *C. tolfino* and *C. setulosus* as well as in untangling the confusion around the identities of *C. luniger* and the previously undescribed *C. whuljensis*. In the case of *C. setulosus*, the synonymy had previously been published by Shatrovskiy (1992) but simply overlooked by the systematics community, as recent catalogues still cite *C. tolfino* as a valid species (Short and Fikáĉek 2011, Bousquet *et al.* 2013).

The confusion over the identities of *C. luniger* and *C. whuljensis*, however, arises from two errors in previous descriptions (Hatch 1965; Smetana 1978, 1988), the first being that they described variation in coloration and microsculpture patterns within *C. luniger* when these variations actually correspond to two separate species. The second is that illustrations and descriptions of genitalia were based on individuals of the undescribed species, *C. whuljensis* which has narrow parameres, wheras the lectotype has widened parameres as was illustrated for *C. spathifer*. Because of this, *C. luniger* was described twice as both *C. luniger* and *C. spathifer* based on the two genitalia shapes (Smetana 1978), while the undescribed species, in fact, remained undescribed within the concept of *C. luniger*. Thus, all records of *C. spathifer* refer to *C. luniger*, while records of *C. luniger* may be correct but may also refer to *C. whuljensis* and require confirmation.

For differentiating females of *Cercyon numerosus* and *C. symbion*, the anterior margin of the furcal arms of the metafurca is the most consistent character. Other characters such as the metaventral tablet and scutellum shapes (Fig. 100A–D) which are somewhat different between the two species but these characters are not stable enough to reliably be used in identification (in rare cases, these characters may resemble *C. symbion* in *C. numerosus*). In most specimens of *C. numerosus*, the scutellum is longer than wide and in *C. symbion* it is about as wide as long but in some specimens of *C. symbion*, it is longer than wide. Similarly, while the anterior half of the mesoventral tablet is consistently constricted in *C. symbion* and usually evenly tapered in *C. numerosus*, it may be constricted in some specimens of *C. numerosus*. *Cercyon numerosus* also shows a greater variation in coloration than *C. symbion* which is consistently piceous.

Chapter IV:

Terrestrial hydrophilids (Coleoptera) collected from a fallen nest of the giant honeybee *Apis dorsata dorsata* at Bogor Botanical Garden, West Java, Indonesia

Introduction

The giant Asian honeybee *Apis dorsata dorsata* found throughout South and Southeast Asia builds exposed nests consisting of single semi-circular combs which commonly hang from tree branches (Fig.106A), under cliffs, and on overhangs of buildings (Misra *et al.* 2017). These bees perform long distance migrations but tend to return to previously occupied nesting sites in which a few to many colonies can be found in relatively close proximity (Kahono *et al.* 1999). While the worker bees are able to protect the exposed comb with their bodies by forming a "curtain" of bees (Koeniger *et al.* 2017), when these nests do fall, they offer a rare source of nutrition for scavengers. While communities of vertebrates and invertebrates associated with active beehives have been well described, there are few to no studies looking at what happens in the unlikely event of a fallen, discarded, or abandoned nest.

In this study, we had the unique opportunity to observe scavenger invertebrates feeding on the decaying remains of one such fallen nest from the Bogor Botanical Garden, West Java, Indonesia which provides a relatively protected "natural" habitat with large trees on which bees can construct their hanging nests. Kahono *et al.* (1999) mention that there have been reports of bee nests potentially being attacked by animals but honey harvesting by human beings does not occur within the garden. Previously, Hartini *et al.* (2013) recorded the species of mites found in the fallen comb but numerous insect specimens were also collected from the same comb. Most of the insect collected were members of the beetle family Hydrophilidae but a few individuals from four other beetle families, Histeridae, Agyrtidae, Staphylinidae, and Coccinelidae were also collected along with a couple specimens worker ants.

The hydrophilids collected in this study represent the first recorded association with honeybees as well as new distributional records for *Protosternum hainanensis* Fikáček, Liang, Hsiao, Jia and Vondráček, 2018, *Noteropagus obliquus* Orchymont, 1925b, and *N. occlusus* Orchymont, 1932. Additionally, species of the genus *Protosternum* have previously only been collected from banana trees so this is the first recorded collection of a specimen from a different habitat.

Material and Methods

All specimens were collected from a fallen nest of Apis dorsata dorsata (Fig. 106) from the same location and date and are housed in the Systematic Entomology collection at the Hokkaido University Museum:

“Indonesia: Jawa, Kebun Raya Bogor, 30.I.2004. from nest of *Apis dorsata*. Sarang Lebah, Sih Kahono”.

Specimens were identified to genus using keys in Hansen (1990) and Jia *et al*. (2020). For *Dactylosternum* species, a character matrix in Hebauer (2008) was first used and species were confirmed with descriptions in Fikáček and Gimmel (2017) (*D. grouvellei*) and Mai *et al.* (2022) (*D. abdominale* and *D. hydrophiloides*). *Protosternum hainanensis* was first determined to be close to *P. abnormale* from the key in Bameul (1997) and confirmed to be *P. hainanensis* based on the original description in Fikáček *et al*. (2018). *Noteropagus* species were identified using descriptions and keys in Orchymont (1919, 1925, and 1932). *Paraoosternum saundersi* was identified using the key in Hebauer (2006) and confirmed from the description in Fikáček and Jia (2011). *Pachysternum apicalis* was determined from a key in Fikáček, Jia and Prokin (2012). I was unable to identify the *Cercyon* specimens to species level.

Dissections of male genitalia were performed by relaxing specimens in boiled water for about 15 minutes before removing genitalia from the body either through a slit made between abdominal tergites or by removing the terminal two to four segments of the abdomen. Genitalia were then placed in 10% KOH solution for 20–30 minutes at 60˚C before muscle was removed in 70% ethanol and then dyed in lactic acid with 1–2 drops of acid fuchsine for three hours at 60˚C. They were then dehydrated in acetic salicylate (methyl salicylate 1: acetic acid 1) for 15 minutes at 60˚C, followed by xylene for about two minutes at room temperature before examination in α-terpineol under a dissecting microscope (Nikon SMZ645, Nikon SMZ800). α-terpineol was chosen because it has a relatively low refractive index and material can be preserved in it for an extended amount of time. Genitalia were preserved in Canada balsam resin on a small circle of glass glued to cardboard and attached to the specimen.

Habitus photos were taken with a Nikon Digital Sight DS-Fi1 on a Nikon SMZ745T stereomicroscope, SEM photos were taken with a JSM-6510 scanning electron microscope, and all photos were edited using Adobe Photoshop CS6.

Dactylosternum abdominale Fabricius, 1792

(Figs. 107C–D, 110)

Sphaeridium abdominale Fabricius, 1792: 79. – Antilles.

Coelostoma insulare Castelnau, 1840: 59. Syn.: Orchymont, 1925: 274.

Dactylosternum roussetii Wollaston, 1854: 100. Syn.: Wollaston, 1864: 94; Orchymont 1925b: 274.

Cyclonotum mulsanti Murray, 1859: 352. Syn.: Orchymont, 1925: 275.

Cyclonotum natalense Gemminger and Harold, 1868: 495. Syn.: Orchymont, 1925: 274; Balfour-Browne, 1945: 116.

Hydrobius semistriatus Schaufuss, 1887: 108. Syn.: Orchymont, 1925: 277.

Dactylosternum depressum Régimbart, 1903: 46. Syn.: Orchymont, 1934: 265.

Andotypus perezdearcei Moroni, 2000. Syn.: Fikáček *et al.* 2014.

Detailed diagnosis in Mai *et al.* (2022).

Distribution. **Palearctic** (introduced)**:** Algeria, Austria, Azores, Croatia, Cyprus, Czech Republic, Egypt, France, Great Britain, Germany, Greece, Hungary, Iran, Italy, Japan, Madeira, Poland, Spain (incl. Canary Is.), Switzerland, Syria, Tunisia, United Arab Emirates; **Afrotropical:** Benin, Cabe Verde, Comoros, Guinea, Ivory Coast, Madagascar, Mauritius (Mascarene Is.), Nigeria, Senegal, Seychelles, South Africa, Togo, Yemen, Zaire; **Oriental:** China (Guangdong, Guangxi, Macao, Nei Mongol), India (incl. Andaman Is.), Indonesia (Java, Sumatra), Malaysia, Philippines, Singapore, Sri Lanka Taiwan; **Australian:** (Australian Capitol Territory, Queensland, South Australia, Victoria, Western Australia, Christmas Is.), Fiji, New Caledonia, New Guinea, New Zealand; **Pacific** (introduced)**:** French Polynesia (Gambier Is., Marquesas Is., Society Is.), USA (Hawaii), Samoa; **Neotropical** (introduced)**:** Argentina, Brazil, Cuba, Jamaica, Lesser Antilles, Mexico; **Nearctic** (introduced)**:** USA (Alabama, California, Florida, North Carolina, Texas).

Ecology. Usually found in various decaying organic matter, especially decaying banana tree stumps. Also found in other rotting plant material, domestic waste, and farmyard manure (Mai *et al.* 2022).

Dactylosternum hydrophiloides MacLeay, 1825
(Figs. 107C–D, 111)

Sphaeridium hydrophiloides MacLeay, 1825: 36.
Cyclonotum capense Dejean, 1833: 134. Syn.: Erichson, 1845: 105; Orchymont, 1923: 417.
Coelostoma nitidum Castelnau, 1840: 58. Syn.: Orchymont, 1914: 322; Orchymont, 1935: 198.
Cyclonotum rubripes Boheman, 1858:24. Syn.: Orchymont, 1914: 322.

Detailed redescription in Mai *et al.* (2022).

Distribution. **Afrotropical** (introduced)**:** South Africa; **Oriental:** Bhutan, China (Fujian, Guangdong, Hong Kong, Hainan, Guangxi, Guizhou, Yunnan, Xizang), Nepal, India (West Bengal, Andaman Is.), Indonesia (Borneo, Buru, Java, Sulawesi), Malaysia, Philippines, Singapore, Taiwan, Thailand, Vietnam; **Australian:** Australia, Palau Island; **Pacific** (introduced)**:** USA (Hawaii); **Neotropical** (introduced)**:** Jamaica.

Ecology. Usually found in decaying plant material, especially rotting banana tree stumps but also in rotten bamboo and fruits (Mai *et al.* 2022).

Dactylosternum grouvellei Guillebeau, 1894
(Figs. 107E–F, 112)

Sternosternus grouvellei Guillebeau, 1894: ccvii. – Indonesia: Sumatra.
Dactylosternum seriatum Knisch, 1921: 77. Syn: Fikáček and Gimmel, 2017.

Redescription. Body size small, length 3.0 mm long, width 2.6 mm; very convex, almost semicircular (Fig. 112A). Dorsal and ventral surfaces black to dark testaceous; legs testaceous; maxillary palpi and antennal segments dark fulvous, antennal club yellow (Fig. 107E–F).

Head weakly convex; surface with dense, v-shaped punctures (each consisting of a fine puncture with two short microrugae) becoming very dense anteriorly and laterally; anterior margin of clypeus rounded, almost straight medially, without distinct beading. Eyes of moderate size, interocular space about 6.5x as wide as one eye in dorsal view, weakly emarginate anteriorly.

Pronotum ca. 2.5x as wide as long, widest basally, narrowed anteriorly; pronotal puncation similar to head. Lateral margin weakly curved, with narrow beading which continues around anterior margin and ends at posterior angles. Scutellum triangular, slightly longer than wide. Elytra widest at base; lateral margins weakly curved, almost straight medially, slightly explanate, with very fine beading; surface somewhat shining; 10 deep striae composed of larger punctures connected by grooves; intervals flat, becoming convex posteriorly, with v-shaped punctures, some of which become finely setous posteriorly (Fig. 112B).

Mentum as in Fig. 112C, slightly widened anteriorly, sides weakly curved, surface with deep setous punctures laterally, setae rather long and fine, anterior margin straight to weakly sinuate, weakly emarginate at center, rather concave behind. Maxillary palpomeres subequal in length, covered in sparse fine pubesence and microrugae; segment 2 swollen apically; palpomere 4 fusiform, apex with a deep pore; segment 3 slightly widened apically.

Central area of proventrite as in Fig. 112D, weakly convex, almost flat, lacking median carina but anterior margin carinate and center with a small tubercle; posterior margin with weak beading; lateral areas with very shallow antennal grooves which are not clearly delineated. Mesoventral process as in Fig. 112E–F, medially raised and forming a keel with the anterior apex of the metaventrite; anterior portion forming an “arrowhead” shape with anterior apex acute, anterior margin protruding and carinate laterally, sloping out and towards body posteriorly; posteriorly confluent with anterior apex of mesoventral disc, surface with very fine and sparse punctation. Lateral areas of metaventrite densely pubescent, lacking femoral lines; central disc strongly raised medially, almost flat at center; surface posteriorly with short median longitudinal groove; surface glabrous, with fine sparse punctures consistent with those on mesoventral process; posterior margin weakly emarginate, with row of pubesence (Fig. 112G–H).

Abdomen with 5 segments, first segment carinate medially, surface densely pubescent; apex of segment 5 rounded.

Ventral surface of femorae glabrous with fine setous punctation and sinuate microrugae. Ventral surface of tarsi with long yellow setae which are curved apically; metatarsi with segment 1 shorter than segements 2 and 3 combined.

No male specimen available for genitalia dissection.

Distribution. **Oriental:** Indonesia (Enggano, Java, Mentawei Is., Sumatra), Vietnam.

Ecology. The ecological habit of this species is not well recorded, but it is likely to also inhabit banana tree stumps and various decaying organic material.

Protosternum hainanensis Fikáček, Liang, Hsiao, Jia and Vondráček, 2018
(Figs. 109E–F, 113)

Protosternum hainanensis Fikáček, Liang, Hsiao, Jia and Vondracek, 2018. – Hainan Island.

Detailed description in Fikáček *et al.* (2018).

Distribution. China (Hainan Island), Indonesia (Java) [new record].

Ecology. Species of the genus Protosternum are previously thought to be exclusively found in rotting banana stems and it is likely that they are obligately associated with them, particularly during their larval and pupal stages (Fikáček *et al.* 2018).

Remarks. While this specimen can be placed as a member of the *P. abnormale* species group based on [characters], the sole individual collected was female and thus the species could not be confirmed based on the genitalia. It fits best the description of *P. haianensis* which is known only from Hainan island in Southern China (Fikáček *et al.* 2018) based on the weakly curved anterolateral ridge of the metaventrite which reaches the lateral margin of the metaventrite more posteriorly. The other species known to have this characteristic is P. obscurum from southern India but the current specimen differs from this species in having a short tooth at the intersection of the transverse and longitudinal carinae of the mesoventral process (Hebauer 2007).

Noteropagus obliquus Orchymont, 1925
(Figs. 109A–B, 114–115)

Noteropagus obliquus Orchymont, 1925: 305. – Malaysia, Pinang Is.

Redescription. Body size minute, length 1.4 mm long, width 0.9 mm; strongly convex (Fig. 114A). Dorsal coloration dark reddish-brown, head black dorsally, lighter on clypeus and lateral margins; labrum, maxillary palpomeres, and antennae light yellow-brown, including club. Ventrites dark reddish-brown, lighter on epipleura, lateral areas of pronotum, middle of mesoventral process, middle of apical abdominal ventrite, and legs (Fig. 109A–B).

Head strongly convex, with clypeus strongly deflected; with fine, sparse punctures separated by about 2x their diameter and strong microrugae; frontoclypeal suture indiscernible; anterior margin of clypeus truncate, with strong marginal beading. Eyes small, interocular space about 7x as wide as one eye in dorsal view. Labrum exposed, anterior margin sinuate.

Pronotum ca. 2.4x as wide as long; pronotal puncation as on frons but lacking distinct microrugae, shining. Lateral margin almost straight, with strong narrow beading which continues around anterior angles, posterior margin without beading or a transverse series of coarser punctures. Elytra shining, with elytral suture deeply impressed posteriorly; 9 striae composed of larger punctures which are larger and coarser laterally, 1–4 becoming indistinct on anterior about 1/4, 5–9 not continuing on about anterior 1/3; intervals flat anteriorly, posteriorly with odd intervals (3 and 5) somewhat convex; with smaller, fine punctures and each with a row of small fine pubesence posteriorly (Fig. 114B).

Mentum as in Fig. 114C, covered in long golden pubesence, anterior margin strongly emarginate. Maxillary palpomere 2 swollen apically, palpomere 4 fusiform, about as long as palpomere 2, male without adhesive discs, stipes with long golden pubesence.

Raised median area of proventrite as in Fig. 114D, triangular, separated from lateral areas by coxal cavities, tectiform, carinate medially and along anterior margin, lateral areas with antennal grooves almost reaching lateral margins. Mesoventral process as in Fig. 114E, pentagonal, transverse, convex posteromedially, anterior margin strongly marginate, with apical process, posterior margin strongly curved, closely attaining anterior margin of metaventrite. Lateral areas of metaventrite with deep coarse punctures; raised central area about 1.5x longer than wide, with a median groove on posterior 1/5, surface with much finer punctation and indistinct microrugae. Abdomen with 5 segments, first segment weakly carinate medially, segments 1–3 with coarse punctures laterally, segments 4–5 with only fine, indistinct punctation (Fig. 114F).

Anterior surface of procoxae with fine granulate microsculpture, metacoxae with an even row of punctures of decreasing size laterally. Femora triangular, shining, posteromedial angle of mesofemora distinctly extending posterior to trochanters. Outer margin of tibiae with a row of small indistinct spines and meso- and metatibiae with small apical spines. Tarsi ventrally with dense pubesence.

Male genitalia as in Fig. 115, about 0.35 mm long, paramera about 1.5x as long as phallobase. Median lobe with sides weakly sinuate on basal about 1/2, straight on apical about 1/2, converging to a blunt point apically, corona located at apical about 2/5ths, opening very wide. Paramera wide narrowed to blunt tips apically, phallobase symmetrical, pointed basally. Accessory sclerite (9th ventrite) long, about 2/3 length of aedeagus, sides sinuate, narrowed near based and widened apically before converging to meet at an ange, with wide median ventral ridge; lateral arms subequal in length paramera, apices truncate.

Distribution. **Oriental:** Indonesia (**Java [new record]**, Sulawesi), Malaysia; **Pacific** (introduced)**:** Hawaii.

Ecology. No ecological information specific to this species is described but two other Noteropagus species were recorded from "on wild banana" in Orchymont, (1932) and also collected by Fikáček *et al.* (2018) in rotten banana stems. Members of this genus are likely generalists on decaying organic matter.

Noteropagus occlusus Orchymont, 1932
(Figs. 109C–D, 116)

Noteropagus occlusus Orchymont, 1932: 682. – Indonesia, S. Sumatra.

Redescription. Body size small, length 1.4 mm long, width 0.9 mm; strongly convex (Fig. 116A). Dorsal coloration dark reddish-brown, including head; labrum, maxillary palpomeres, and antennae light yellow-brown, including club. Ventrites reddish-brown, lighter on epipleura, lateral areas of pronotum, middle of mesoventral process, middle of apical abdominal ventrite, and legs (Fig. 109C–D).

Head strongly convex, with clypeus strongly deflected; with fine, sparse punctures separated by about 2x their diameter and fine indistinct microrugae; frontoclypeal suture indiscernible; anterior margin of clypeus truncate, with strong marginal beading. Eyes small, interocular space about 7x as wide as one eye in dorsal view. Labrum exposed, anterior margin sinuate.

Pronotum ca. 2x as wide as long; pronotal puncation as on frons, surface shining. Lateral margin almost straight, weakly curved, with strong narrow beading which continues around anterior and posterior angles, posterior margin medially without beading or a transverse series of coarser punctures. Elytra shining, completely lacking elytral suture; 10 striae composed of larger punctures which are not coarser posteriorly, 1 and 8 very short and only discernible apically, 9 and 10 obsolete; intervals flat throughout; with smaller, fine punctures and very short pubesence on apical 1/5 (Fig. 116B).

Mentum as in Fig. 116C, covered in long golden pubesence, anterior margin strongly emarginate. Maxillary palpomere 2 not swollen apically.

Raised median area of proventrite as in Fig. 116D, triangular, separated from lateral areas by coxal cavities, convex, very weakly carinate medially, lateral areas with antennal grooves almost reaching lateral margins. Mesoventral process as in Fig. 116E, pentagonal, transverse, convex posteromedially, anterior margin strongly marginate, without apical process, posterior margin weakly curved, closely attaining anterior margin of metaventrite. Lateral areas of metaventrite with deep coarse punctures; raised central area about 1.5x longer than wide, with a median groove on posterior 1/5, surface with much denser, finer setous punctation and indistinct microrugae. Abdomen with 5 segments, first segment carinate medially, segments 1–3 with coarse punctures laterally, segments 4–5 with only fine, indistinct punctation (Fig. 116F).

Anterior surface of procoxae with fine granulate microsculpture. Femora triangular, shining, posteromedial angle of mesofemora distinctly extending posterior to trochanters. Outer margin of tibiae with a row of small indistinct spines and meso- and metatibiae with small apical spines. Tarsi ventrally with dense pubesence.

No male specimen available for genitalia dissection.

Distribution. **Oriental:** Indonesia (**Java [new record]**, Sumatra); **Afrotropical:** Madagascar, Mauritius (Mascarene Is.).

Ecology. The type specimen described in Orchymont (1932), was collected from "Waterfall Kapala Tjurup by Tjurup on wild banana". It is likely also a generalist on decaying organic matter.

Paroosternum saundersi Orchymont, 1925
(Fig. 109G–H, 117)

Oosternum Saundersi Orchymont, 1925: 289. – Singapore.
Paroosternum saundersi: Hansen, 1991: 261.
Anchorosternum sinsensis Jia, Wu and Pu, 2001: 177. Syn.: Fikáček and Jia 2011.

Detailed redescription in Hebauer (2006). Genitalia illustrated in Fikáček and Jia (2011).

Distribution. Singapore, Myanmar, Vietnam, Thailand, Nepal, Indonesia (Java, Sumatra).

Ecology. This relatively common species is widely distributed throughout Southeast Asia and is commonly collected from mammal dung, particularly that of cattle.

Cercyon (*Clinocercyon*) sp. 1
(Figs. 108A–B, 118–119)

Description. Body size small, length 1.9–3.0 mm long, width 1.3–1.6 mm; very convex, slightly compressed dorsoventrally in some specimens (Fig. 118A). Body and legs testaceous, only anterior portion of head sometimes lightened; maxillary palpi and antennal segments dark fulvous, antennal club yellow-brown (Fig. 108A–B).

Head convex, clypeus deflexed anterior to eyes; shining, with coarse, finely setous punctures separated by about 1–2x their diameter, becoming finer anteriorly and laterally, without apparent microsculpture; anterior margin of clypeus very weakly sinuate, rounded laterally, with distinct beading. Eyes large, interocular space about 6.3x as wide as one eye in dorsal view, very weakly emarginate anteriorly.

Pronotum ca. 2.5x as wide as long; pronotal puncation similar to frons but slightly finer, shining. Lateral margin weakly curved, with strong coarse beading which continues a short distance around anterior and posterior margins. Scutellum triangular, slightly longer than wide. Elytra widest at base; lateral margins with deep fine beading; surface shining; 10 deep striae composed of larger punctures connected by deep grooves; intervals flat, becoming convex posteriorly, with sparse, very fine, setous punctures; interspaces without discernable microsculpture (Fig. 118B).

Mentum as in Fig. 118C, glabrous, with a few sparse, fine punctures around lateral and posterior margins, anterior margin sinuate, weakly emarginate only at center, weakly depressed behind. Maxillary palpomere 2 slightly swollen apically; palpomere 4 fusiform, apex with a fine hair emerging from a deep pore; segment 3 subequal in length to segment 4, slightly widened apically.

Proventrite as in Fig. 118D, tectiform, strongly carinate medially, anterior margin also carinate, confluent with median carina; lateral areas with shallow antennal grooves. Mesoventral process raised medially, forming a fusiform tablet as in Fig. 118E, widest just behind about half length, anteriorly sloping towards body, posterior apex rounded, not contacting mesoventral disc, surface with indistinct fine setous punctation, punctures separated by about 3x their diameter. Lateral areas of metaventrite densely pubescent, lacking femoral lines; central disc about as long as wide, median anterior apex produced weakly angled, surface glabrous, with fine sparse punctures irregularly arranged and separated by 4–6x their diameter, posterior margin rounded, with row of pubesence (Fig. 118F).

Abdomen with 5 segments, first segment strongly and finely carinate medially, surface densely pubescent; apex of segment 5 pointed.

Ventral surface of femorae glabrous with fine setous punctation, without discernable microsculpture, setae on mesofemorae stouter than on metafemorae. Ventral surface of tarsi with dense yellow pubesence; metatarsi with segment 1 about as long as segements 2 and 3 combined.

Male genitalia as in Fig. 119, ratio of median lobe:tegmen = 1.14. Median lobe with sides weakly curved to straight from base to apical 1/7 which is curved to apex, corona located just behind tip. Paramera, wide until near tip at which the inner margin curves outward to form points apically, inner margins near apices very thin, almost membranous. Accessory sclerite (9th ventrite) long, about 1/2 length of aedeagus, strongly pointed apically and curved to one side, with distinct median ventral ridge; lateral arms longer than paramera, apices pointed.

Cercyon sp. 2

(Figs. 108C–D, 120)

Description. Body size small, length 2.7 mm long, width 1.5 mm; compressed dorsoventrally (Fig. 120A). Head testaceous, pronotum fulvous but somewhat darkened centrally, elytra fulvous, with somewhat darkened area reaching from near humeral angles to about 1/2 length, scutellum dark; ventral base coloration brown, lightened on lateral areas of pronotum, epipleura, and proventral process; legs fulvous with testaceous spines on tibiae; maxillary palpi and antennal segments fulvous, antennal club yellow brown (Fig. 108C–D).

Head weakly convex, clypeus not deflexed anterior to eyes; shining, with irregularly shaped punctures separated by about 1/2–1x their diameter, becoming finer anteriorly and centrally, interspaces without apparent microsculpture; anterior margin of clypeus very weakly sinuate, rounded laterally, with distinct beading. Eyes large, interocular space about 5x as wide as one eye in dorsal view, weakly emarginate anteriorly.

Pronotum ca. 2x as wide as long; pronotal puncation coarser than on frons, interspaces shining. Lateral margin weakly curved, with strong beading which continues around anterior margin and ends some distance beyond posterior margins and with indistinct row of minute spines. Scutellum triangular, longer than wide, surface with a few coarse punctures. Elytra widest at about half length; lateral margins with deep fine beading and a uniform row of minute spines; surface shining; with 10 striae composed of larger punctures connected by deep grooves; intervals flat, except for near apex, with fine dense punctures separated by 1–2x their own diameter; interspaces without discernable microsculpture (Fig. 120B).

Mentum as in Fig. 120C, glabrous, with a few sparse, fine punctures around lateral and posterior margins, interpaces with dense fine microrugae, anterior margin weakly sinuate, weakly emarginate only at center, weakly carinate and depressed behind. Maxillary palpomere 2 swollen apically; palpomere 4 fusiform, apex with a fine short hair emerging from a pore; segment 3 distinctly shorter than segment 4, widened apically.

Proventrite as in Fig. 120D, tectiform, strongly carinate medially, anterior half of carina robust, abruptly becoming finer and less protruding at about half length posteriorly; anterior margin also carinate, confluent with median carina; lateral areas with shallow antennal grooves. Mesoventral process raised medially, forming a narrow fusiform tablet as in Fig. 120E, widest just behind about half length, anteriorly sloping towards body, posterior apex very sharply pointed, not contacting mesoventral disc but protruding ventral to it; surface with about 10–12 punctures separated which are by about 1x their diameter. Lateral areas of metaventrite densely pubescent, lacking femoral lines; central disc about as long as wide, surface glabrous, uniformly covered in coarse punctures separated by 1–2x their diameter, posterior margin weakly angled, without row of pubesence (Fig. 120F).

Abdomen with 5 segments, first segment strongly and finely carinate medially, carina not reaching anterior margin, surface densely pubescent; apex of segment 5 rounded.

Ventral surface of femorae glabrous with fine setous punctation, with sparse shallow microrugae irregularly covering surface, setae on mesofemorae stouter than on metafemorae. Ventral surface of tarsi with yellow pubesence; metatarsi with segment 1 longer than segments 2 and 3 combined.

No male specimen available for genitalia dissection.

Cercyon sp. 3
(Figs. 108B–C, 121–122)

Description. Body size very small, length 1.6 mm long, width 1.0 mm; convex but dorsoventrally compressed (Fig. 121A). Dorsal coloration light testaceous; head fulvous ventrally, proventrite fulvous except along median carina and anterior and posterior margins which are darkened, mesoventrite light testaceous, darkened on median process, other ventrites fulvous to light testaceous; maxillary palpi and antennal segments fulvous, antennal club yellow (Fig. 108E–F).

Head weakly convex, clypeus deflexed anterior to eyes; surface densely covered in irregularly (bowtie) shaped setous punctures which are separated by about 1x their diameter, setae long but fine, interspaces without apparent microsculpture; anterior margin of clypeus weakly curved, rounded laterally, with distinct beading. Eyes moderate, interocular space about 6.25x as wide as one eye in dorsal view, very weakly emarginate anteriorly.

Pronotum ca. 2.4x as wide as long, widest just before base; pronotal setous puncation consistent with that on head. Lateral margin weakly curved, with indistinct fine beading which starts at anterior angles and ends a short distance before posterior angles, inside margin with coarse groove which starts at anterior angle and continues a distance around posterior angle; with small spines along margin. Scutellum triangular, about as long as wide. Elytra widest at about anterior 1/5 length of elytra; lateral margins with coarse beading, with row of regularly spaced spines; 10 striae composed of larger punctures connected by deep grooves; intervals flat, becoming convex posteriorly, densely covered in small, round, setous punctures, setae long and golden; interspaces without discernable microsculpture (Fig. 121B).

Mentum as in Fig. 121C, almost semicircular, roundly narrowed from just before base, anterior margin sinuate, emarginate, weakly carinate, weakly concave behind; surface glabrous, smoothly bumpy, covered in coarse punctures separated by a 2–3x their diameter, interspaces without distinct microsculpture. Maxillary palps with sparse long pubesence; palpomere 2 swollen apically; palpomere 4 about 1/2 length of palpomere 2, fusiform, almost pointed apically, apex with a fine hair emerging from a deep pore; segment 3 subequal in length to segment 4, slightly widened apically.

Proventrite as in Fig. 121D, tectiform, strongly carinate medially, anterior margin also carinate, confluent with median carina; lateral areas with shallow antennal grooves. Mesoventral process raised medially, forming a very narrow almost carinate tablet as in Fig. 121E, widest at about anterior 1/3 length, anteriorly sloping towards body, posterior apex rounded, not extended under but not contacting mesoventral disc, surface with approximately 15 deep setous punctures, punctures dense anteriorly, becoming much less dense posteriorly. Lateral areas of metaventrite densely pubescent, lacking femoral lines; central disc wider than long, median anterior apex with wide margin, produced under center of mesoventrite and mesoventral process (Fig. 121F), surface covered in setae anteriorly and laterally, posteriorly glabrous on center, with coarse dense punctures centrally, punctures separated by 1–2x their diameter, posterior margin rounded with shallow emargination centrally, posterior surface without row of setae.

Abdomen with 5 segments, first segment strongly and finely carinate medially, surface densely pubescent; apex of segment 5 angled.

Ventral surface of femorae glabrous with fine setous punctation, with shallow microrugae, setae on mesofemorae stouter than on metafemorae. Ventral surface of tarsi without dense yellow pubesence; metatarsi with segment 1 about as long as segements 2 and 3 combined.

Male genitalia as in Fig.122, ratio of median lobe:tegmen = 1.18. Median lobe elongate triangular, sides straight, converging to tip, with minute pubesence on apical 1/4, corona located just behind tip. Paramera also narrowed to tip, tips very thin and flexible, tips rounded. Accessory sclerite (9th ventrite) about 6/7ths length of aedeagus, pointed apically and curved to one side, median ventral ridge short, weak; lateral arms subequal to paramera, apices pointed.

Pachysternum apicatum Motschulsky, 1863

(Fig. 109I–J)

Pachysternum apicatum Motschulsky, 1863: 448. – India.

Diagnosis. Detailed description and diagnosis in Fikáček, Jia and Prokin (2012).

Distribution. Widely distributed in southeast Asia. India, Southern China, Thailand, Laos, Vietnam, Malaysia, Indonesia (Sumatra, Java, Bali, Lombok, Sulawesi, Borneo) (Fikáček, Jia and Prokin 2012).

Ecology. This species seems to be a generalist on decaying organic matter including both plant and animal matter but unlike many other Pachysternum, it has not been recorded from fecal material (Fikáček, Jia and Prokin 2012).

Discussion

Due to the lack of knowledge on the fate of fallen nests of *Apis dorsata dorsata*, we cannot be sure of how common this resource really is in the wild, but because fallen honeycomb is such a valuable nutritional resource, it is likely that in the wild, such material is very quickly consumed by larger animals such as mammals and birds. Additionally, Kahono *et al.* (1999) indicate that the event of one of these nests falling is a rather rare occurance. Therefore, fallen nests of A. *dorsata dorsata* are likely not a common enough habitat for such scavenger insects to specialize on it, though given the opportunity, it seems that they are still quite attractive to saprotrophic beetles.

Terrestrial hydrophilids are commonly found in and on various types of decaying organic material including plant matter, carrion, mammal dung, and seaweed wrack (Short and Fikáček 2011, Bloom *et al.* 2014, Arriaga-Varela *et al.* 2021). The larvae are generally carnivorous, feeding on the larvae of flies and other insects while the adults are thought to feed on biofilms, dung, and other decaying material (Kobayashi 2009, Archangelsky *et al.* 2016, Kobayashi and Ôhara 2017, Fikáček *et al.* 2018). With the exception of a few groups including the beach-dwelling members of the genera *Cercyon* and *Cercyodes* which are almost exclusively found in decaying seaweed (Smetana 1978, Ôhara 2008; Inari *et al*. 2018, Suzumura *et al.* 2019), most species of terrestrial hydrophilids are somewhat flexible in the types of habitats where they can occur. Members of the genus *Sphaeridium* are most commonly found in dung but have also been reported from carrion (Heo 2011), indicating that while there is a strong preference for dung, they can also reside in other somewhat similar microhabitats if necessary.

Of the beetles collected from the nest, a large majority of them were from the family Hydrophilidae, with only a few representatives from a few other families. Most have previously been known mainly from decaying plant material or less commonly, from dung. With the possible exception of the three species of *Cercyon* which I was unable to identify to species level, none of the species collected are known to colonize carrion. While most species collected seem to be relatively generalist in habitat, the only species that is known to have a very specific habitat was the single specimen from the genus *Protosternum* which are thought to have an obligate relationship with banana trees (Fikáček *et al.* 2018). A few specimens of three species of *Dactylosternum* which are not exclusive to but very commonly collected from banana trees as well as several specimens of two species of *Noteropagus*, the ecology of which is not well known but has also previously been collected from banana trees (Orchymont 1925, Orchymont 1932), were also present.

We might predict that the organic material present in a decaying bee nest is most likely dead bee brood, pollen, and honey, with fungus, bacteria, and other arthropods so, like other temporally limited saprotrophic microhabitats, there are many fast-moving factors at play. The large number of species which seem to be plant associated indicates that this habitat may have some similarities to the microecosystems of decaying plant materials but without more information on other factors such as biodiversity of other organisms present (fungi, diptera, etc.) and nutritional resources available, it is impossible to know whether there is a specific relationship.

Chapter V:

Miscellaneous studies on other beetles living in decaying material on beaches (Coleoptera: Byrrhidae, Tenebrionidae)

Part 1. Records of the introduced Australian genus *Microchaetes* (Hope, 1834) (Coleoptera: Byrrhidae) in Japan with a new prefectural record from Miyazaki

Microchaetes Hope, 1834 is a genus of Byrrhidae comprised of 12 valid species with nine species recorded from Australia (including Tasmania) (Lawrence *et al*. 2013) and with three species recently described from Chile by Solervicens (2016) and Solervicens and Elgueta (2019). An undetermined introduced species thought to be endemic to Tasmania is also known from an urban park in Aukland, New Zealand where it may have been introduced via root clusters of imported city trees (Pütz 2004). Unexpectedly, it was also recorded from Japan by Pütz (2004) from specimens collected from Chiba and Tokyo prefectures during 1996 and Ibaraki prefecture during 1999 and appeared to be the same as the specimens collected from

Aukland (Pütz 2004). In Japan, they have been collected from both coastal and inland regions and seem to inhabit a variety of habitats including, but not limited to, beaches, riverbeds, on mosses, and in urban parks (Tsuji 2017). Reliable species level identification of the Japanese specimens is however not currently possible pending significant revision of the Australian members of the genus (Pütz 2004, A. Slipinski personal communication November 24, 2021) and as such, neither the number of species in Japan nor any habitat specificity at the species-level can be determined at present. Genus-level identification can however be easily performed even from photographs as this group is quite distinct among the Japanese fauna.

Entomology is a popular hobby in Japan and species distributions are documented not only by researchers but also by amateurs who record their collected specimens in detail in small local journals and online blogs. Because of this, the distributions of Japanese insects are quite well known among Japanese insect collectors and researchers but often not known outside this community. Publications produced by "konchudokokai" or "mushi-no-kai", local entomology societies (or "insect lovers' clubs") mainly publish regional data from local collectors and researchers. The journal, Gekkan-Mushi ("Insects Monthly") is published by a private company specializing in selling field guides and insect breeding and collecting equipment and contains collecting records of collectors and amateur researchers nationwide. Some publications are available through the online book dealer Roppon-Ashi Entomological Books, but many journals and newsletters put out by smaller local groups remain difficult to obtain outside of Japan.

Records of the undetermined *Microchaetes* species in Japan were previously summarized in Japanese in Tsuji (2017) who included records from Ibaraki prefecture to as far south as Hiroshima and Kagawa prefectures but several more records have since come to light. We have translated and updated this list of records compiled from both professional academic publications and environmental assessment reports as well as from amateur sources such as local publications and newsletters published by local entomology societies to better show the distribution of the genus in Japan. As a result, there were reports from 19 publications, 12 of which were produced by local entomological societies (Table 2) and the beetle has been found in 15 prefectures including Aichi, Chiba, Gifu, Hiroshima, Hyogo, Ibaraki, Kagawa, Kanagawa, Kyoto, Miyazaki, Oita, Okayama, Osaka, Tokyo, and Yamaguchi, with Ibaraki being the northernmost and Miyazaki the most southern (Fig. 125) indicating that this species is rather widely distributed across central to southern Japan, particularly in coastal regions of the Pacific Ocean and Seto Inland Sea.

Following the initial report of *Microchaetes* in Japan by Pütz (2004), a specimen of the distinctive beetle collected by Dr. Kurosa in August 1999 from Kanagawa prefecture was found and reported in Takizawa (2005) along with another specimen collected during June 2005. The beetle next appeared in Hyogo prefecture where it was collected first during 2001 and later during 2007 and reported by Yoshida (2008) which was followed by reports of specimens collected in Okayama (Suenaga and Takizawa 2004) and Kyoto (Mizuno and Arata 2005) as early as 2002. The first report from the southern island of Kyushu was made in Okamoto and Miyake (2006) in which they were collected during light trap surveys in the northern part of Oita prefecture during 2005. This was followed by the first record for Shikoku Island from Kagawa prefecture during 2006 (Satô 2007) and a specimen collected during 2008 in Osaka City represented the next new prefectural record for Osaka prefecture (Shiyake *et al.* 2020) followed by a 2012 specimen from Aichi prefecture (Nisshin History Compilation Committee 2015). The second author collected one specimen during 2015 from Iwakuni, Yamaguchi prefecture and reported it during 2017 along with other previously existing reports of the genus in Japan and the same year, three specimens of *Microchaetes* were also collected in nearby Hiroshima prefecture and reported in Kosaka and Yano (2017) and during 2020 one specimen was collected in Gifu prefecture (Nakano 2020).

Most recently, one specimen (Figs. 123 and 124) was collected in April of 2021 by the first author by shaking seaweed wrack through a metal sifter over a white pan and collecting beetles as they fell through. Locality data for those specimens are: Japan, Miyazaki prefecture, Aoshima, Aoshima beach, 31.803031N, 131.470418E, 8 April 2021, seaweed wrack on sand beach. This represents a new prefectural record from Miyazaki. The genus was confirmed using the key and illustrations provided in Lawrence *et al.* (2013). Its habitus was photographed using a Nikon Digital Sight DS-Fil on a Nikon SMZ74T steromicroscope and terminalia illustrations were created by tracing photos on an iPad Air 3 using Procreate software and edited in Adobe Illustrator. Terminology for terminalia follows Solervicens and Elgueta (2019) and Tshernyshev and Sergeev (2020). The specimen is deposited in the Hokkaido University systematic entomology collection.

Part 2. Review of the northern Pacific genus, *Phaleromela* Reitter, 1916 (Coleoptera: Tenebrionidae)

Introduction

The genus *Phaleromela* Reitter represents a rather small genus of five described species of which four, *P. humeralis* Laporte, *P. prohumeralis* Triplehorn, *P. picta* Mannerheim and *P. variegata* Triplehorn are recorded from the western United States and one, *P. subhumeralis* Reitter, occurs in coastal regions throughout the Far east from eastern Russia and northeast China throughout Japan and South Korea (Kawauchiya and Ôhara 2015). Many of these species with the exception of *P. subhumeralis* which has been treated by South Korean and Japanese researchers (Jung et al. 2009, Kawauchiya and Ôhara 2015) however lack comprehensive redescriptions lacking photos, illustrations, and detailed descriptions of genitalia.

In particular, the taxonomic status of the two species *P. humeralis* and *P. prohumeralis* from California remain unknown. In his 1961 catalog of the genus, Triplehorn discussed these species and stated that it is likely that they are synonymous with each other but was not able to resolve the issue at the time. With the type specimens of both species unknown and having only limited descriptions which detail little more than coloration, it may not be possible to determine the exact species that either or both Laporte (1840) and Horn (1874) were referring to at this time. As such, redescriptions of these two species are not included and their names are listed as “incertae sedis”.

The remaining three species however represent a rather interesting complex in their morphological range from fully winged to apterous and differences and in their preferences of habitat between backshores of sandy beaches to riverbeds. Additionally, the geographical divide between the far eastern *P. subhumeralis* and western North American *P. picta* and *P. variegata* presents many interesting questions as to the origin and evolutionary history of these three species. As such, we herein redescribe these three species based on collected specimens of *P. picta*, and *P. subhumeralis* as well as museum specimens of *P. variegata* with hope that this revision may aid in future studies on the biogeographic history of this genus as well as of coastal insects in the northern Pacific in general.

Materials and Methods

Specimens of *P. picta* and *P. subhumeralis* were collected from the backshores of sandy beaches by digging near vegetation and sifting sand through a metal mesh colander or flour sifter with a mesh size of a couple millimeters (Fig. 127B, D, E) or by collecting beetles directly from the surface of the sand, often under driftwood and other dried plant material (Fig. 127C).

Dissections were performed by relaxing specimens in boiled water for about 15 minutes before removing genitalia from the body by either removing the whole abdomen or through a slit made along the lateral margin of the abdomen. Genitalia were then placed in 10% KOH solution for 20-30 minutes at 60°C before removing muscle in 70% ethanol solution. They were then dyed in lactic acid with 1–2 drops of acid fuchsine for about 3 hours at 60°C. They were then dehydrated in acetic salicylate (methyl salicylate 1: acetic acid 1) for 15 minutes at 60°C and then immersed in xylene for about two minutes at room temperature before examination in α-terpinol under a dissecting microscope (Nikon SMZ800). α-terpinol was chosen due to its relatively low refractive index and material can be preserved in it for an extended amount of time. Genitalia were finally preserved in Canada balsam resin on a small circle of glass glued to cardstock and attached to the specimen.

Habitus photographs were taken on a Nikon Digital Sight DS-Fil on a Nikon SMZ745T stereomicroscope and SEM images were taken with a JSM-6510 scanning electron microscope. Illustrations were created in Procreate on an iPad Air 3.

Specimens of *P. variegata* were borrowed from the Oregon State Arthropod Collection (OSAC), Oregon State University, Corvallis, Oregon, USA (collection manager: Christopher Marshall).

Systematics

Phaleromela Reitter, 1916

Phaleromela Reitter, 1916: 4. Type species: *Phaleria subhumeralis* Marseul, 1876, monotypy.

Diagnosis. Body size small, length 2.5–5.0 mm; shape oblong to almost circular, dorsoventrally convex. Anterior margin of head evenly arcuate between eyes, clypeus not strongly defined from frons; eyes small, widely separated both dorsally and ventrally, anterior margin not emarginate; antennae extending beyond base of pronotum and gradually broadened apically.

Pronotum narrower than elytra at base, densely punctate, with distinct to indistinct microsculpture at least near posterior corners; proventrite, extending posterior to procoxae, deflexed apically, with long hairs at center, lateral areas rugous. Elytra with eight distinct punctate striae, lacking short striae paralleling margins of scutellum. Mesoventrite deeply recessed between pro- and mesocoxae. Anterior tibiae conspicuously flattened and slightly to strongly expanded apically, margined with stout spines, all tibiae with conspicuous apical spurs. Tarsi 5-5-4, claws simple.

Key to species:

1. Fully winged, body elongate, coloration as in Fig. 126C, apical margin of protibiae straight, outer angle not forming a distinct lobe (Fig. 130C); western North America.
   Phaleromela variegata Triplehorn

- Apterous, body rounded, coloration not as in Fig. 126C, apical margin of protibiae convex, outer angle forming a distinct lobe (Figs 130A, B).
  …2

2. Light colored with or without dark markings on elytra (Fig. 126A), elytra fused, male genitalia short and stout, penis rods much shorter than aedeagus (Fig. 130A); western North America.
   Phaleromela picta Mannerheim

- Black and shagreened, with orange humeral spots on elytra (Fig. 126B), elytra not fused, male genitalia longer, penis rods not shorter than aedeagus (Fig. 130B); Palearctic, coastal regions of the Far East

Phaleromela subhumeralis Reitter

*does not include *P. humeralis* and *P. prohumeralis*.

Phaleromela picta Mannerheim, 1843

(Figs. 126A, 127E, 128A-B, 129A, 130A, 131)

Phaleria picta Mannerheim, 1843: 277.

Phaleromela globosa LeConte, 1857: 51. Syn: Bousquet *et al*., 2018.

Description. Size small, length 2.5–4.5 mm, width 1.5–2.7 mm. Habitus globular, round, dorsoventrally strongly convex. Light colored, head testaceous, pronotum testaceous to fulvous, elytra base color fulvous with or without variable dark brown markings as in Fig. 126A; ventrum, legs, antennae, and mouthparts pale, fulvous to light testaceous.

Head very densely and coarsely punctured on frons, punctures separated by less than their own diameter, often confluent, interspaces without discernable microsculpture; labrum wide, anterior margin rounded, surface and margin with sparse but strong and erect golden setae and superficial microsculpture; eyes of moderate size, visible ventrally but widely separated. Antennae reaching just beyond posterior angles of pronotum, with antennomeres of increasing width, without distinctive club, arranged as follows: scape rounded, only slightly longer than wide, pedicel about as long as wide, narrower than other segments, 1 and 2 longer than wide, 3 about as long as wide, 4–8 wider than long, 9 (terminal) round, a little wider than long, as wide as segment 8. Terminal segment of maxillary palpi elongate, fuciform, more than twice as long as wide, tip tapered, covered in sparse pubesence.

Pronotum (Fig. 128A) transverse, about twice as wide as long, maximum width at about ½ length, lateral margins rounded, with or without superficial laterobasal depressions, without marginal bead; surface matte, with distinct granulate microsculpture throughout though superficial at center, stronger laterally and posteriorly, with coarse punctation which is less dense than on head, punctures separated by about 1–2x their diameter; hypomeron strongly microrugous throughout, without punctures; prosternum (Fig. 128B) beaded along anterior margin, surface anterior to coxae covered in very sparse setous punctures, the setae of which are very long, interspaces with microsculpture, punctation continuing onto area of prosternal process between procoxae, prosternal process only slightly widened posterior to coxae, sides almost parallel apex rounded.

Elytra not elongate, pointed at apex, fused, with distinct uniform grooved punctate striae, lateral margins not explanate, with marginal bead from anterior angle to just before posterior tip, surface weakly shining, elytral intervals with fine uniform punctures separated by about 1–2x their diameter and sparse microreticulation. Epipleura shining with fine, indistinct punctures, punctures setous along lateral margin, with stout golden setae which are visible along lateral margins of elytra when viewed dorsally. Scutellum very narrow transverse triangle, more than twice as wide as long, may be covered by posterior margin of pronotum, margins straight, with a few coarse punctures anteriorly and dense, fine granulate microsculpture. Apterous.

Mesoventrite (Fig. 128B) wider, middle portion strongly recessed, forming a strongly concave wide groove which is separated from the prosternal process, with setous punctures on recessed portion. Metaventrite (Fig. 128B) narrow, glabrous, covered in sparse setous punctation, without microsculpture with distinct median longitudinal groove on posterior 3/4ths, and anterior marginal bead, anterior margin between mesocoxae convex, posterior coxae also margined with strong marginal beads.

Legs covered in long golden pubesence and short spines; protibiae apically dilated, apical margin concave, outer angle forming a distinct lobe (Fig. 129A), meso- and metatibiae narrower than protibiae.

Abdominal segments glabrous with setous punctures which are moderately dense throughtout and indistinct granulate microsculpture on segments 3–5. Male genitalia as in Fig. 130A, genital ratio (basal piece:paramera) = 0.52, aedeagus short and stout, penis rods much shorter than tegmen, apex of penis pointed; gastral spicula about 4/5 length of aedeagus.

Sexual dimorphism. Segments 2–3 of male protarsi distinctly expanded, wider than long and wider than segment 4 while segments 1–4 in female each not wider than long, subequal in length.

Distribution. Western coastal North America, Alaska through California, Idaho (Bousquet *et al.* 2018, Grant et al. 2020, Santa Barbara Museum of Natural History 2020, Sikes 2020, Ueda 2021). Map: Fig. 131.

Ecology. These beetles are numerous in many backshore sand and dunes throughout California and as far north as Alaska. Compared *P. subhumeralis*, they are more commonly found buried in the sand but remain rather close to the surface and can be easily collected by sifting them out of the sand with a metal kitchen colander (Fig. 127B, D, E). While they are mainly found in coastal habitats, Papp and Pierce (1960) recorded finding them feeding directly on stored grain products in the Mojave Desert and there are also several specimens recorded from northern Idaho in the Field Museum Collection (Grant *et al.* 2020).

Examined material. **California:** San Francisco, Nr. Ocean Beach Fire pit, 37.743442°N, 122.508267°W, 25.VIII.2019, sand beach/dune, [CA19MO103] M. Ôhara (30 exs.), A. Suzumura (4 exs.) and H. Nose (2 exs.) leg.; McKinleyville, Clam Beach County Park, 40.994444°N, 124.117500°W, 30.VIII.2019; sand beach, [CA19MO124] M. Ôhara (8 exs.) and H. Nose (2 exs.) leg.; Trinidad, Trinidad State Beach, 41.057500°N, 124.149722°W, 30.VIII.2019; sand dune, [CA19MO125] M. Ôhara leg. (6 exs.). **Oregon:** Port Orford, Battle Rock Wayside Park, 42.742001°N, 124.491623°W, 31.VIII.2019; sand beach/dunes, [OR19AS128] A. Suzumura leg. (2 exs.); Nr. Glasgow, Horsfall Beach, 43.453917°N, 124.277343°W, 31.VIII.2019; sand beach, [OR19AS131] A. Suzumura (31 exs.) and H Nose (1 ex) leg.; Dune City, Stilcoos Beach, 43.882644°N, 124.153432°W, 31.VIII.2019; sand beach/dunes, [OR19AS131] M. Ôhara (17 exs.) and A. Suzumura leg. (26 exs.). **Washington:** Seattle, Golden Gardens, 48.692593°N, 122.404922°W, 11.IX.2019; sand beach, [WA19AS133] A. Suzumura leg. (2 exs.); Same location but 2018.VIII.14 (28 exs). **British Columbia:** Vancouver, Sunset Park Beach, 49.279741°N, 123.139735°W, 2018.III.17, sifting sand [BC18AS004] A. Suzumura leg. (16 exs.)

Phaleromela subhumeralis Marseul, 1876
(Figs. 126B, 127C, 128C-D, 129B, 130B, 131)

Phaleria subhumeralis Marseul, 1876: 102.

Phaleromela subhumeralis: Gebien, 1939: 743 (502); Kim and Kim, 2002: 243; Jung *et al.*, 2009: 147.

Redescription. Size small, length 2.7–5.0 mm, width 1.8–2.5 mm. Habitus oval though not elongate, dorsoventrally convex. Dark-colored, head piceous, pronotum and elytra base color piceous to dark testaceous, elytra with two bright yellow to orange humeral spots which extend from the humeral angles diagonally towards center of elytra as in Fig. 126B; ventrum piceous to dark testaceous, sometimes lightened to a brown at center of pro-, meso-, and metaventrites; legs and antennae piceous to dark testaceous, maxillary and labial palps dark, white at tips.

Head densely and coarsely punctured on frons, punctures separated by less than their own diameter, interspaces without discernable microsculpture; labrum wide, anterior margin rounded, surface and margin with sparse but strong and erect golden setae; eyes small, barely visible ventrally, widely separated. Antennae reaching just beyond posterior angles of pronotum, with antennomeres of increasing width, without distinctive club, arranged as follows: scape rounded, only slightly longer than wide, pedicel about as long as wide, narrower than other segments, 1 and 2 longer than wide, 3–5 about as long as wide, 6–8 wider than long, 9 (terminal) round, about as long as wide, as wide as segment 8. Terminal segment of maxillary palpi stout, less than twice as long as wide, apex obliquely truncate, the margin of which is excavated and filled with dense short felt-like pubesence, outer surface with a few sparse hairs.

Pronotum (Fig. 128C) transverse, about 1.7 times as wide as long, maximum width from anterior about 1/3 throughout base, lateral margins subparallel on posterior 2/3s, with deep laterobasal depressions, with marginal bead from around anterior angles throughout lateral and basal margins; surface glabrous, with distinct granulate microsculpture throughout though superficial at center, stronger laterally and posteriorly, with coarse punctation which is less dense than on head, punctures separated by about 1–2x their diameter; hypomeron strongly rugous at center, lateral margins with strong granulate microsculpture; prosternum (Fig. 128D) beaded along anterior margin, surface anterior to coxae covered in coarse setous punctures which are sparser at center and dense laterally and the setae of which are very long near center and much shorter laterally, interspaces with microsculpture, punctation continuing onto prosternal process which is only slightly widened posterior to coxae, apex rounded.

Elytra only slightly elongate, not fused, apex rounded, with distinct uniform grooved punctate striae, lateral margins very narrowly explanate on about 1/2 width of anterior portion of lateral-most strial interval, with marginal bead from anterior angle to posterior tip, surface strongly shining, almost metallic with sparse superficial microreticulation, interspaces with fine uniform punctures separated by about 1–2x their diameter. Epipleura shining with fine, indistinct punctures, lacking pubesence. Scutellum broadly trianglular, margins weakly rounded, with no to very few punctures (2 or 3) and dense, fine granulate microsculpture. Apterous.

Mesoventrite (Fig. 128D) short, middle portion strongly recessed, forming a strongly concave wide groove which is separated from the prosternal process, with sparse setous punctures on recessed portion. Metaventrite (Fig. 128D) glabrous, covered in sparse setous punctation and very superficial granulate microsculpture which is more distinct laterally, with indistinct median longitudinal groove on posterior half and anterior marginal bead, anterior margin between mesocoxae convex, posterior coxae also margined with strong marginal beads.

Legs covered in pubesence and short spines; protibiae apically dilated, apical margin concave, outer angle forming a distinct lobe (Fig. 129B), meso- and metatibiae narrower than protibiae.

Abdominal segments glabrous with fine setous punctures which are moderately dense throughtout and increasingly distinct granulate microsculpture on segments 3–5. Male genitalia as in Fig. 130B, genital ratio (basal piece:paramera) = 0.53, aedeagus long and narrow, penis rods slightly longer than tegmen, apex of penis narrowly truncate, apical margin not convex, often slightly concave; gastral spicula about 3/4 length of aedeagus.

Sexual dimorphism. Segments 1–3 of male protarsi distinctly expanded, much wider than segment 4 while segments 1–4 in female of about the same width.

Distribution. Russia (Khabarovsk, **Primorsky [new record]**, Sakhalin, Kamchatka, Kuril Archipelago: Shumshu, Paramushir, Onekotan, Matua, Ushishir-Yankicha, Simushir, Chirpoi, Urup, Iturup, Kunashir, Shikotan), northeast China, Korea, Japan (Hokkaido, northern Honshu) (Jung et al. 2009, Kawauchiya and Ôhara 2015). Map: Fig. 131.

Ecology. Very common on sandy beaches throughout the Pacific Far East. They can easily be found walking on the surface of or buried in sand near vegetation and under dried plant material on upper shores of sandy beaches from Spring through Fall.

Examined material. **Japan, Honshu:** Yamagata-ken, Tsuruoka-shi: Yunohama, 8.VIII.1954/H.Hasegawa leg.//0000060574, Sys.Ent, Hokkaido Univ., Japan [SEHU]//NAKANE Coll. SEHU Japan 1999 (1 ex..); Aomori-ken, Kitatsugaru-gun: Nakadomari-machi: Kodomari, 1.VIII.1960/A.Abe leg.// 0000072649, Sys.Ent, Hokkaido Univ., Japan [SEHU]//NAKANE Coll. SEHU Japan 1999 (1 ex.). **Hokkaido:** Hyakkuninhama, 41.990285°N, 143.252244°E, 17.IV.2018, sifting sand, [HK18AS007] A.Suzumura leg. (3 exs.); Sakakimachi, Hamanaka, 43.132739°N, 145.122644°E, 18.VI.2018, under wrack, [HK18AS021] A.Suzumura leg. (3 ex.); Zenibako, Sunset Beach, 43.149954°N, 141.184106°E, 5.VI.2018, sargassum wrack, [HK18AS015] A.Suzumura leg. (1 ex.); Niikappu, 46.361932°N, 142.304293°E, 16.IV.2018, backshore on sand, [HK18AS002] A.Suzumura leg. (3 exs.); near Apoi, 42.081905°N, 143.009635°E, 18.IV.2018, dry wrack, [HK18AS010] A.Suzumura leg. (3 exs.); Rebun Is., Funadomari town, 45.438572, 141.033611, 28.VIII.2020, sand beach, A.Suzumura leg. (1 ex.). **Korea:** [KR-16-MO-056] Gangwon Prov., Goseong-gun, Hyeonnae-myeon, Chodo-ri, Hwajinpo Beach, 38˚28'56.10"N 128˚26'17.25"E (38.48160N, 128.43738E), 16m, 3.X.2016, M. Ôhara (1 ex.); [KR-16-MO-051] Gyeongbuk Prov., Yeongdeok-gun, Namjeong-myeon, Jangsa-ri, Jangsa Beach, 36˚16'58.53"N, 129˚22'31.15"E (36.28291N 129.37533E), -4m, 2.X.2016, M. Ôhara (1 ex.). **Russia, Kuril Archipelago:** Paramushir, Kuril Arch., Russia, [IKIP-PA-96-MO-001A] 1-Aug-96, 50°37.73N, 156°08.21E, Utesnyy riv., near mouth of river, under pebbles and logs on sandy beach, M. Ôhara; Urup, 45-56.60'N:150-10.44'E. 29.VIII.1995, Inland coastal margin of Negodnaya bay: environs of Vstrechnyi river. [V.Roth]. By hand and forceps. UR-95-VR-035A (1 ex.); Urup, Kuril Arch., Russia, [IKIP-UR-96-MO-048B], 20-Aug-1996, 45°35.20'N, 149°32.30'E, Ukromnaya bay, under stone or wood piece on seashore, hand picking, forceps, M. Ôhara (1 ex.). **Sakhalin:** H.Kôno, Haga, Shimizu//0000060014, Sys.Ent, Hokkaido Univ., Japan [SEHU] (1 ex.).

Phaleromela variegata Triplehorn, 1961
(Figs. 126C, 128E-F, 129C-D, 130C, 131)

Scaphidema pictum Horn, 1874: 36 [junior primary homonym of *Phaleromela picta* Laporte, 1840].

Phaleromela variegata Triplehorn, 1961: 126. Replacement name for *Phaleromela picta* (Horn 1874).

Redescription. Size small, length 2.8–3.8 mm, width 1.3–2.0 mm. Habitus elongate oval, moderately flattened dorsoventrally. Head black to dark testaceous, pronotum and scutellum testaceous, elytra base color fulvous with variable testaceous to dark brown markings as in Figs. 126C; ventrum testaceous, antennae and mouthparts often lightened.

Head densely and coarsely punctured on frons, punctures separated by less than their own diameter, interspaces without discernable microsculpture; labrum wide, anterior margin rounded, surface and margin with sparse but strong and erect golden setae; eyes of normal size, visible ventrally but widely separated; antennae reaching just past posterior angles of pronotum, with antennomeres of increasing width, without distinctive club, arranged as follows: scape rounded, only slightly longer than wide, pedicel about as long as wide, narrower than other segments, 1–3 longer than wide, 4 and 5 about as long as wide, 6–8 wider than long, 9 (terminal) oval, slightly narrower than segment 8. Terminal segment of maxillary palpi elongate, fuciform, more than twice as long as wide, tip rounded, covered in short pubesence and sparse longer golden hairs.

Pronotum (Fig. 128E) transverse, about 1.6 times as wide as long, maximum width at base which is only a little wider than at about anterior 1/3, lateral margins sinuate, convex in anterior half, straight to slightly concave in posterior half, with deep laterobasal depressions, entire margin with irregular marginal bead which is widest along posterior margin, very narrow at middle of anterior margin; surface glabrous, with or without distinct granulate microsculpture around posterior angles, with coarse punctation which is less dense than on head, punctures separated by about 1–2x their diameter; hypomeron glabrous, with very sparse, short pubesence centrally and anteriorly; prosternum (Fig. 128F) beaded along anterior margin, surface anterior to coxae sparsely and uniformly covered in very long white erect setae, prosternal process coarsely punctate, long golden setae arising from punctures, widened posterior to coxae, apex rounded.

Elytra elongate, not fused, apex weakly pointed, with distinct uniform grooved punctate striae, lateral margins narrowly explanate, with marginal bead to posterior tip, surface shining, interspaces with fine uniform punctures separated by about 2x their diameter. Epipleura with fine, indistinct punctures, lacking long pubesence. Scutellum broadly trianglular, margins somewhat rounded, with fine dense punctures anteriomedially. Fully winged.

Mesoventrite (Fig. 128D) short, middle portion strongly recessed, forming a strongly concave wide groove for reception of prosternal process, with long pubesence on edges along inner margins of mesocoxae. Metaventrite (Fig. 128D) glabrous, covered in coarse setous punctation, with distinct median longitudinal groove on posterior 2/3 and anterior marginal bead, anterior margin between mesocoxae straight, posterior coxae also margined with strong marginal beads.

Legs covered in long pubesence and short spines; protibiae apically dilated but apical margin straight, outer angle not forming a distinct lobe, meso- and metatibiae only slightly narrower than protibiae.

Abdominal segments glabrous with fine setous punctures which are sparse along middle, increasingly dense laterally. Male genitalia as in Fig. 130C, genital ratio (basal piece:paramera) = 0.62, aedeagus long and narrow, penis rods slightly longer than tegmen, apex of penis slightly explanate, apical margin often convex; gastral spicula about 3/4 length of aedeagus.

Sexual dimorphism. The sexes of this species are not easily distinguishable from each other. The protarsi of both male and female specimens are moderately expanded and not distinctly different from each other.

Distribution. Western North America: Canada (Alberta, British Columbia, Northwest Territories, Saskatchewan, Yukon) and United States (California, Idaho, Oregon, Washington, **Montana [new record]**) (Bousquet *et al.* 2018). Map: Fig. 131.

Ecology. Unlike the above species, they are found along freshwater riverbanks under rocks and pieces of wood from coastal regions to as far inland as Saskatchewan and Montana.

Examined material. **Canada, British Columbia:** Kennedy Lake, VI., BC//15.VI.1951, R. Guppy//Lake shore//12312//ex. G. Stace-Smith collection, purchased 1960 (2 exs.); North Vanc., 24.V.52, Lazorko N.// 12312 (3 exs.); B.C. Kitimat, 15.VII.1979, G.G.E.Scudder// 15 mi N (1 ex.); BC, Bear Lake, 10 km S, Hwy 97, 6.VIII.1982, G.G.E.Scudder (1 ex.); Cheakamus R, BC, 3.IV.1983, L.Vasington (1 ex.). **United states, Idaho:** IDAHO: Smith's Ferry, 23.VI.1938, M.C. Lane//OSAC_0000314018 (1 ex.). **Montana:** Sanders Co. MONT, 13m NE St. Regis, 15.VII.1967, L. Russell 2500'//OSAC_0000295691, OSAC_0000295693, OSAC_0001084529-OSAC_1084533, OSAC_0001084536 (8 exs.). **Oregon:** West Woodburn, Ore. 9.VI-1913//OSAC_0001084581 (2 ex.); BearSpringOre, 6.V.1937, KM and IM Fender// OSAC_0001084591 (1 ex.); McMinnville Ore., 18.IV.1956, KM and IM Fender//OSAC_0001084592 (1 ex.); Pinehurst, Oregon, Jackson County, 24.V.1958, Joe Sehuh, coll.//rotting log aggregation//OSAC_0001084580 (1 ex.); Oreg., Jackson Co., Dead Indian Soda Sprg., 12 mi. SE Lakecreek, 2500' 21.V.1964// J.D. Lattin Collector//OSAC_0001084579 (1 ex.); Benton Co., Ore., 21.X.1975, S. Vernoff, aggregated in rotting log near Mary's River//OSAC_0001084571-OSAC_0001084574, OSAC_0001084537 (6 exs.); OREGON Benton Co, Corvallis, 21.X.1975, S. Vernoff, near Mary's River//OSAC_0001084538 (1 ex.); OREGON; Benton Co, Willamette River, 12.X.1977, coll J D Lattin, ex willow//OSAC_0001084537 (1 ex.). **Washington:** Seattle, Wash.//OSAC_0001084582 (1 ex.); Cooks, WASH., 13.VIII.1913//OSAC_0001084575 (1 ex); Mt. Ranier, WASH., White R. Camp, 6.IX1934, M. H. Hatch//OSAC_0001984584-90 (8 exs.).

Species incertae sedis

Phaleromela humeralis (Laporte, 1840).

Phaleria humeralis Laporte, 1840: 219.

Phaleromela humeralis, Gebien, 1939: 743; Triplehorn, 1961: 126; Bousquet *et al.*, 2018: 291.

Distribution. California.

Phaleromela prohumeralis Triplehorn, 1961.

Phaleria humeralis Horn, 1870: 377 [junior primary homonym of *Phaleria humeralis* Laporte, 1840].

Phaleromela prohumeralis Triplehorn, 1961: 127 [replacement name for

Phaleromela humeralis (Horn, 1870); Triplehorn, 1961: 126; Bousquet *et al.*, 2018: 291.

Distribution. California.

Notes. While it seems that *P. humeralis* and/or *P. prohumeralis* are likely not synonymous with the other North American species, Triplehorn (1961) speculated that it is highly possible that they are synonymous with each other. Based on the original descriptions written by Laporte (1840) and Horn (1874), and in his Marseul's 1874 description of *P. subhumeralis*, this species seems to be superficially similar to *P. humeralis* but differs in being slightly smaller, with spots of the elytra being of a different shape, punctation less dense on the head, elytral striae more distinct, with more widely spaced and distinct punctation. After examining many specimens of *P. subhumeralis* from Japan, Russia, and South Korea, there is enough variation within this species that this diagnosis as well as the original descriptions of

P. humeralis and *P. prohumeralis* do not provide sufficient information to differentiate either of these species from *P. subhumeralis*.

Chapter VI:

General Discussion

Preface

The groups of beetles treated in this work are linked along several different axes most prominently but not limited to phylogenetic relationship and habitat preference. While the main goal of my work it to generate taxonomic resources that can be used by other researchers to properly identify insects inhabiting heterotrophic systems, some insight can also be drawn from comparing the groups treated in the four main sections of this thesis. The projects in each section were not conducted in a standardized manner nor on the same ecological scope as each other and thus cannot be compared one-to-one but by better understanding of the diversity of beetles present in each different system may lead to further research on the benefits and constraints of different systems.

Taxonomy and Biogeography

The two main taxonomic projects included in this thesis serve to fill large gaps in resources for the genus *Sphaeridium* in Asia and the beach-dwelling members of the hydrophilid genus *Cercyon*. Treatments of Asian species *Sphaeridium* in particular were previously scattered, mainly consisting of single species descriptions with few visual references. Examination of species included in the SEHU insect collection revealed that Asian members of the genus, while including several closely related species, comprise at least 19 species and can largely be differentiated based on external morphological characteristics. Ventral characters which historically were not as emphasized in descriptions (perhaps due to the tradition of mounting insects in ways that obscure ventrites) showed to be particularly valuable in species determination. In particular, the mesoventral protrusion which is located at the center of the mesoventrite (Fig.11C–F) in between the mesocoxae takes a unique form within the genus and shows a wide variation in shape. Other characters found to be useful included the shape and presence of a terminal spine on the median part of the proventrite, the shape and surface sculpture of the metaventrite, and the shape of the male protarsus.

The placement of *Sphaeridium* within the Hydrophilidae as a whole has been known for some time. Even based on morphological characters, it is distinct enough that it has long been placed in its own tribe which has more recently been confirmed by molecular phylogenetics (Short and Fikáĉek 2013, Bloom *et al.* 2014). Incomplete information on specific species has however been insufficient to explore the relationships between species within the genus. Based on the morphological revision in this thesis, several species can be grouped based on the abovementioned characters, but molecular analysis is still necessary to confirm these groupings and determine relationships between species and species groups proposed herein. Establishing species delineations however may help inform any further work on this group.

In comparison, the beach dwelling *Cercyon* represent a much smaller group and most species had been treated more recently with keys to species included in Ôhara and Jia (2006) and Shatrovskiy (1992) for the far east and Smetana (1988) for the west coast of North America. The genus *Cercyon* is however considerably larger than just the beach species or *Sphaeridium* and has been considered polyphyletic for some time with strong evidence in Arriaga-Verala and Fikáĉek (2021) and is thus quite difficult to study. Whether or not the beach *Cercyon* represent a monophyletic clade remains to be shown but the finding that two species are distributed on both sides of the Pacific indicates greater connectivity between the two seemingly disjunct regions. It also bears the question of how the species occurring in both regions are related if monophyletic. Do species on either side represent monophyletic groups and if not, how many times have species moved across the Pacific and by which routes? Morphologically, the north Pacific *Cercyon* seem to form a monophyletic group joined by their rather flat habitus, posterior apex of mesoventral tablet contacting metaventrite at a single point, and broad protibial, but the origin of the group as well as its relationship to the other four species beach dwelling *Cercyon* still needs to be confirmed. The existence of the Australasian genus *Cercyodes* shows that the adaptation to beach habitats has occurred at least twice within the megasternini but within the *Cercyon*, molecular work is still needed to better understand the intergeneric relationships at play.

The tenebrionid genus *Phaleromela* has also lacked revision in recent years with the most recent treatment being Triplehorns's 1961 paper on the genus which lists the species known from North America but does not redescribe or illustrate them and does not fully compare them to the one Far East species, *P. subhumeralis*. Though it hasn't been well studied, the two beach dwelling members, *P. picta* and *P. subhumeralis*, are rather ubiquitous and widely distributed along the coasts of the North Pacific and along with the inland species, *P. variegata*, show an interesting range of morphological differences reflective of differences in their preferred habitats. Like *Cercyon*, the trans-pacific distribution raises questions as to the origin of the genus and its relationship to other members of the tribe Diaperiini. Interestingly, the related coastal genus *Phaleria* is also present in both North America and the Far East though its distribution is more southern, generally starting at the southernmost distributions of the two beach *Phaleromela* (Triplehorn and Watrous 1979). In many ways, *P. variegata* resembles members of *Phaleria* the closest, being winged and more elongate in body shape but more closely resembles the other species of *Phaleromela* ecologically as they are known to mainly inhabit beach habitats. The little overlap in ranges suggests that perhaps the beach *Phaleria* and *Phaleromela* occupy similar niches and exert competitive pressure on each other but more information on the natural history of both genera is needed to know for sure.

In the past, North America and Asia have commonly been considered as separate regions when looking at biological systems though in reality, these regions are strongly connected not only by the proximity of Alaska and Far East Russia but also by ocean current and the movement of humans. This become rather apparent when examining the diversity of beach-dwelling insects, which are more restricted by inland terrestrial habitats than by the ocean. Several possible routes of transmission across this wide region exist including gradual movement along coastlines, more direct transmission via human trade or potentially ocean debris, or a combination of the two. Both the beach *Cercyon* and the members of the tenebrionid genus *Phaleromela* present interesting models for examining this dynamic as well as the evolutionary process for adaptation to beach habitats.

In particular, the recent discovery of the Far East species *C. dux* in British Columbia and Washington raises the possibility that this species may have been introduced to North America following the great East Japan earthquake tsunami disaster in 2011 via debris generated by the tsunami. An estimated 5 million tons of debris were washed into the Pacific Ocean from the Japanese coast, of which roughly 1.5 million tons did not sink and were spread across the Pacific, including many large items including large pieces of wood, boats, and even whole docks (NOAA 2015, Murray *et al*. 2018). While Japanese debris is known to travel to Pacific Northwest coasts of North America regularly, carried by the Kuroshio and Oyashio currents which join to form the north Pacific current, the debris influx in Washington State was found to be about ten times baseline levels (Murray *et al.* 2018). As a result, a number of marine species including foraminifers, sponges, hydroids, chitons, copepods, ostracods, and fish were found to have traveled across the ocean on large rafts of accumulated debris (Carlton and Fowler 2018). One Japanese species of soil-dwelling orbatid mite was also found to have arrived in Haida Gwaii as a result of oceanic rafting by Lindo (2020) which indicates the potential for small terrestrial arthropods with some salinity tolerance to be distributed directly across the Pacific via debris. *Cercyon* species, being beach specialists, are salinity tolerant and are able to resist submersion due to the hydrofuge pubesence that covers their ventral surface so the possibility of their survival on a large enough raft, particularly with seaweed accumulation, is possible. Since the initial discovery of *Cercyon dux* from Vancouver Island in 2014, it seems to also be expanding its range southward, based on my own collecting from 2016–2019, appearing on beaches in northern Washington where it had not been previously collected (Fig. 99).

Habitat flexibility and heterotrophic systems

Sphaeridium, while strongly preferring dung, is known to also occasionally colonize carrion (Heo *et al.* 2011) though this isn't a common occurrence, particularly in more northern regions, and whether or not it is only a character in some species is not yet known. The mouthparts in *S. lunatum* show strong morphological similarities to those of coprophilous scarabaeid beetles (Holter 2004) indicating specialization to a coprophagous lifestyle in this species but it is currently believed that the species *S. huijbregtsi* may be more necrophilous as it has only been collected from carrion-baited pitfall traps (Berge Henegowen 1986, Fikáĉek and Kopráĉek 2015). Nevertheless, there seems to be some flexibility in habitat choice for *Sphaeridium* as a genus and it is perhaps likely that under more historical conditions in which widespread ranching hadn't yet provided an abundance of high-quality dung (Holter and Scholtz 2007), lesser connectivity of desired habitat made some degree of flexibility more necessary for survival.

The species collected from the fallen bee nest also indicate the potential for opportunistic utilization of higher quality resources for more habitat-flexible species. Most species collected from the beehive are known mainly from plant matter, which seems to vary quite a bit from the potential resources available in the bee nest which likely contains bee brood, pollen, and honey. Only one of the fully identified species, *Paroosternum saundersi* is known from dung (as well as plant matter) and none of the collected species seemed to be common on carrion which may simply be a result of proximity to plants and not dung or carrion but also may indicate some nutritional similarity between the rotting bee nest and decaying vegetation. This however represents the first and only study of a bee nest as a heterotrophic system so whether or not it is representative outside of this particular circumstance cannot be determined.

In contrast the nine Pacific species of beach *Cercyon* are found only in seaweed wrack and no other hydrophilids seem to consistently live in this detritus in the north Pacific. Of the three systems examined in this work, only these hydrophilids seemed to live exclusively in this type of detritus. Additionally, other than the unrelated Australasian megasternine genus *Cercyodes*, no other genus of hydrophlids is known to live in beach wrack indicating that existing in this habitat may require more specialization than others. While the integument of most terrestrial insects is generally well waterproofed and highly impenetrable by salts, challenges related to the ingestion of high salinity foods remain and the proximity to seawater also necessitates specific adaptations for preventing submersion (Cheng *et al.* 1976). Most beach *Cercyon* also live in the wrack zone which occurs at or just below the high tide line and may be periodically submerged so physiological and behavioral adaptations for avoiding periods of higher tide are also necessary.

Like beach dwelling *Cercyon*, the two beach dwelling members of the tenebrionid genus *Phaleromela, P. picta* and *P. subhumeralis,* also inhabit beach habitats. *Phaleromela* however, tend to prefer to live at and around the roots of backshore vegetation and under older, more dry wrack deposited well above the high tide line on sandy beaches. Much of the debris found in this wrack is in a much more advanced state of decomposition and despite relatively close proximity to the fresh wrack, differs distinctly from the fresh wrack in moisture content, available resources, and insect community present. While there is some movement of species between the two types of wrack, beach *Cercyon* are not often found living in the dry beach wrack where there is considerably less activity of other invertebrates for the larvae to prey on. These differences may indicate that the heterotrophic systems of either wrack zone are different though connected.

For both groups the substrate under wrack piles does seem to matter to some degree, with *Phaleromela* tending to occur only on sandy beaches and *Cercyon* species varying in their tolerance for different substrates, with species like *C. aptus* and *C. fimbriatus* occurring on both sand and cobble beaches while some other species occurring mainly on cobble beaches. The type of substrate of a beach is rather important for the decomposition of seaweed wrack not only in its relation to the type of seaweed that washes up but also moisture retention and in the wrack community of invertebrates (Orr *et al.* 2005). Whether or not the substrate is important for hydrophilids in other heterotrophic systems is still not well studied but based on differences in diversity between cobble and sand beaches and the characteristic of the expanded protarsi in beach *Cercyon*, it seems to be quite important in this type of system.

Conclusion

While able to fill several gaps in the classification of the groups treated in this thesis, it shows that there is still a lot of work to do to more fully understand the diversity and life histories of coleoptera living in heterotrophic systems. North Pacific beach ecosystems present particularly interesting questions as to the routes of movement of different taxa across the region but morphological taxonomy alone is not sufficient to fully understand the phylogenetic relationships of these groups. For the *Sphaeridium* as well, while external characters and the shape of the male genitalia are sufficient for species determination, relationships within the genus would require molecular methods to confirm. More studies on the biology and life histories of these beetles are also warranted to better understand their roles in decomposer communities. How larvae and adults alter the physical structure of detritus and their role in the food webs of these communities may give us a much more complete idea of the processes at play.

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Tables and Figures

Tables

Table 1. List of species and numbers of individuals collected from *Apis dorsata dorsata* nest.

Taxa	**number of specimens**
Coelostomatini	
Dactylosternum abdominale Fabricius, 1792	2
Dactylosternum hydrophiloides MacLeay, 1825	3
Dactylosternum grouvelli Guillebeau, 1894	1
Protosternini	
Protosternum hainanensis Fikáček, Liang, Hsiao, Jia & Vondráček, 2018	1
Omicrini	
Noteropagus obliquus Orchymont, 1925	12
Noteropagus occlusus Orchymont, 1932	1
Megasternini	
Paroosternum saundersi Orchymont, 1925b	35
Cercyon (*Clinocercyon*) sp.1	95
Cercyon sp.2	2
Cercyon sp.3	1
Pachysternum apicalis Motschulsky, 1863	56

Table 2. Literature records of *Microchaetes* sp. in Japan.

Prefecture	Records of Microchaetes
Aichi	Takamatsu, Orido Town, Nisshin City, 15.VII.2012 (Nisshin History Compilation Committee 2015).
Chiba	Miyako Town, Chuo Ward, Chiba City, 6.VII.1996 (Pütz 2004)
Gifu	Hinata, Motosu City, 30.VII.2020 (Nakano 2020).
Hiroshima	Akiota Town, 9.VII.2016 (Participants of collecting event 2016); Ajinadai, Hatsukaichi City, 8.VIII–10.VIII.2017 (Kosaka and Yano 2017); 9.VI–25.IX.2018 (Kosaka and Yano 2018); 2019 (Kosaka and Yano 2019); 9.VI-23.VII.2020 (Kosaka and Yano 2020).
Hyogo	Kakogawa City 14.I.2001; Himeji City, 9.VI.2007; Shiso City, 7.VIII.2007 (Yoshida 2008).
Ibaraki	Hasaki, Kamisu City, 20.VII.1999 (Pütz 2004).
Kagawa	Mt. Iwaseo, Takamatsu City, 2.VII.2006; Hazama, Mannou Town, 3.VII.2006 (Sato 2007); Kawanabe Town, Takamatsu City, 19.VII.2015; Shinhama Town, Marugame City, 18.IX.2017; Yashimanishi Town, Takamatsu City, 25.II.2019; Ikenobe, Hikame, and Shishibuse, Miki Town, 23.IX.2019; Nagaonishi, Sanuki City, 24.IX.2019 (Waki 2020).
Kanagawa	Yamaguchi, Hayama Town, 22.VIII.1999; Musashikosugi, Kawasaki City (Takizawa 2005); Tsumadaminami, Atsugi City, 15.III.2019–V.2020 (Saito 2020).
Kyoto	Takanodai, Maizuru City, 21.VII.2002 (Mizuno and Arata 2005)
Miyazaki	Aoshima, Aoshima beach, 8.VI.2021.
Oita	Northern Oita, 2005 (Okamoto and Miyake 2006)
Okayama	Nishinoura, Tsurajima Town, Kurashiki City, 5.V.2002 (Suenaga and Takizawa 2004); Ushimado Town, 2.VIII.2004 (Yoshida and Suenaga 2008); Tamagashi, Kita Ward, Okayama City, 31.VIII.2004 (Yamaji 2005).
Osaka	Tsuneyoshi, Konohana Ward, Osaka City, 27.IX.2008; Sugahara, Higashiyodogawa Ward, Osaka City, 27.VII.2015 (Shiyake *et al.* 2020)
Tokyo	Omori, Ota Ward, 12.VII.1996 (Pütz 2004); Motoakasaka, Minato Ward, 19.VIII–2.IX.2003 (Nomura and Hirano 2005).
Yamaguchi	Kawaradani, Iwakuni City, 9.VII.2015; Kuga Machi, Iwakuni City, 14.VI.2016 (Tsuji 2017); Mure, Hofu City, 30.VI.2018, 3.V.2019 (Kogawa 2020); Komatsubara Town, Ube City, 4.X.2019 (Tanaka 2021).

Chapter II

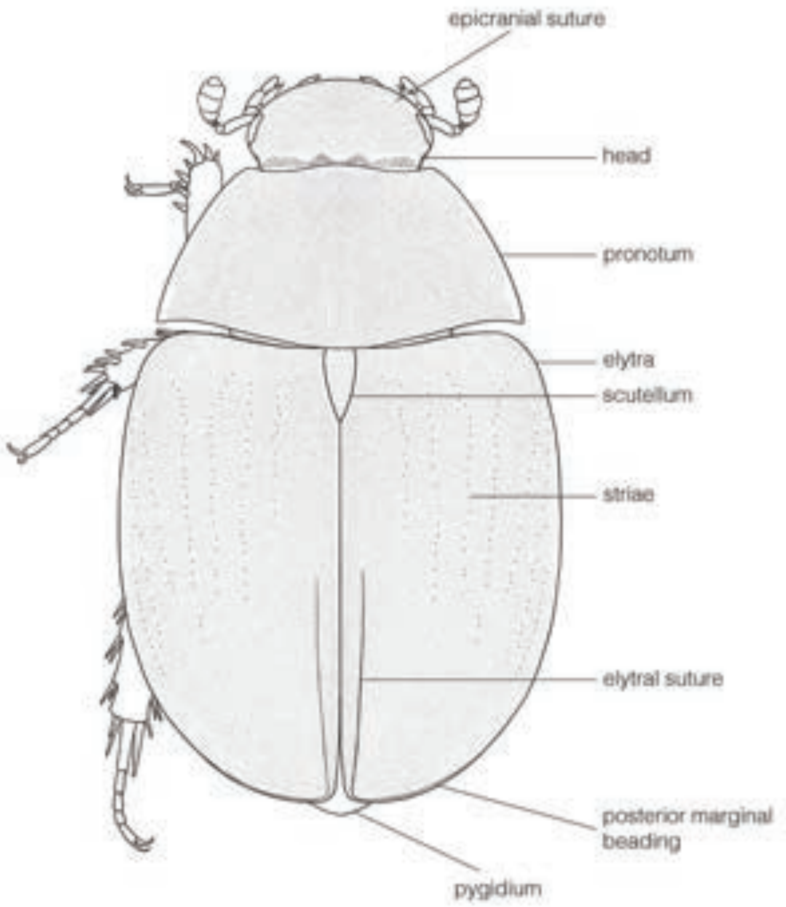

Figure 1. Habitus, dorsal view, schematic.

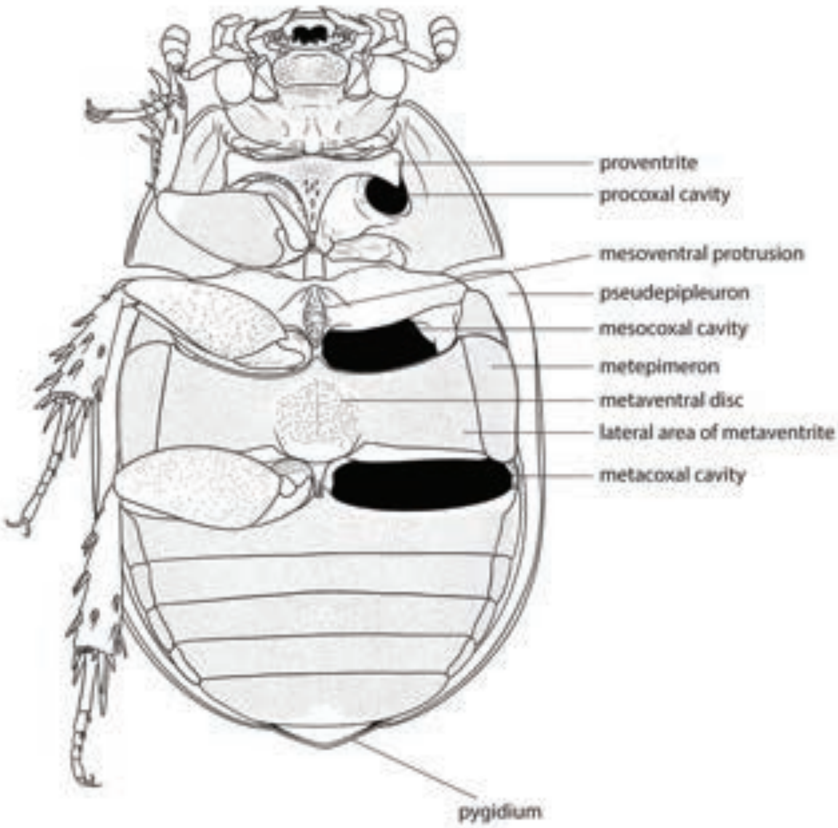

Figure 2. Habitus, ventral view, schematic.

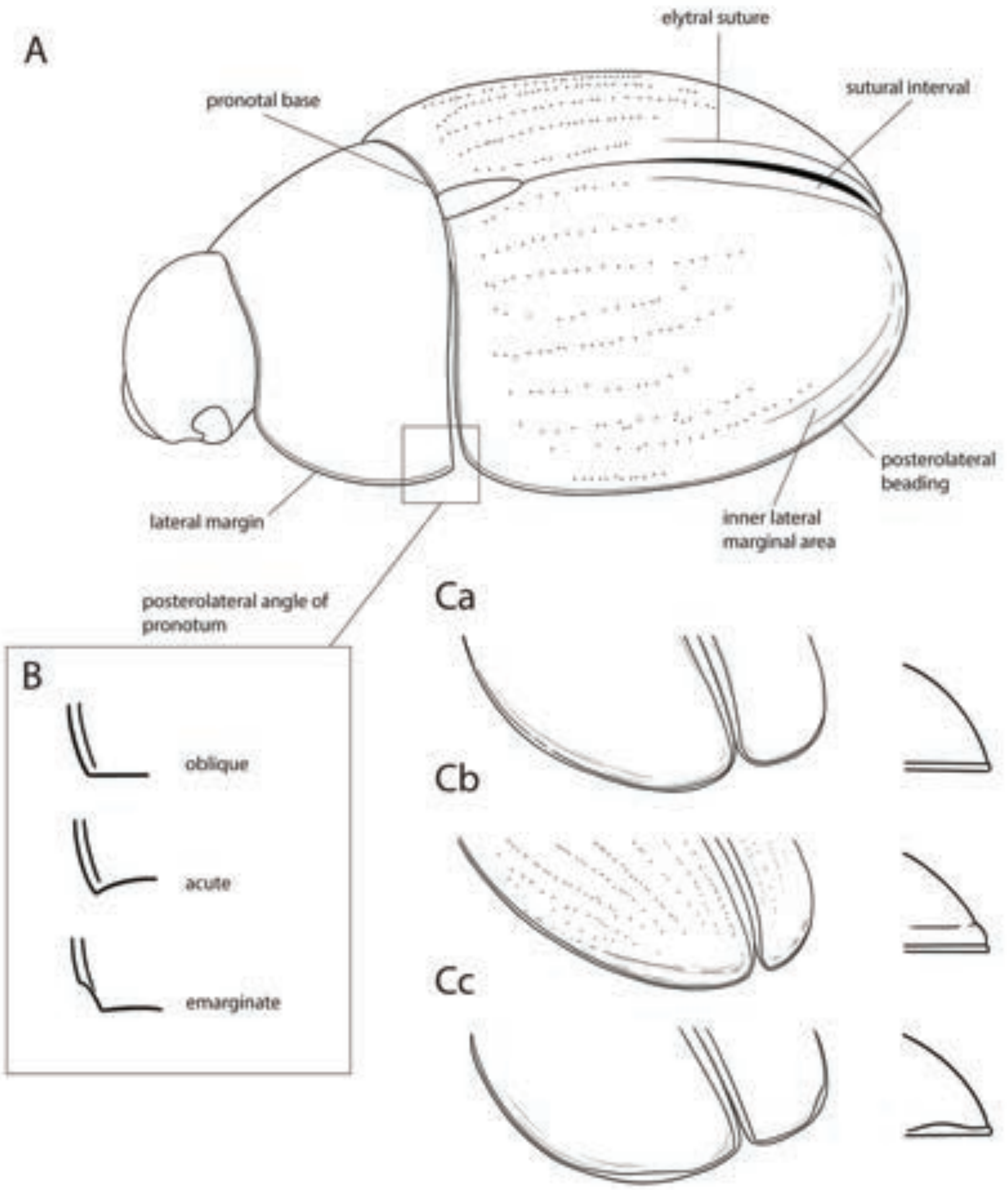

Figure 3. A) Habitus, oblique view, schematic; B) Protonal posterior angle, variation; C) Latero-posterior margin of elytra, oblique and lateral schematic: Ca) *Sphaeridium scarabaeoides*; Cb) *S. severini*; Cc) *S. vitalisi*.

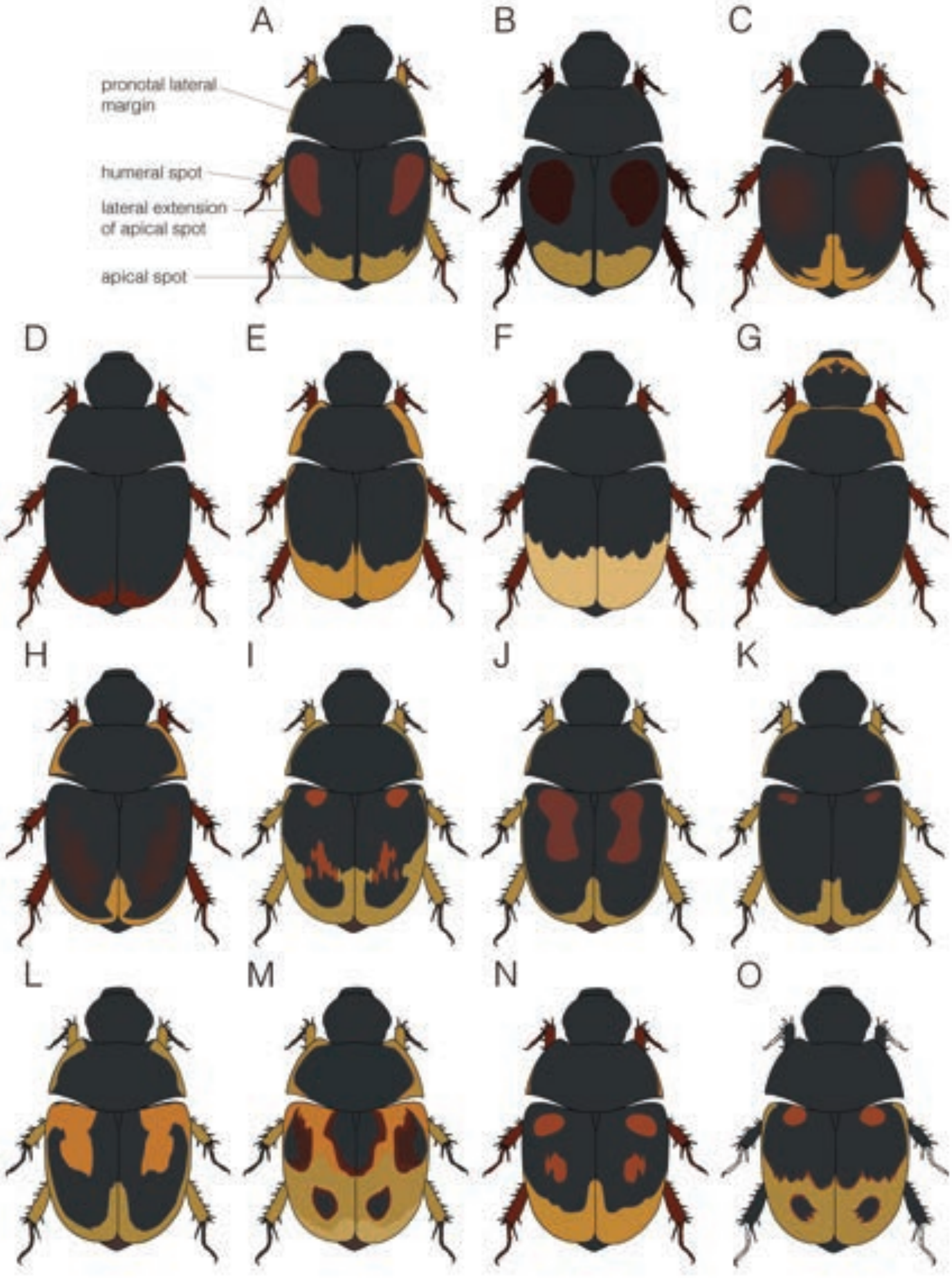

Figure 4. Generalized color patterns. A) *Sphaeridium scarabaeoides*; B) *S. lunatum*; C) *S. bipustulatum*, *S. marginatum*, *S. substriatum*; D) *S. densepunctatum*; E) *S. daemonicum*, *S. huijbregtsi*, *S. kolleri*, *S. seriatum*, *S. severini*, *S. vitalisi*; F) *S. dimidiatum*, *S. discolor*; G) *S. flavomaculatum*; H) *S. sundense*; I–O) *S. quinquemaculatum*; N–O) *S.* sp.1.

Figure 5. Generalized ventral coloration. A) Dark coloration; B) light coloration.

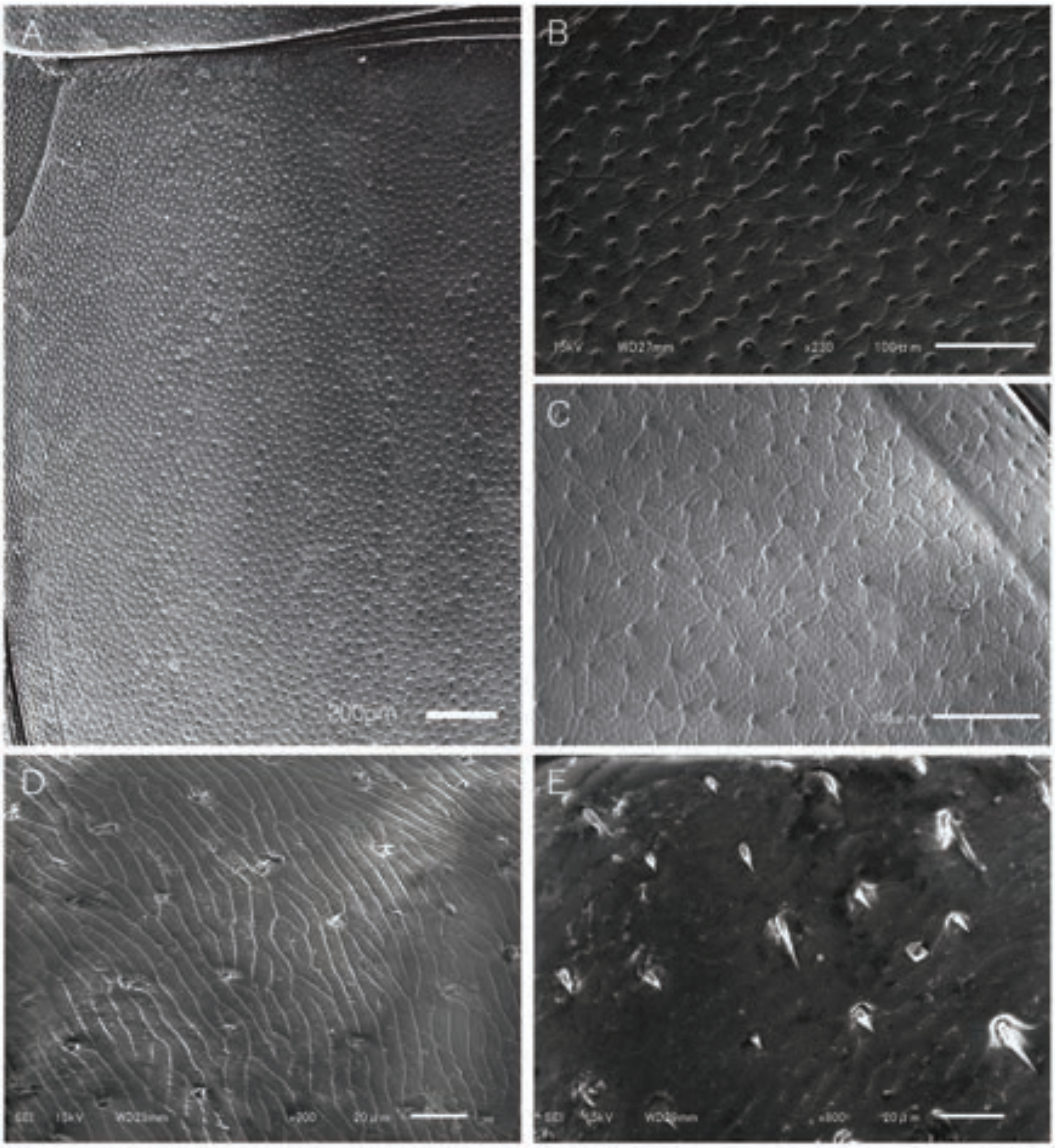

Figure 6. Surface microsculpture. A–C) *Sphaeridium severini*, elytra; A) radiating microrugae; B) reticulate microrugae; C) reticulate microrugae and granulate microsculpture; D) *S. marginatum*, metafemur, microrugae; E) *S. marginatum*, mesoventral field, microrugae.

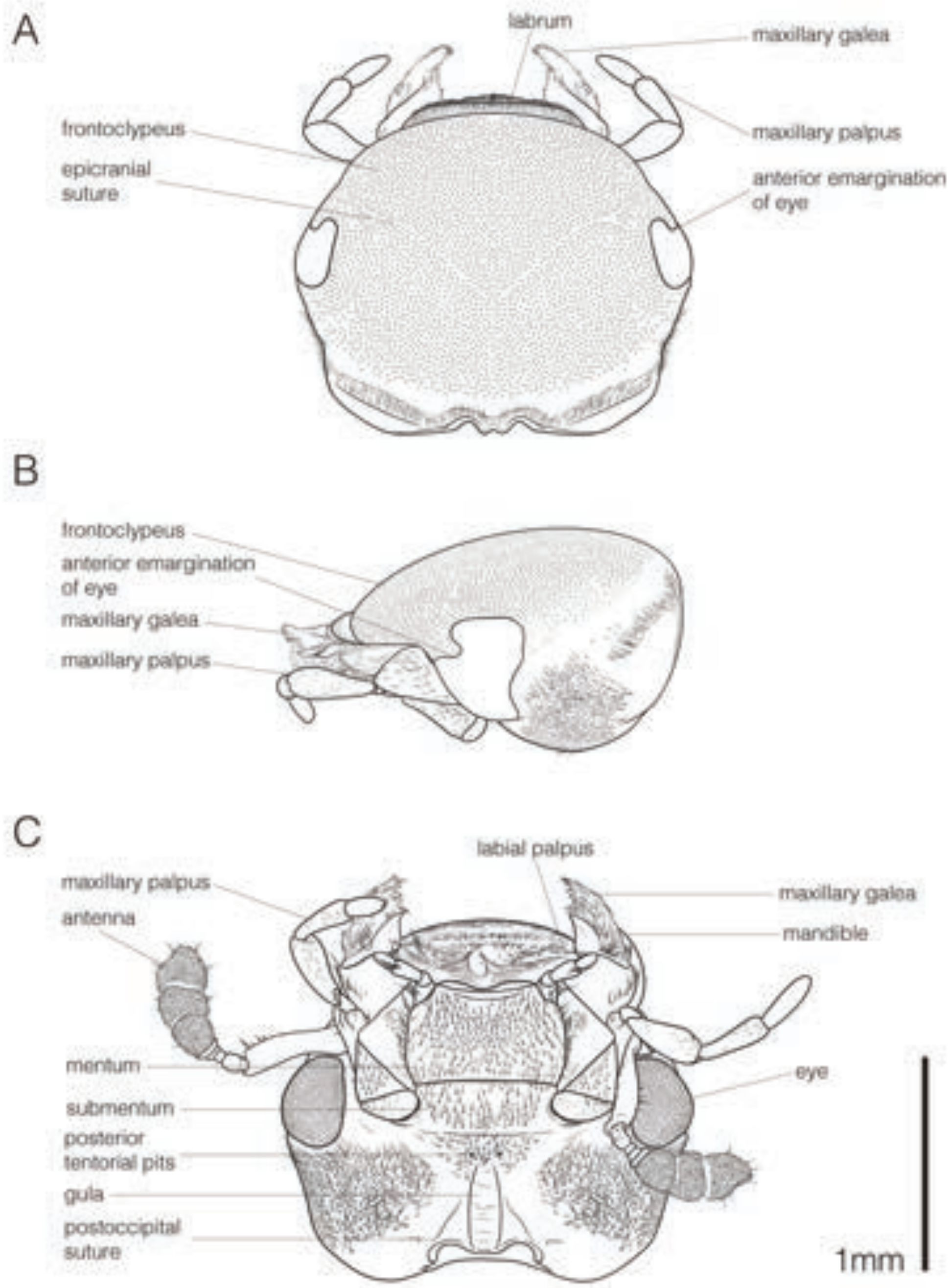

Figure 7. Head. A) Dorsal view; B) lateral view; C) ventral view.

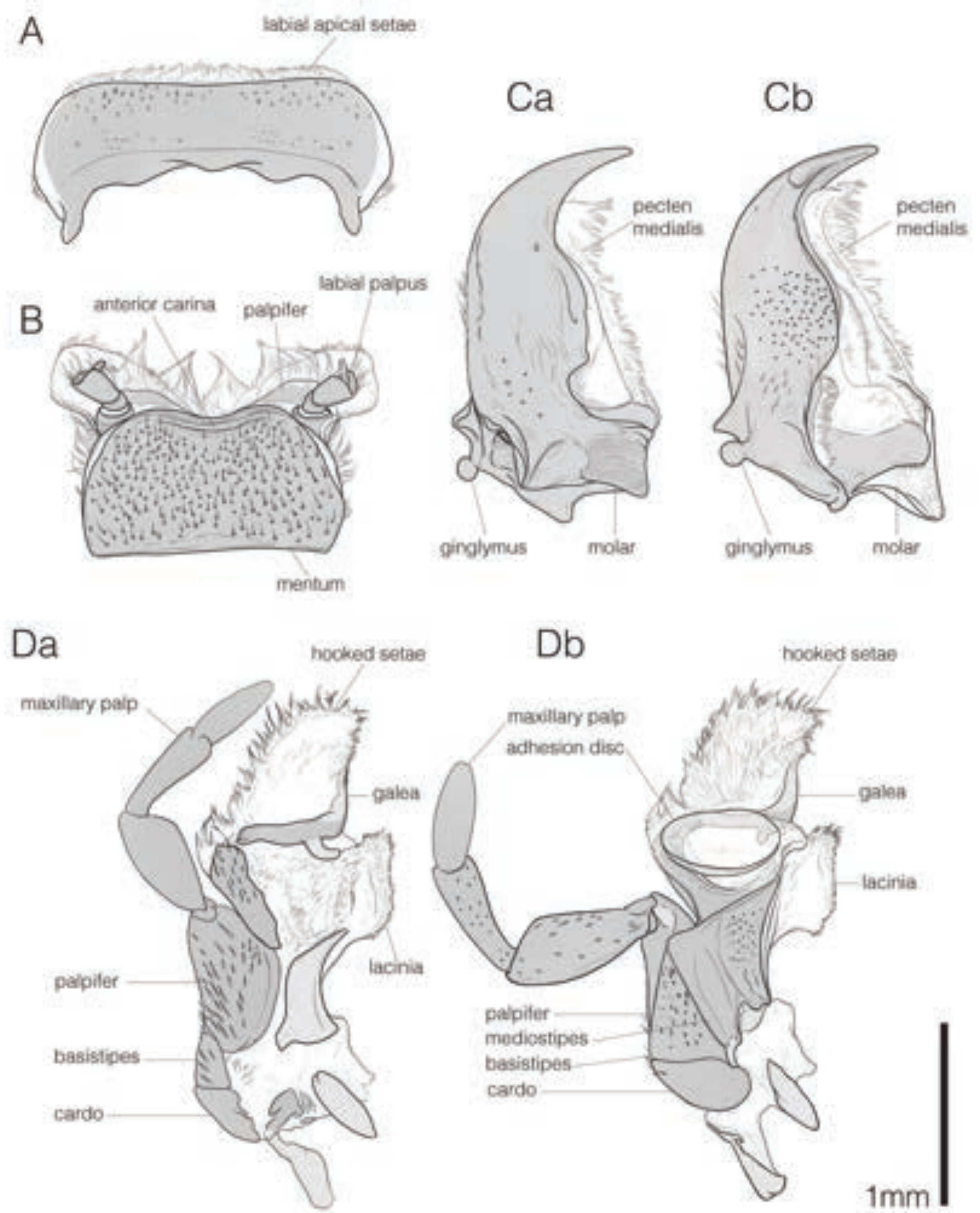

Figure 8. External mouthparts, *Sphaeridium scarabaeoides*, male. A) Labrum, dorsal; B) mentum and prementum, ventral; C) mandibles, a) dorsal, b) ventral; D) maxillae, a) dorsal, b) ventral.

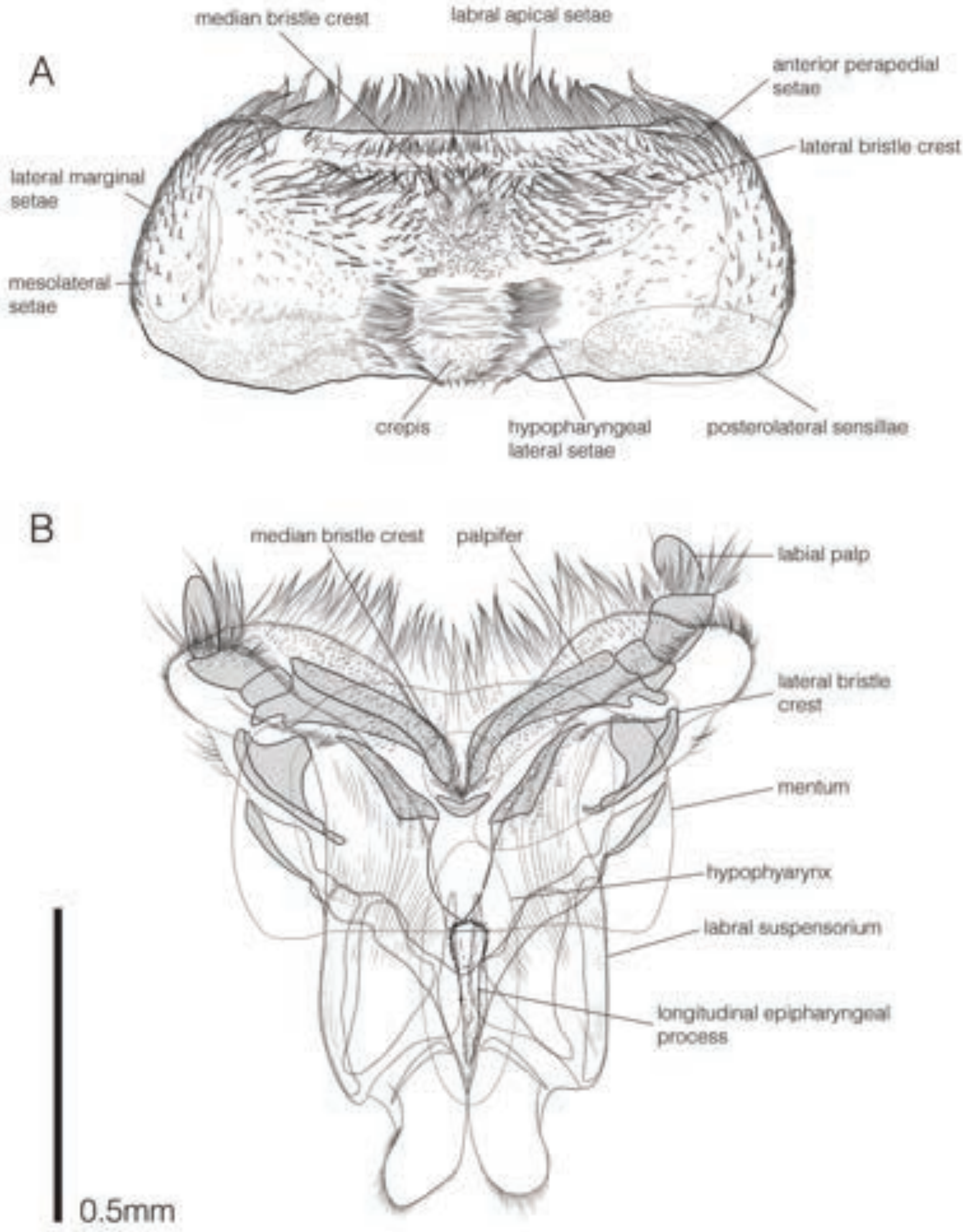

Figure 9. Internal mouthparts, *Sphaeridium scarabaeoides*, male. A) Labrum, ventral (epipharynx); B) labium, dorsal view.

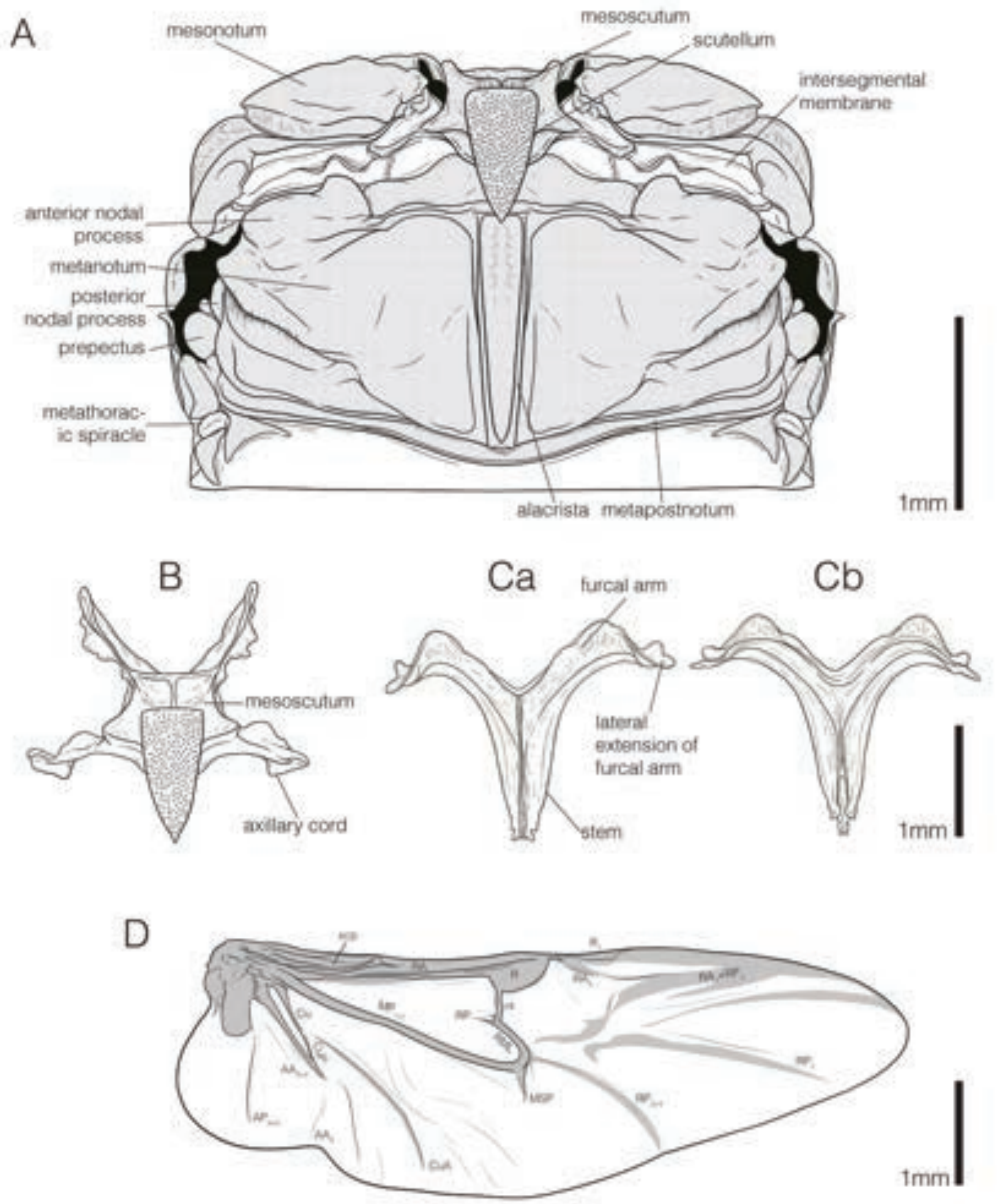

Figure 10. Dorsal and internal thoracic morphology, *Sphaeridium scarabaeoides*. A) Meso- and metanotum, dorsal; B) scutellum, dorsal; Ca) metafuca, dorsal; Cb) ventral; D) wing. Abbreviations: AA, anal anterior; AP, anal posterior; Cu, cubitus; CuA, cubitoanal strut; CuA, cubitus anterior; CuP, cubitus posterior; MP, media posterior; MSP, medial spur; R, radial cell; R_1, radius; r4, radial cross-vein; RA, radius anterior; RML, radiomedial loop; RP, radius posterior; scp, subcostal.

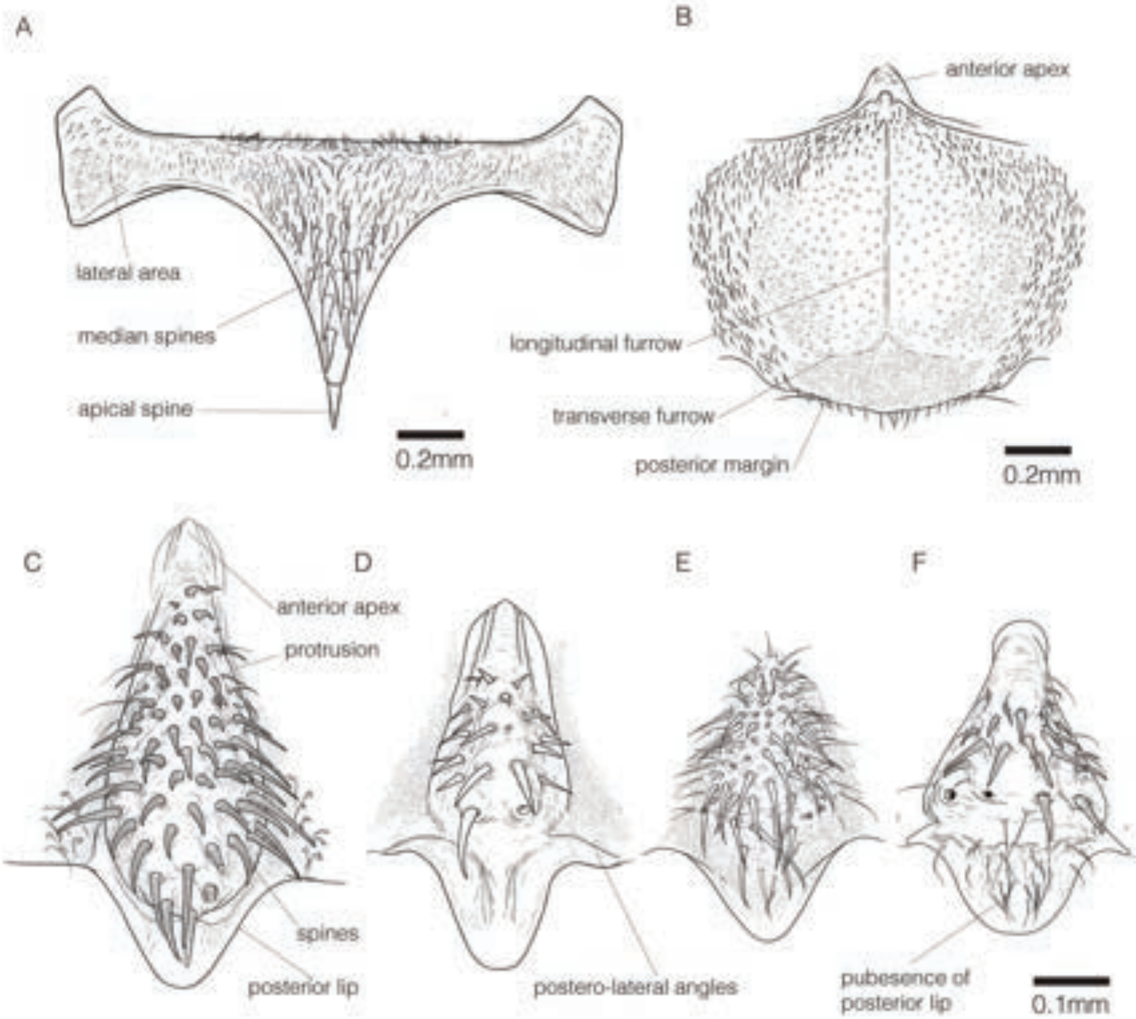

Figure 11. Ventral thoracic morphology. A–C) *Sphaeridium scarabaeoides*; D) *S. substriatum*; E) *S. dimidiatum*; F) *S. quinquemaculatum*; A) proventrite, B) metaventral disc; C–F) mesoventral protrusions.

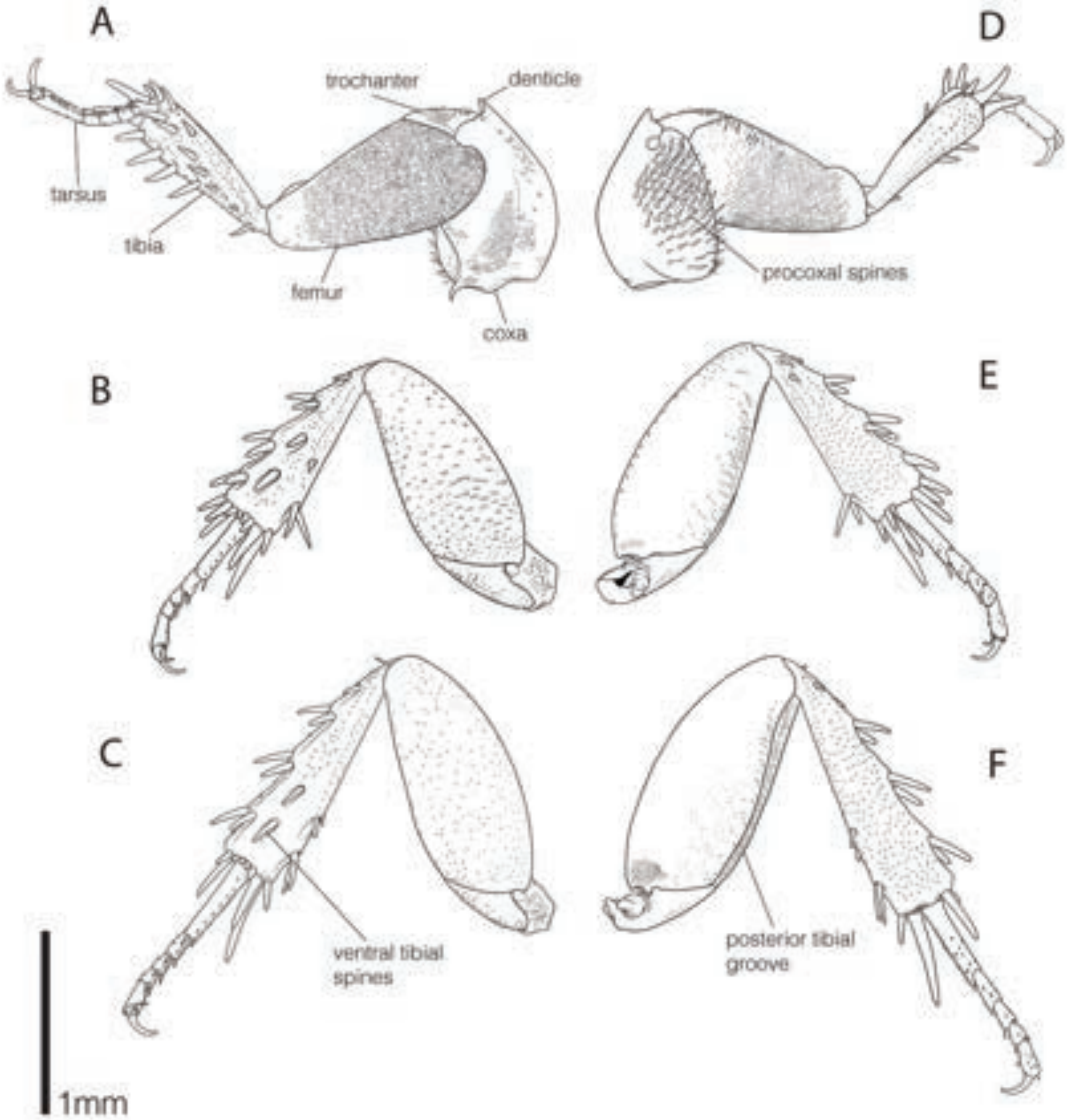

Figure 12. Legs, *Sphaeridium scarabaeoides*, female. A–C) ventral; D–F) dorsal; A, D) proleg (including coxae); B, E) midleg (coxae removed); C, F) hindleg (coxae removed).

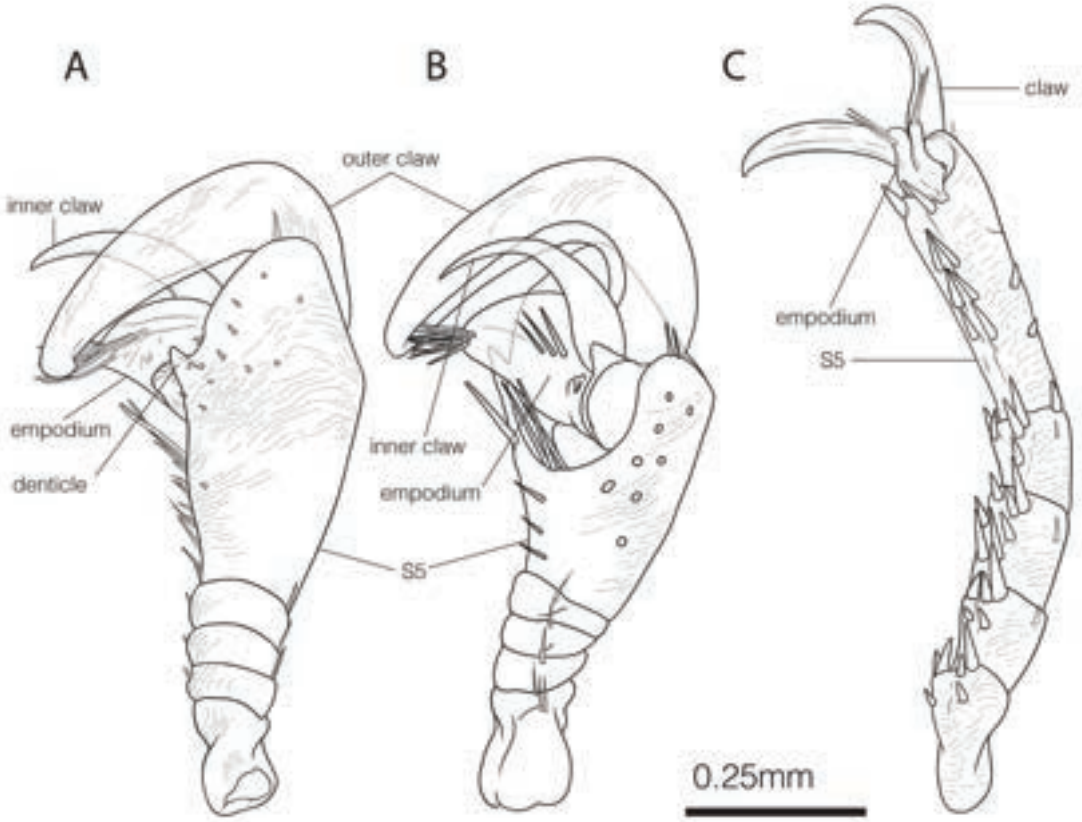

Figure 13. Protarsus, *Sphaeridium scarabaeoides*. A) Male, outer lateral view; B) male, inner lateral view; C) female, ventro-lateral view.

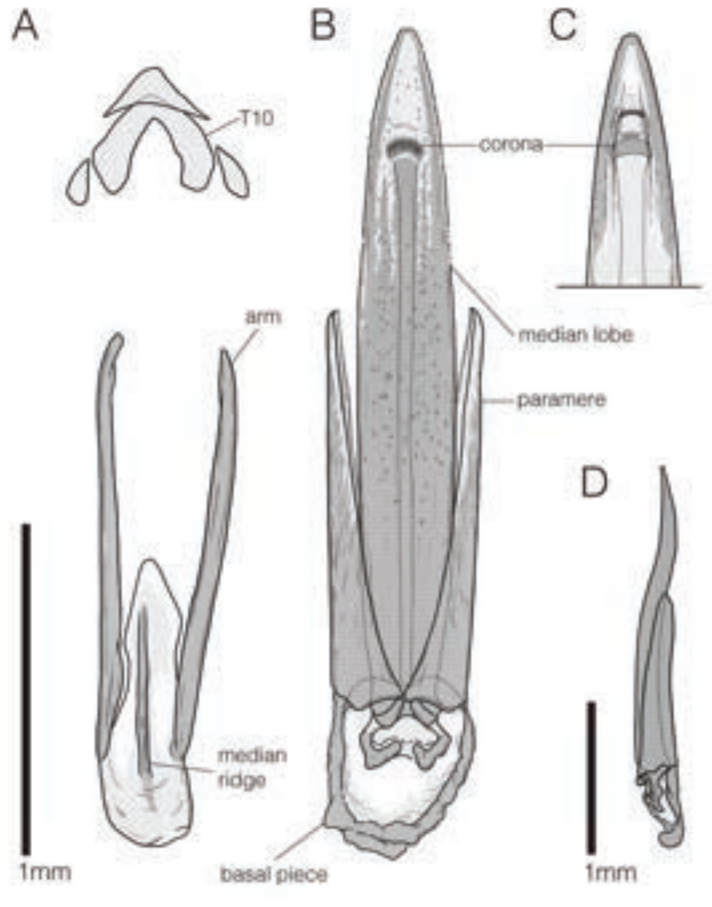

Figure 14. Male genitalia, internal morphology, *Sphaeridium scarabaeoides*. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

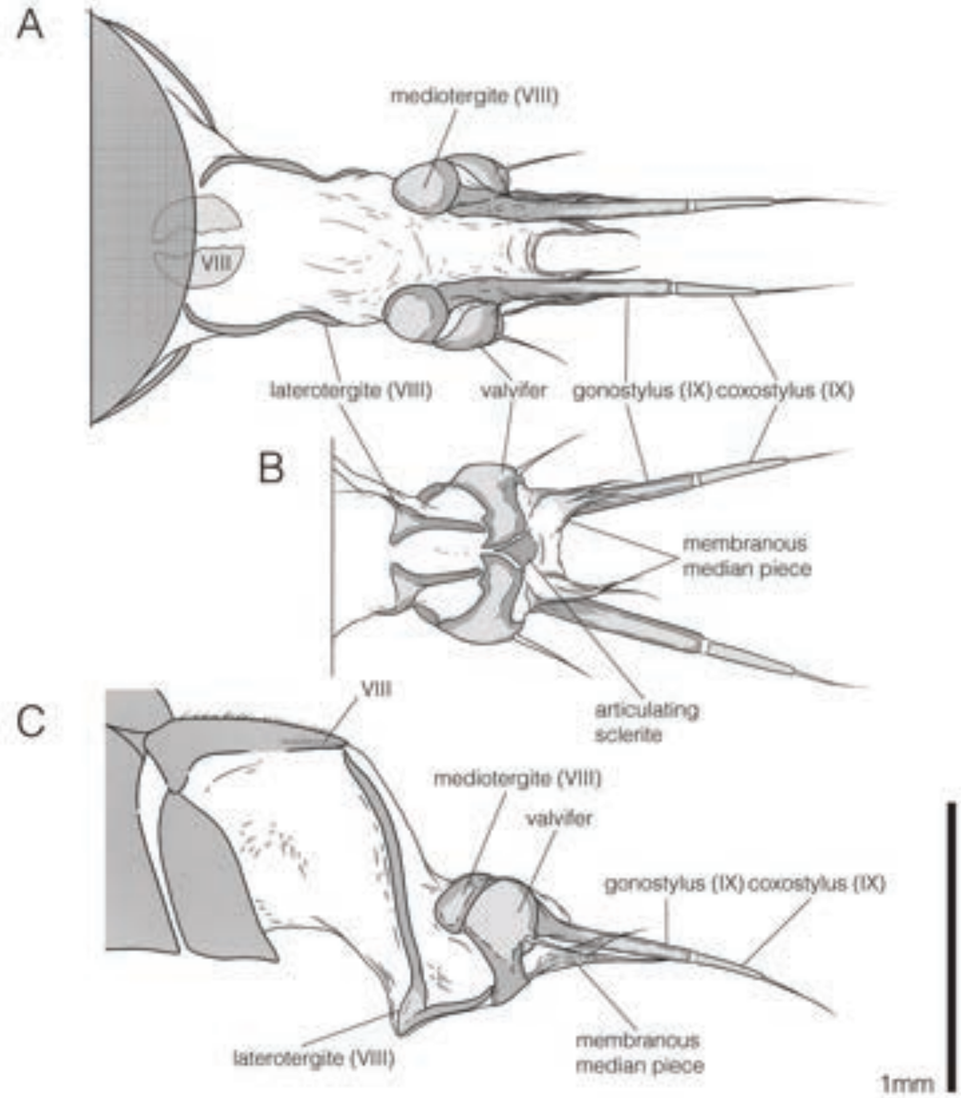

Figure 15. Female genitalia, external morphology, *Sphaeridium lunatum*. A) Dorsal; B) ventral; C) lateral.

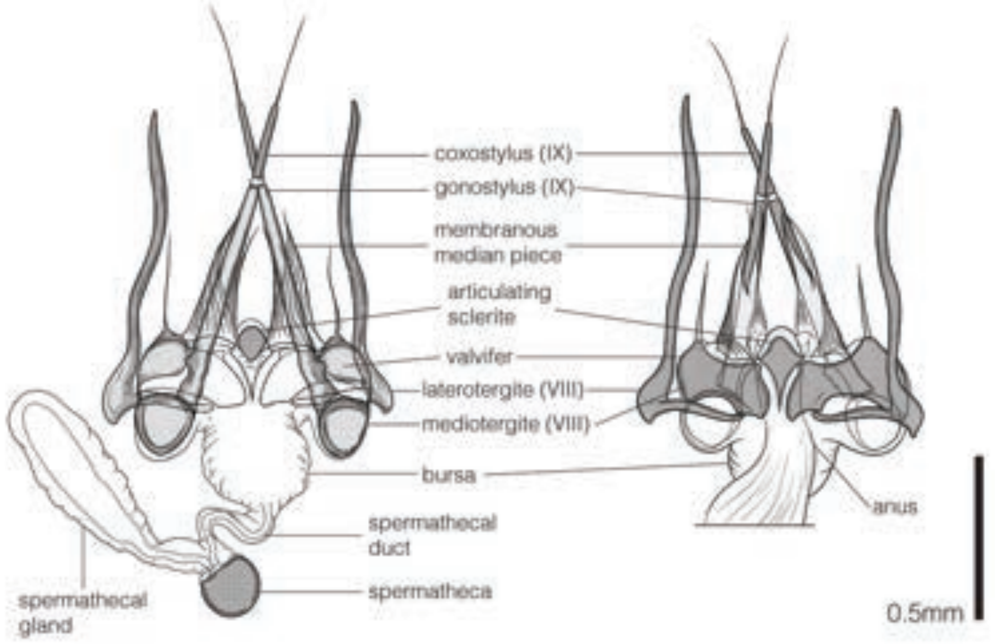

Figure 16. Female genitalia, internal morphology, *Sphaeridium scarabaeoides*. A) dorsal; B) ventral.

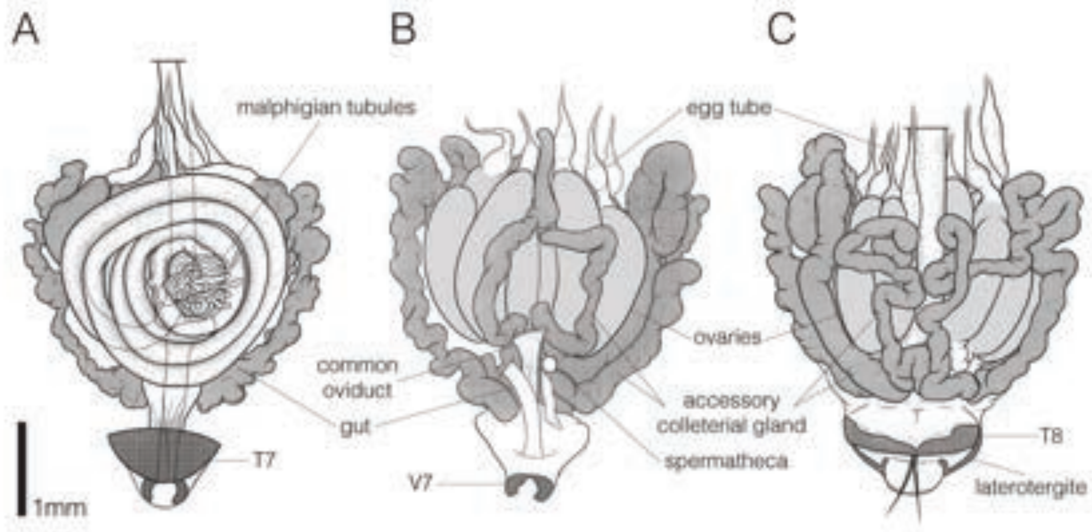

Figure 17. Female, abdominal internal organs, *Sphaeridium scarabaeoides*. A) Dorsal, with gut; B) dorsal, gut removed; C) ventral.

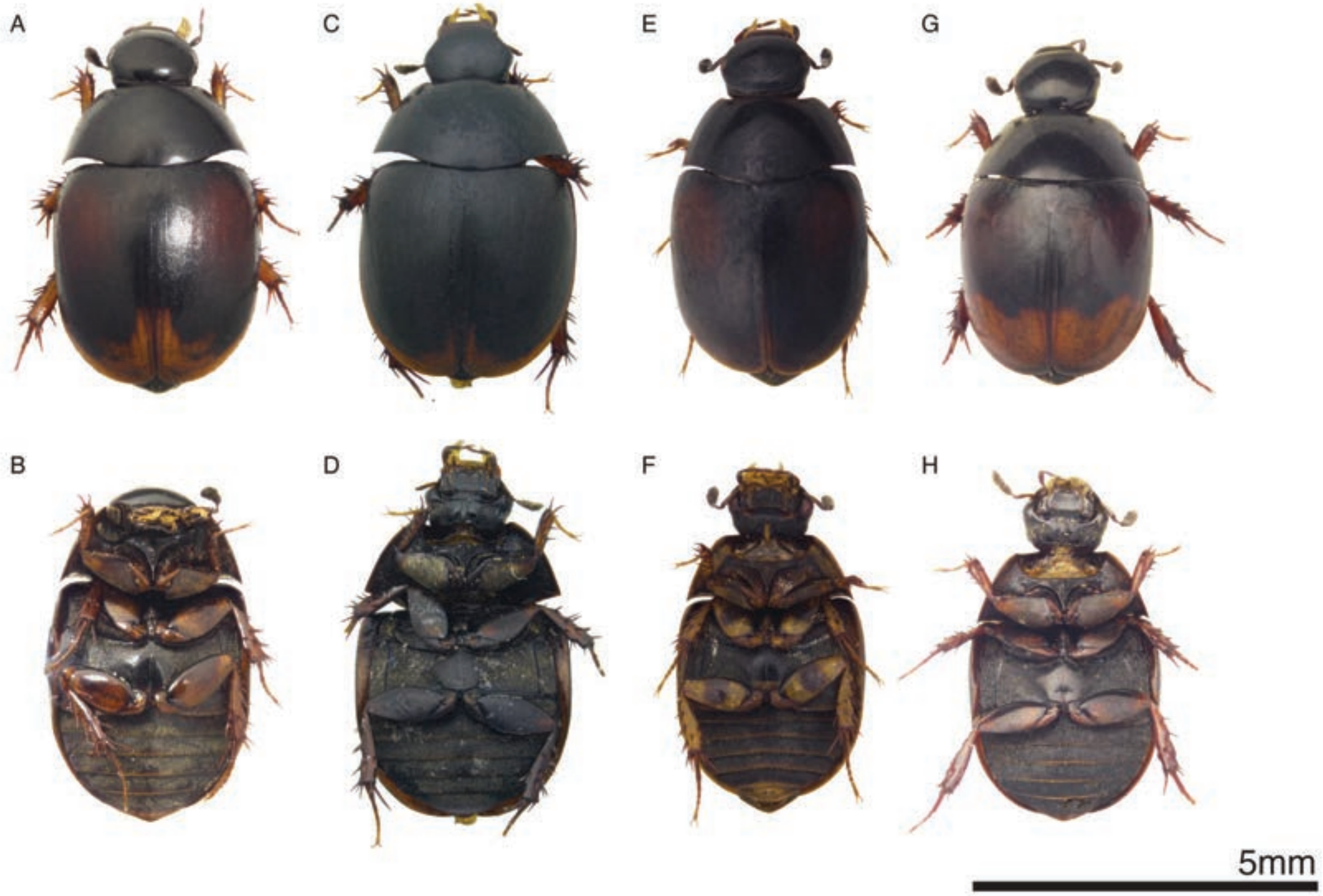

Figure 18. Habitus, *bipustulatum* group. A–B) *Sphaeridium bipustulatum*; C–D) *S. densepunctatum*; E–F) *S. marginatum*; G–H) *S. substriatum*.

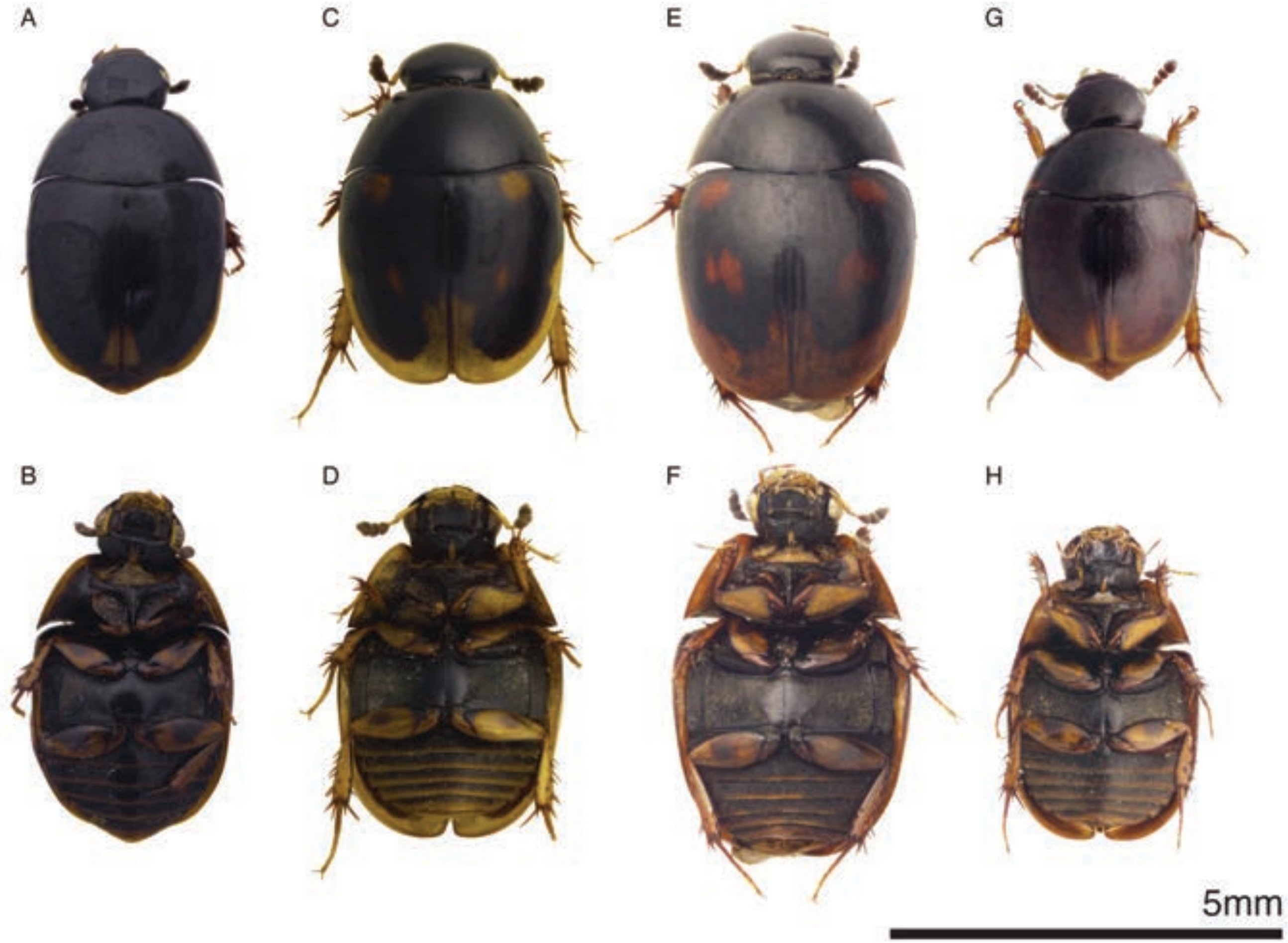

Figure 19. Habitus. A–F) *quinquemaculatum* group: A–B) *Sphaeridium* sp.2; C–D) *S. quinquemaculatum*; E–F) *S.* sp. 1. G–H) *S. sundense*.

Figure 20. Habitus, *seriatum* group: A–B) *Sphaeridium huijbregtsi*; C–D) *S. severini*; E–F) *S. seriatum*; G–H) *S. vitalisi*.

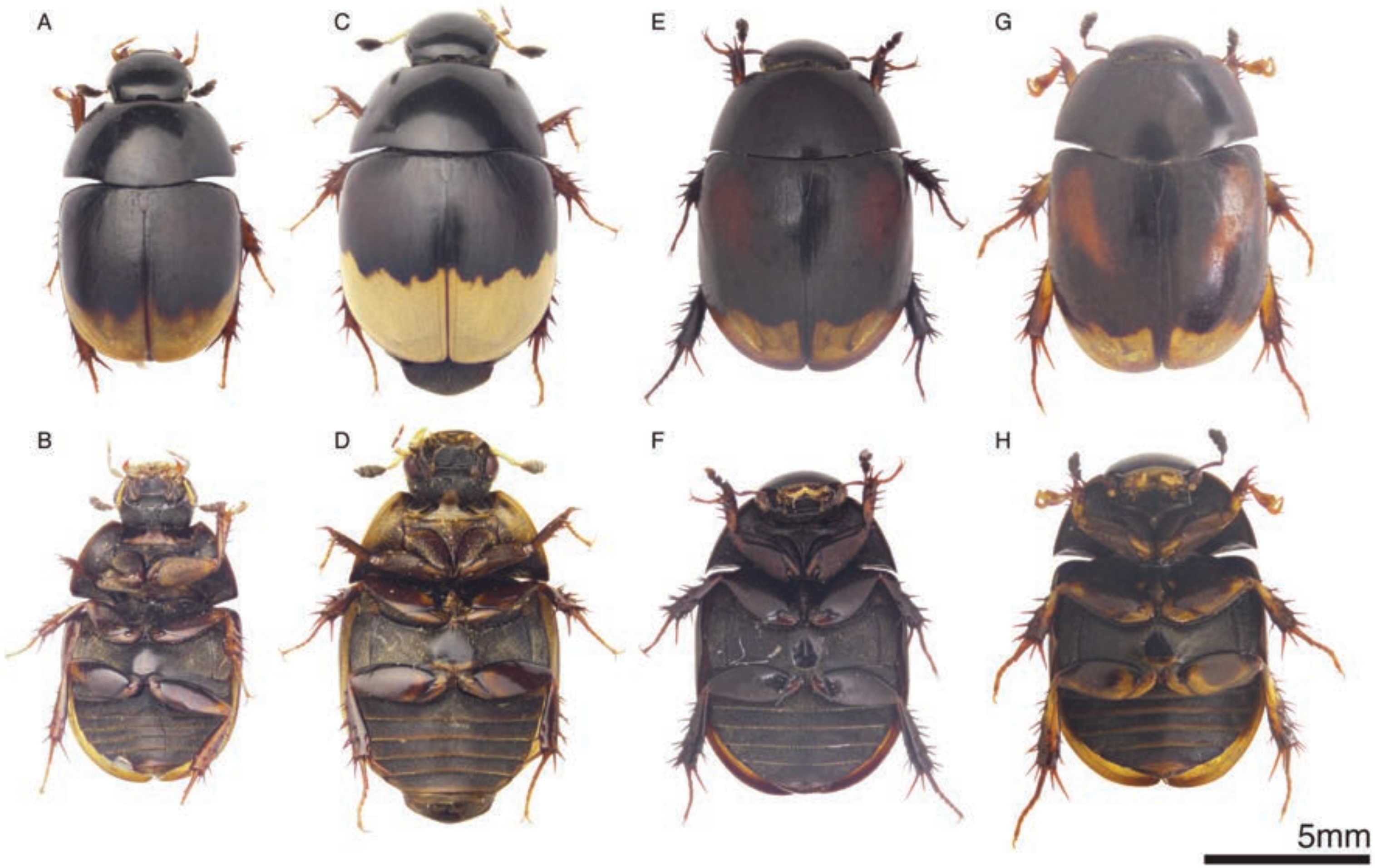

Figure 21. Habitus. A–B) *Sphaeridium dimidiatum*. C–D) *S. discolor*. E–H) *scarabaeoides* group: E–F) *S. lunatum*; G–H) *S. scarabaeoides*.

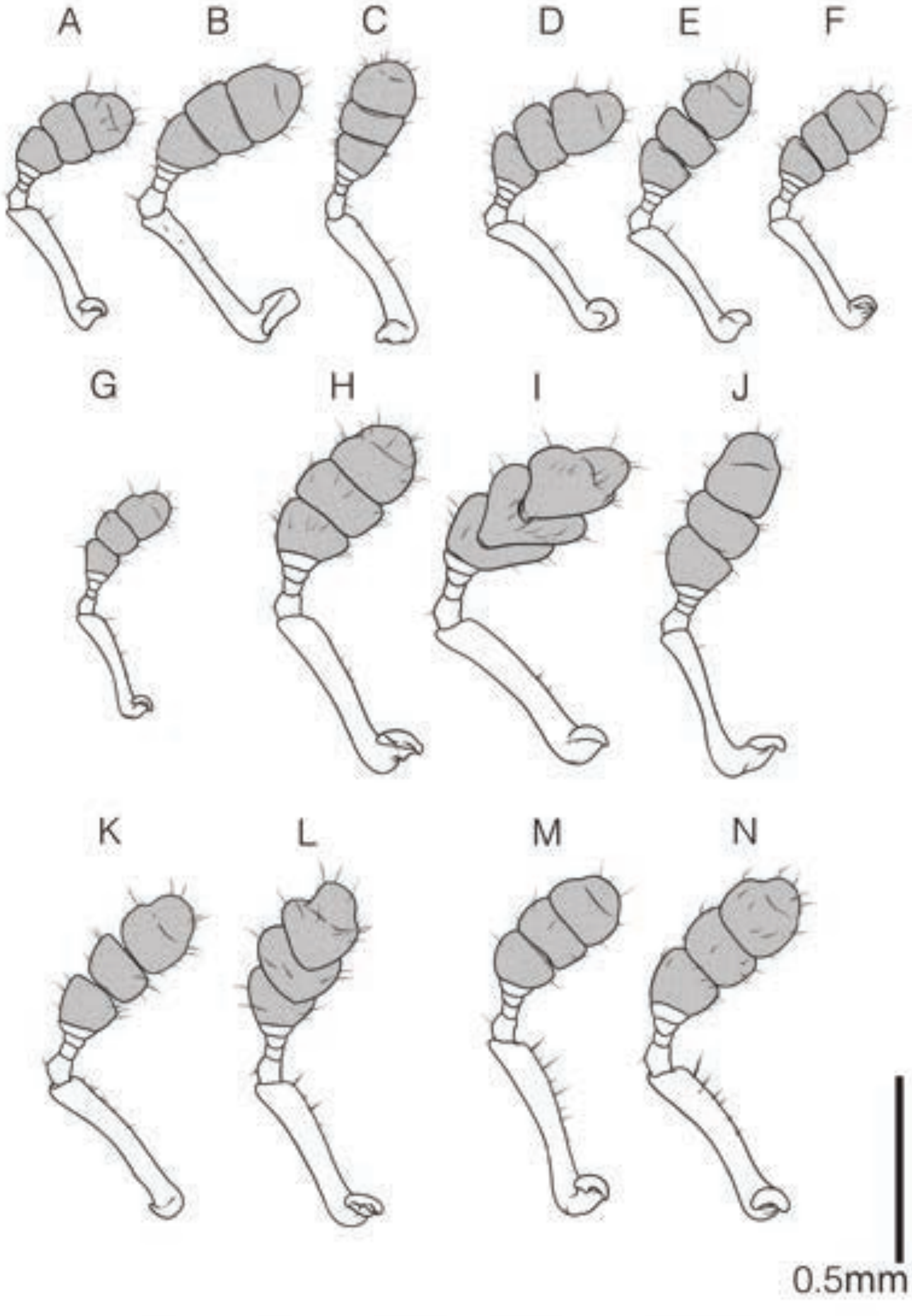

Figure 22. Antennae. A) *Sphaeridium bipustulatum*; B) *S. densepunctatum*; C) *S. substriatum*; D) *S.* sp.2; E) *S. quinquemaculatum*; F) *S.* sp.1; G) *S. sundense*; H) *S. seriatum*; I) *S. severini*; J) *S. vitalisi*; K) *S. dimidiatum*; L) *S. discolor*; M) *S. scarabaeoides*; N) *S. lunatum*.

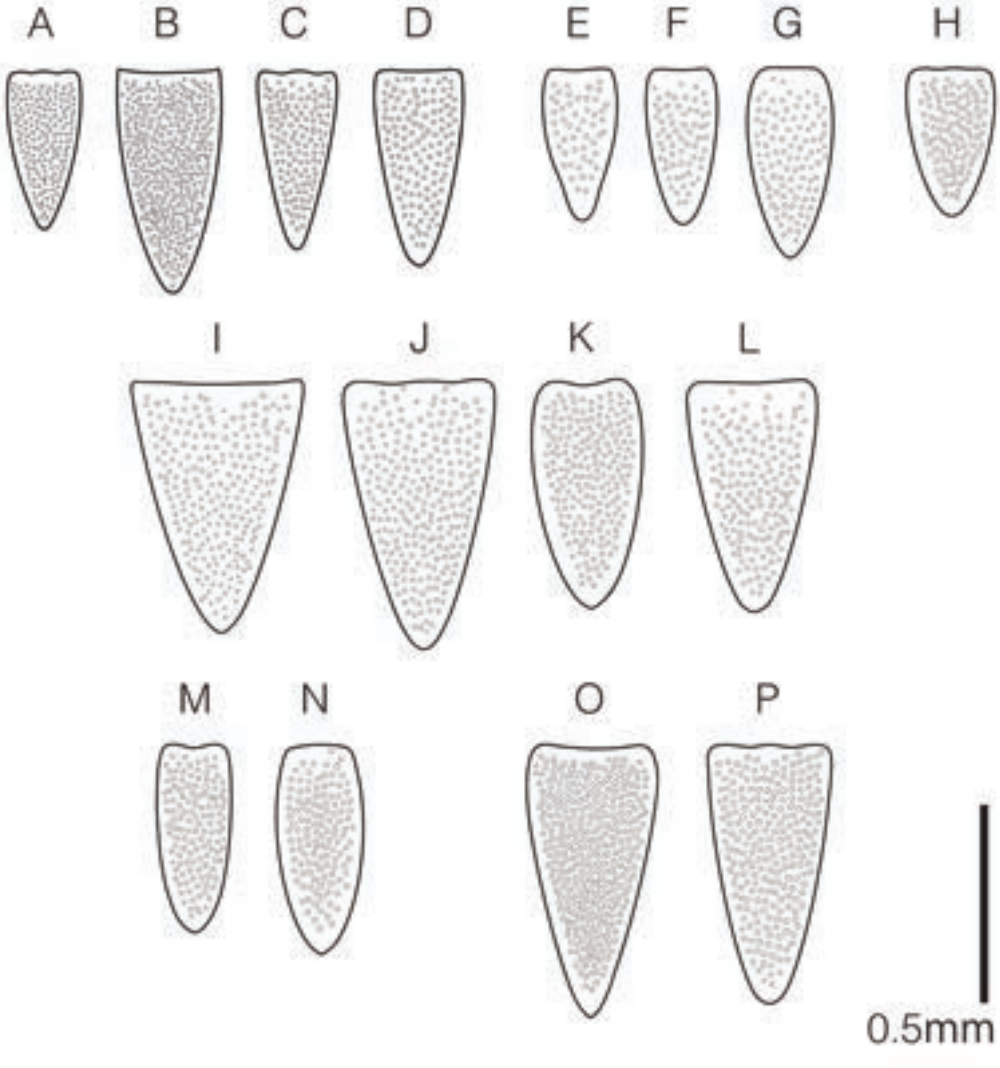

Figure 23. Scutellums. A) *Sphaeridium bipustulatum*; B) *S. densepunctatum*; C) *S. marginatum*; D) *S. substriatum*; E) *S.* sp.2; F) *S. quinquemaculatum*; G) *S.* sp.1; H) *S. sundense*; I) *S. huijbregtsi*; J) *S. seriatum*; K) *S. severini*; L) *S. vitalisi*; M) *S. dimidiatum*; N) *S. discolor*; O) *S. scarabaeoides*; P) *S. lunatum*.

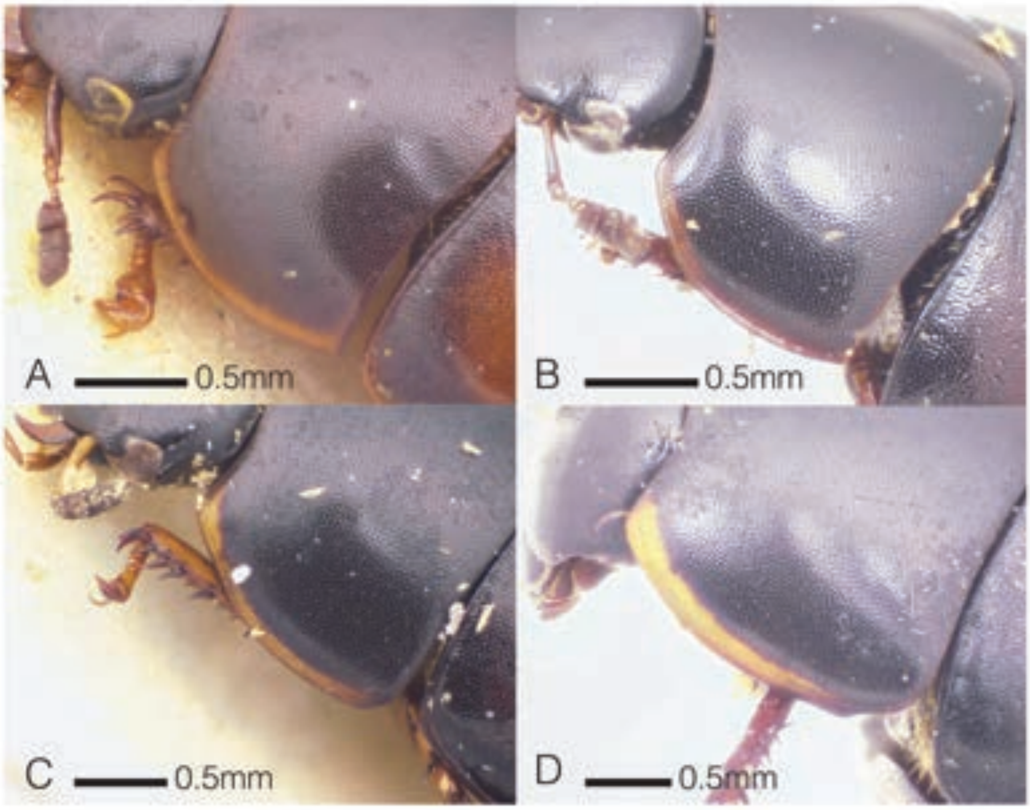

Figure 24. Posterior angle of pronotum. A) 90º angle, *Sphaeridium marginatum*; B) >90º angle, *S. substriatum*; C) small emargination, *S. dimidiatum*; D) large emargination, *S. discolor*

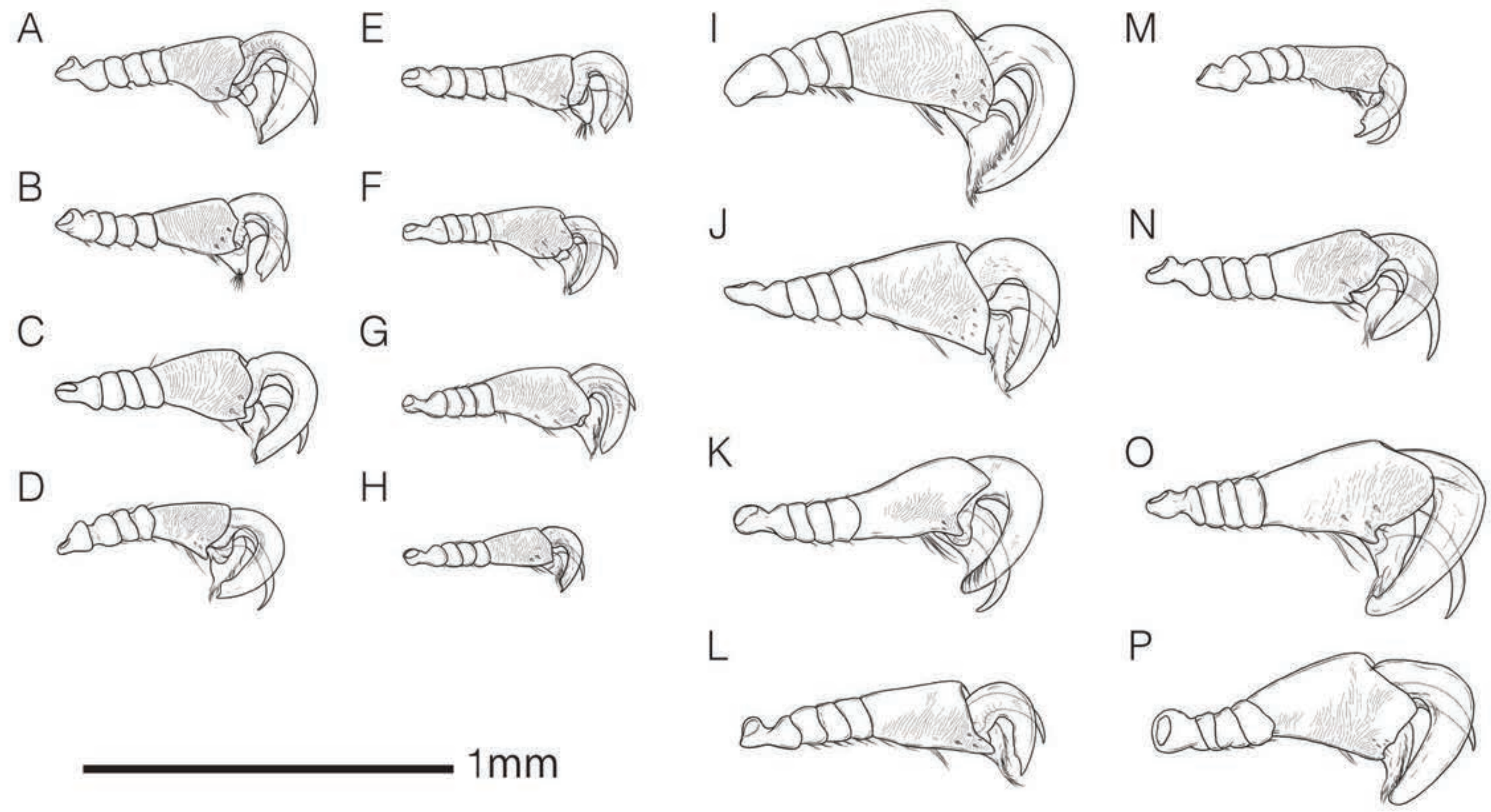

Figure 25. Male protarsi. A) *Sphaeridium bipustulatum*; B) *S. densepunctatum*; C) *S. marginatum*; D) *S. substriatum*; E) *S. kalon*; F) *S. quinquemaculatum*; G) *S.* sp.1; H) *S. sundense*; I) *S. huijbregtsi*; J) *S. seriatum*; K) *S. severini*; L) *S. vitalisi*; M) *S. dimidiatum*; N) *S. discolor*; O) *S. scarabaeoides*; P) *S. lunatum*

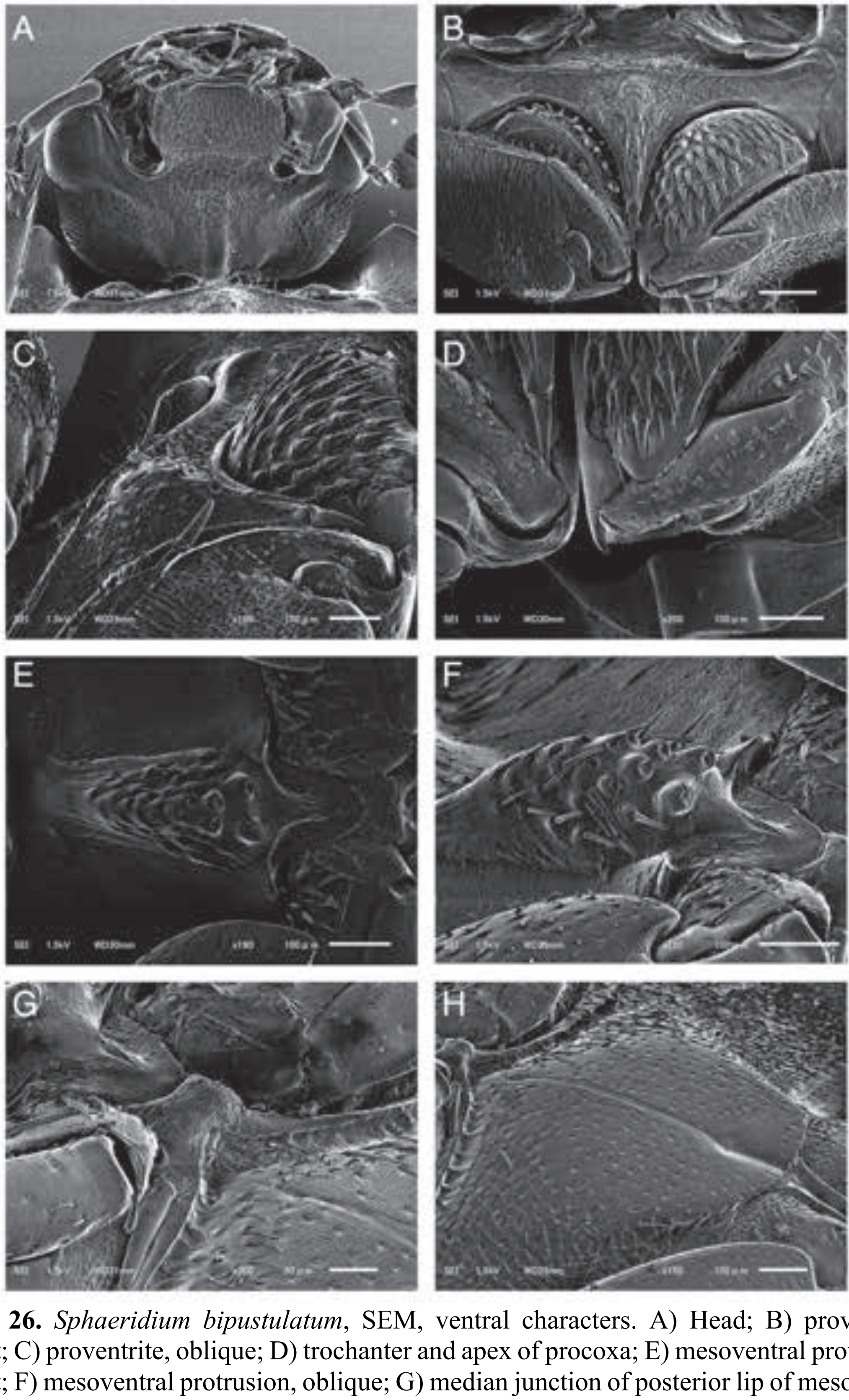

Figure 26. *Sphaeridium bipustulatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

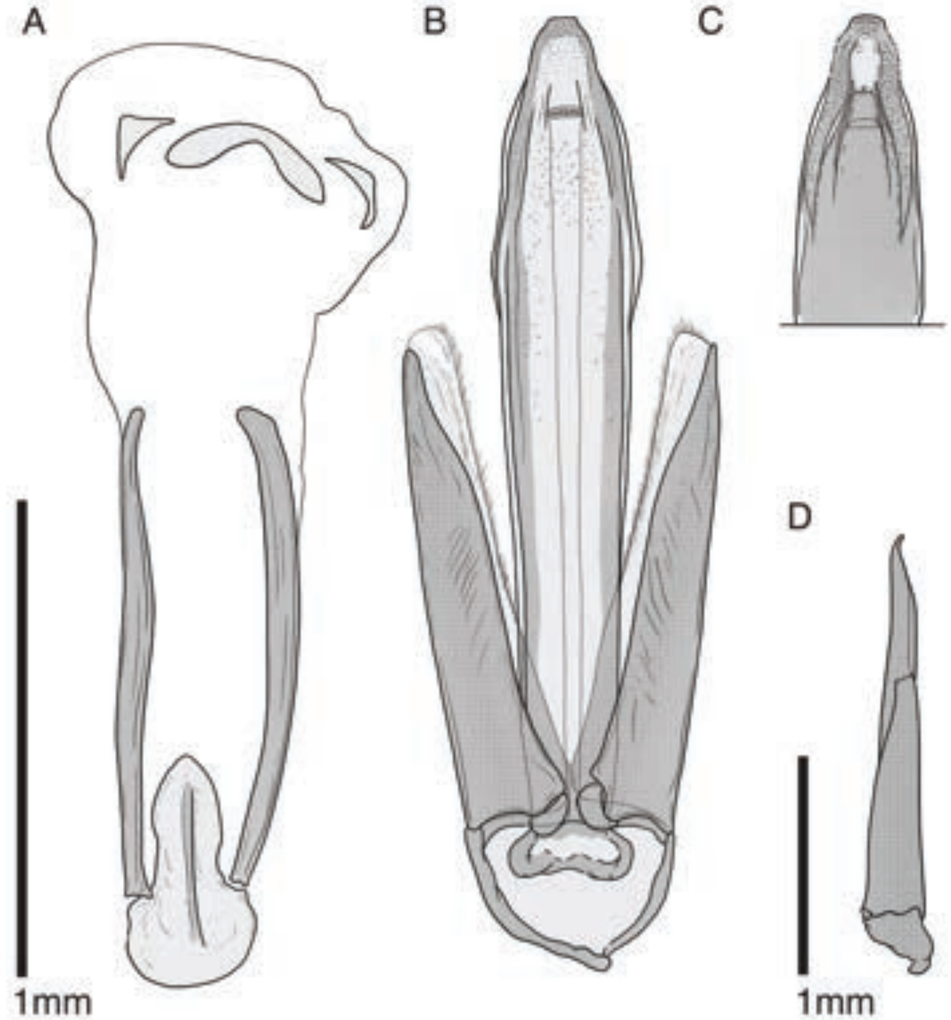

Figure 27. *Sphaeridium bipustulatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

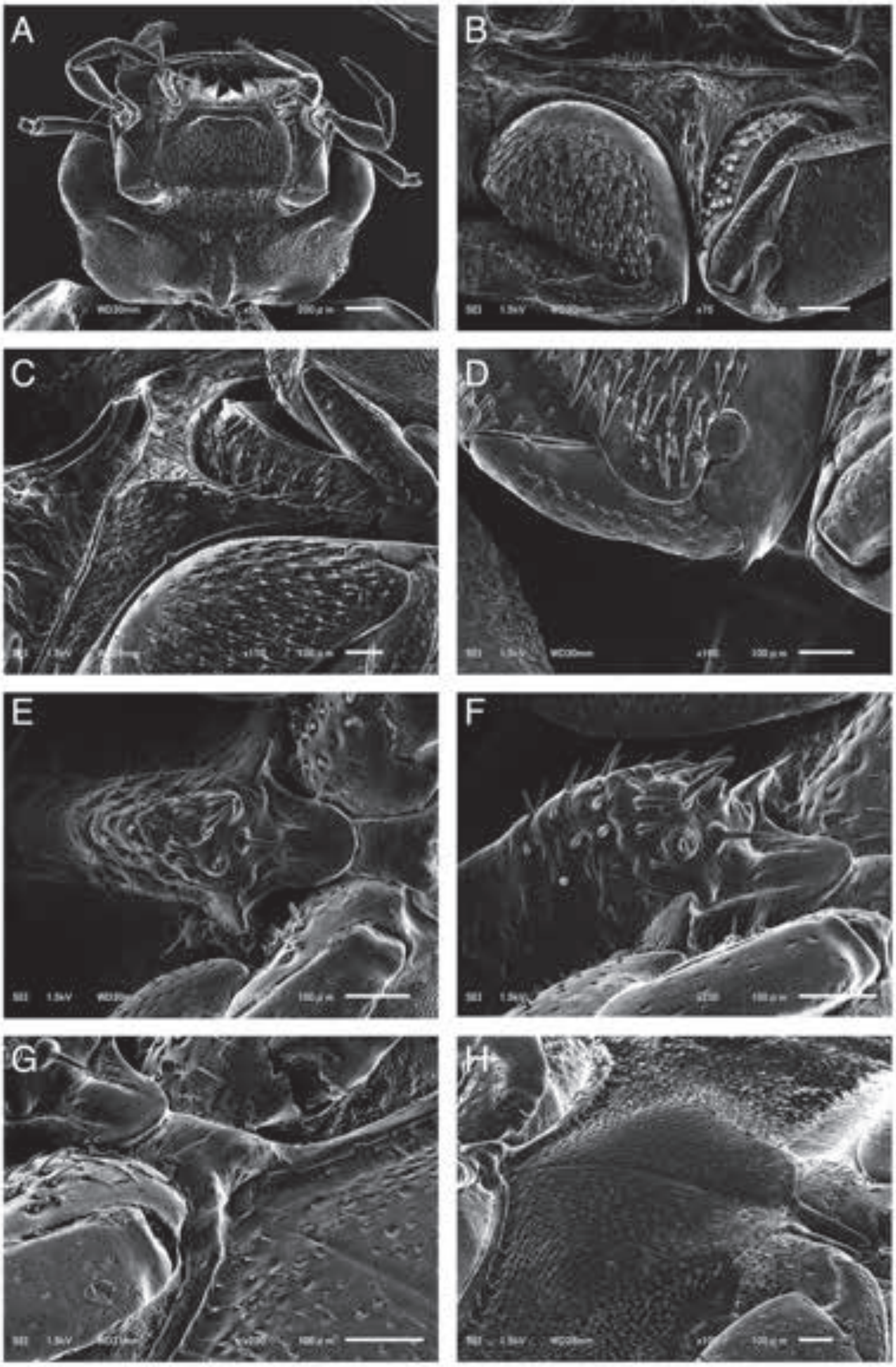

Figure 28. *Sphaeridium densepunctatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

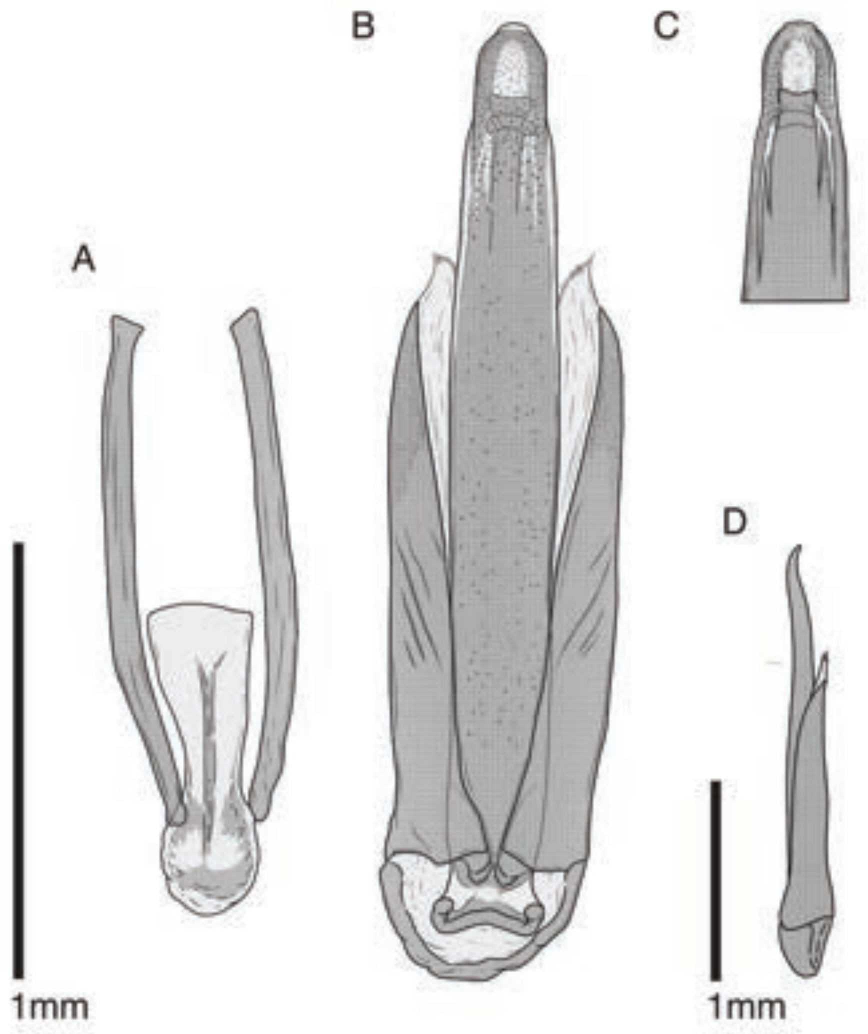

Figure 29. *Sphaeridium densepunctatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

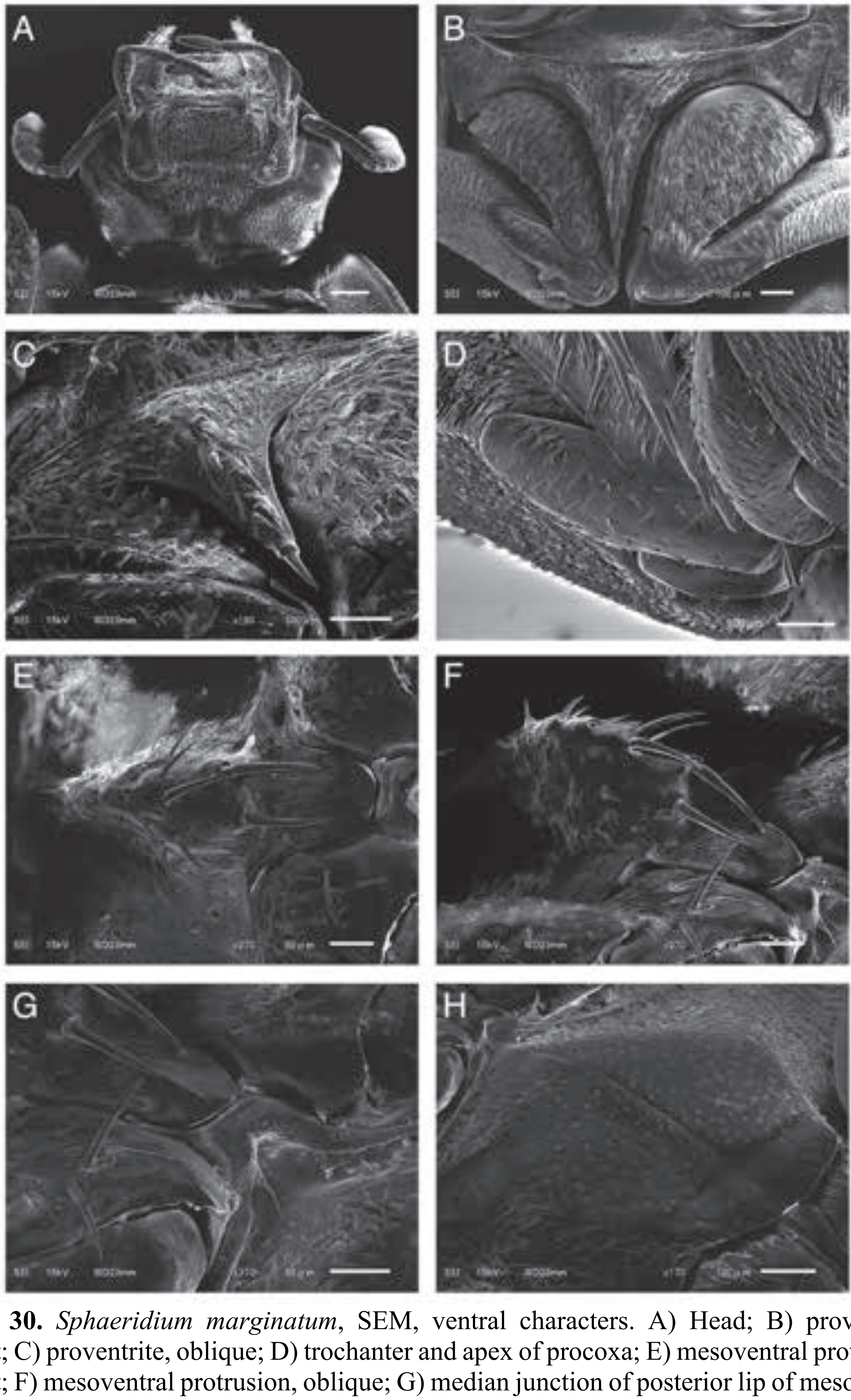

Figure 30. *Sphaeridium marginatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

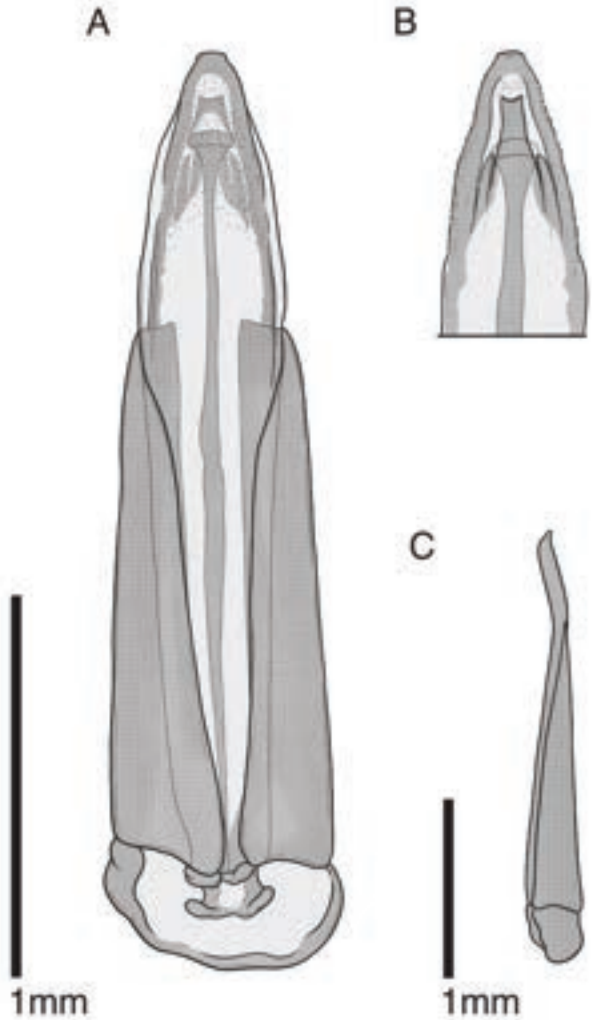

Figure 31. *Sphaeridium marginatum*, male genitalia. A) Tegmen, dorsal; B) apex of median lobe, ventral; C) lateral profile.

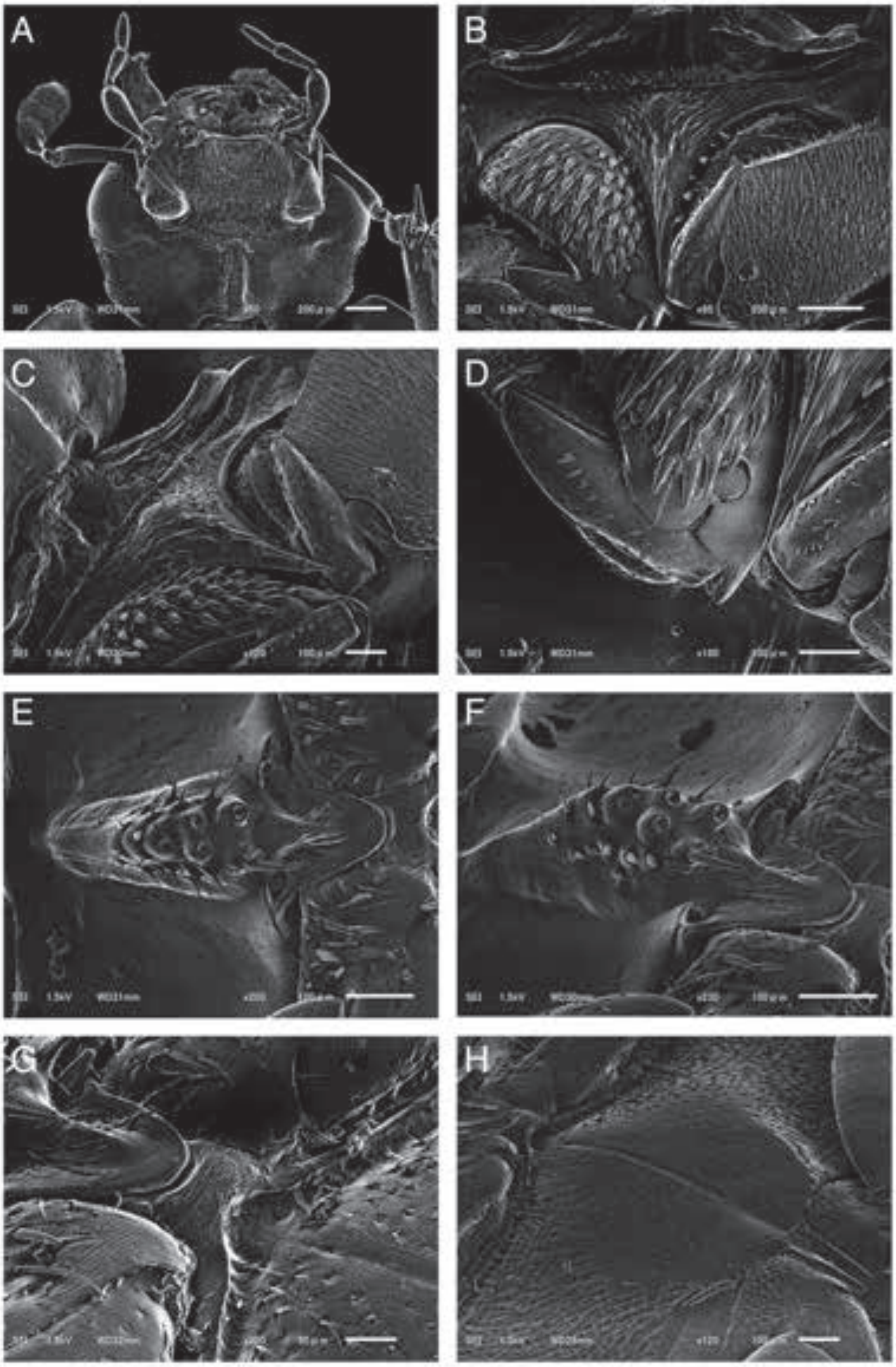

Figure 32. *Sphaeridium substriatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

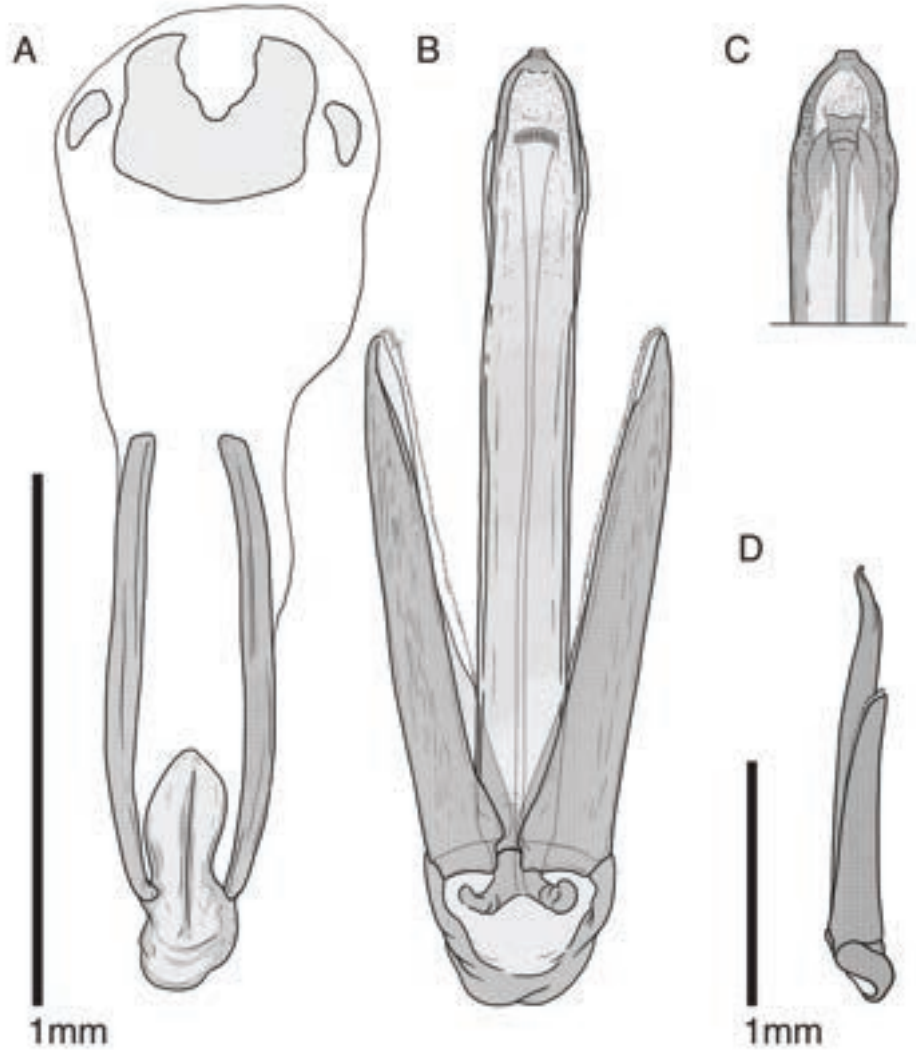

Figure 33. *Sphaeridium substriatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile. (32)

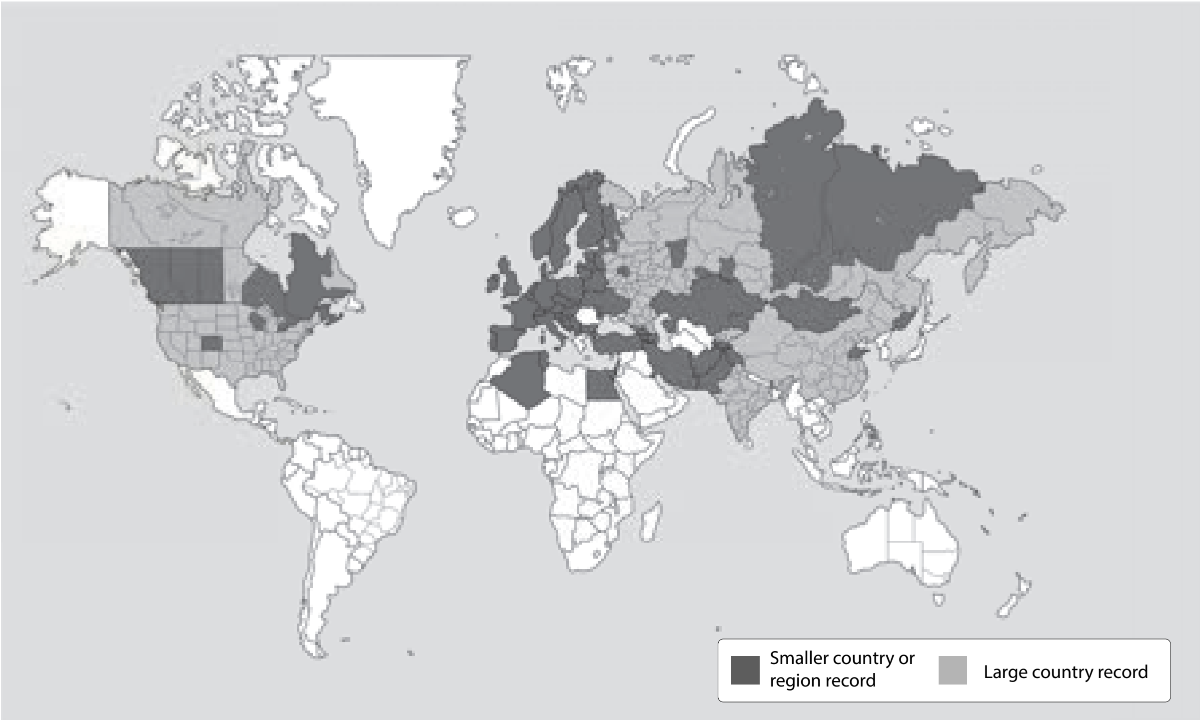

Figure 34. World distribution of *Sphaeridium bipustulatum*. Dark grey – region or smaller country record; Light grey – large country record.

Figure 35. World distribution of *Sphaeridium densepunctatum*. Dark grey – region or smaller country record; Light grey – large country record.

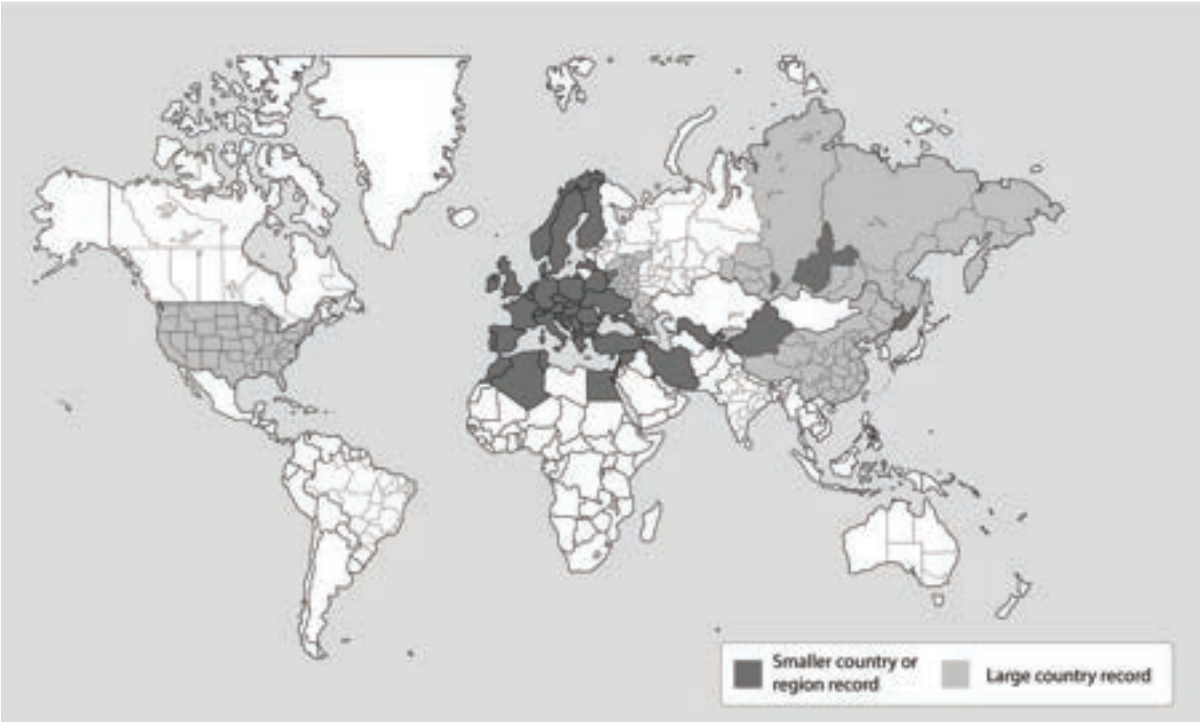

Figure 36. World distribution of *Sphaeridium marginatum.*

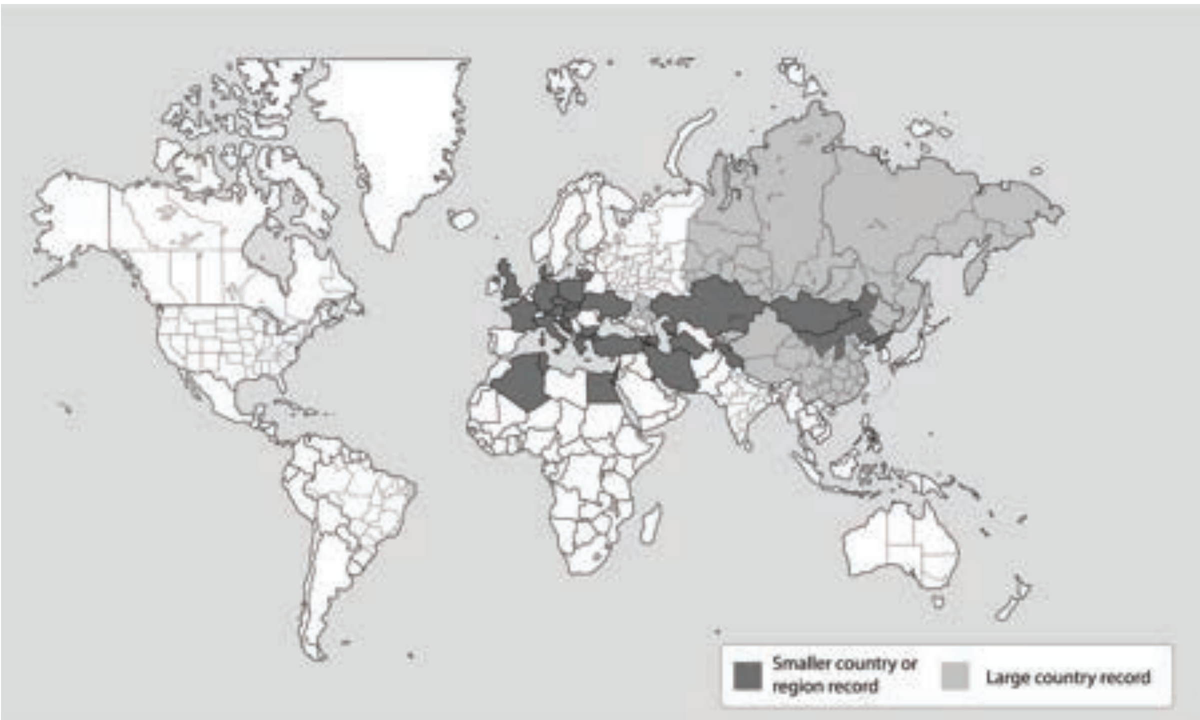

Figure 37. World distribution of *Sphaeridium substriatum*.

Figure 38. World distribution of *Sphaeridium daemonicum*.

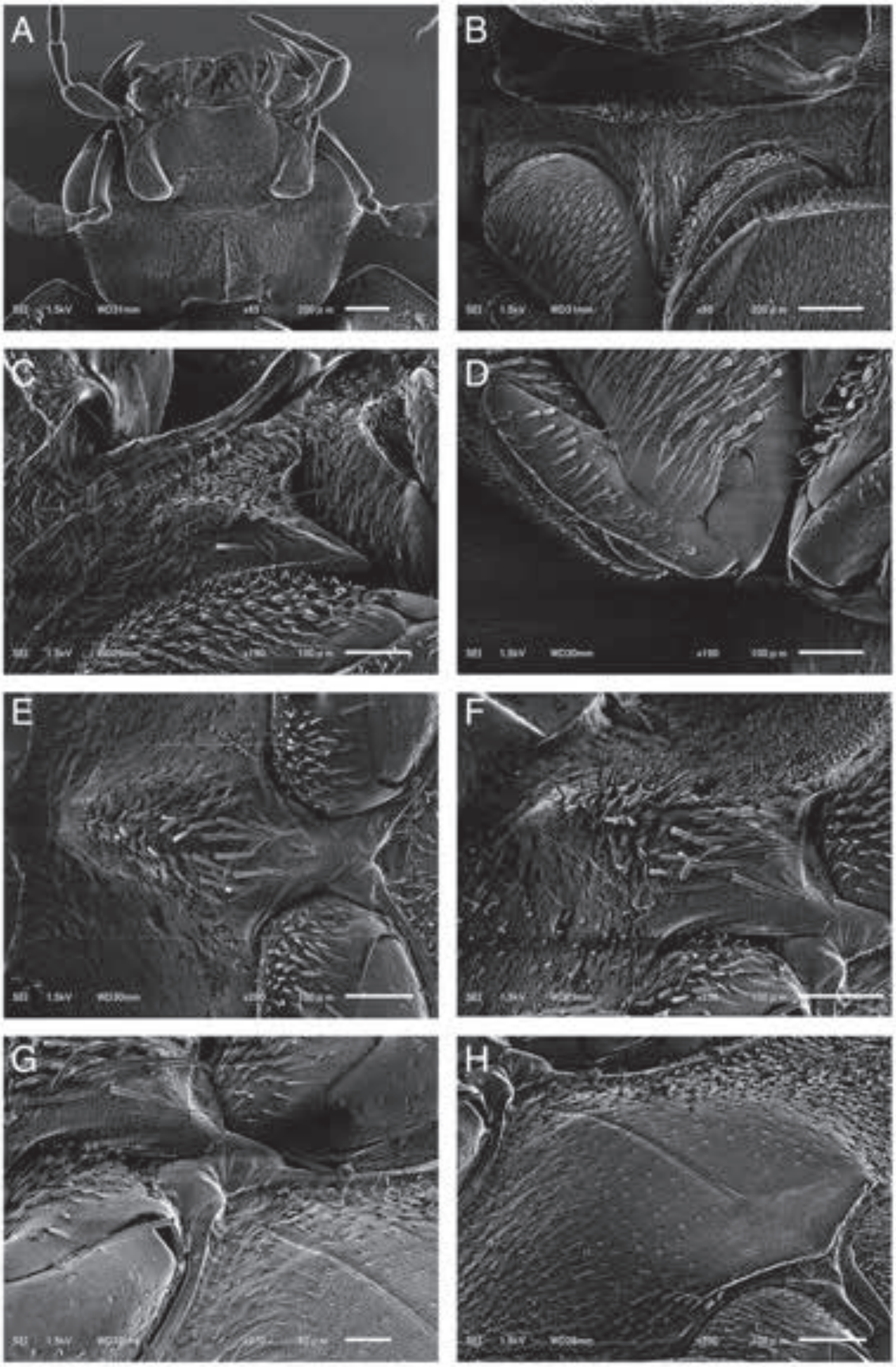

Figure 39. *Sphaeridium dimidiatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

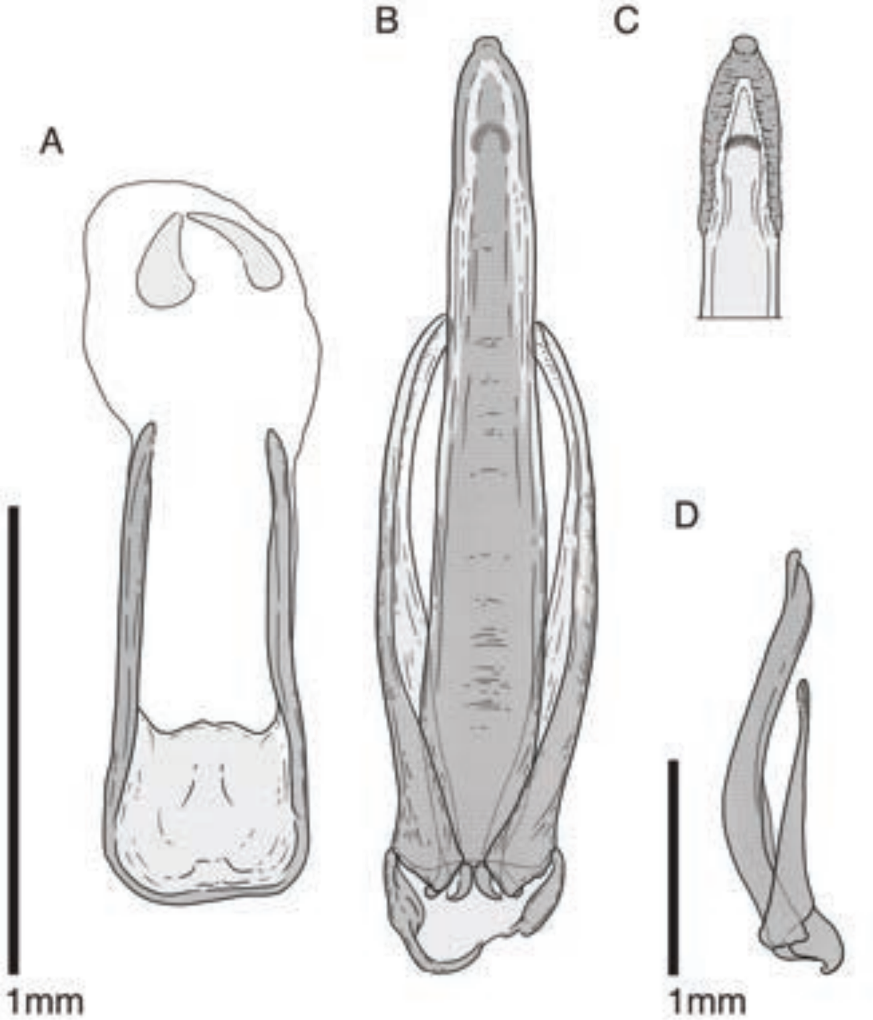

Figure 40. *Sphaeridium dimidiatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

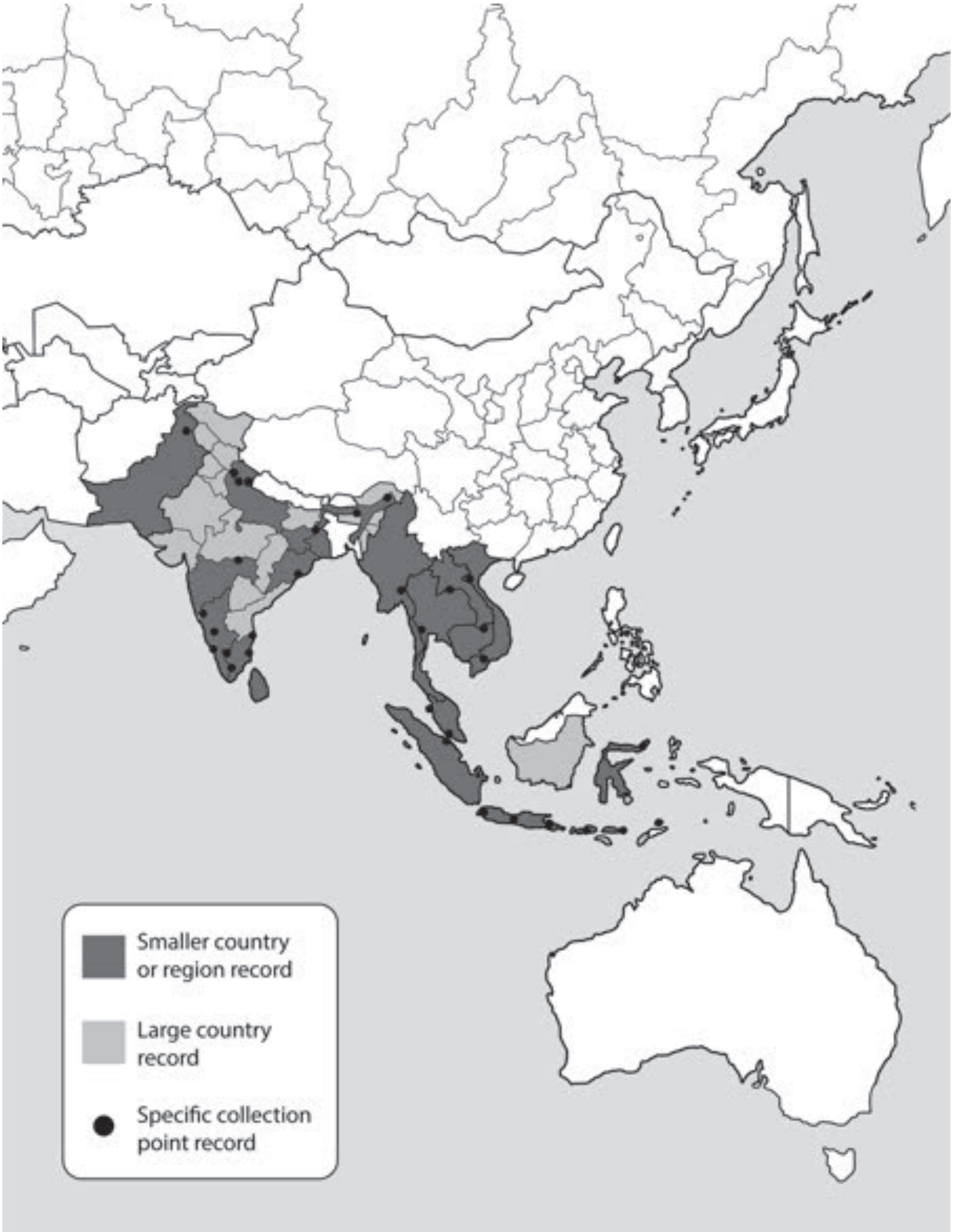

Figure 41. World distribution of *Sphaeridium dimidiatum*.

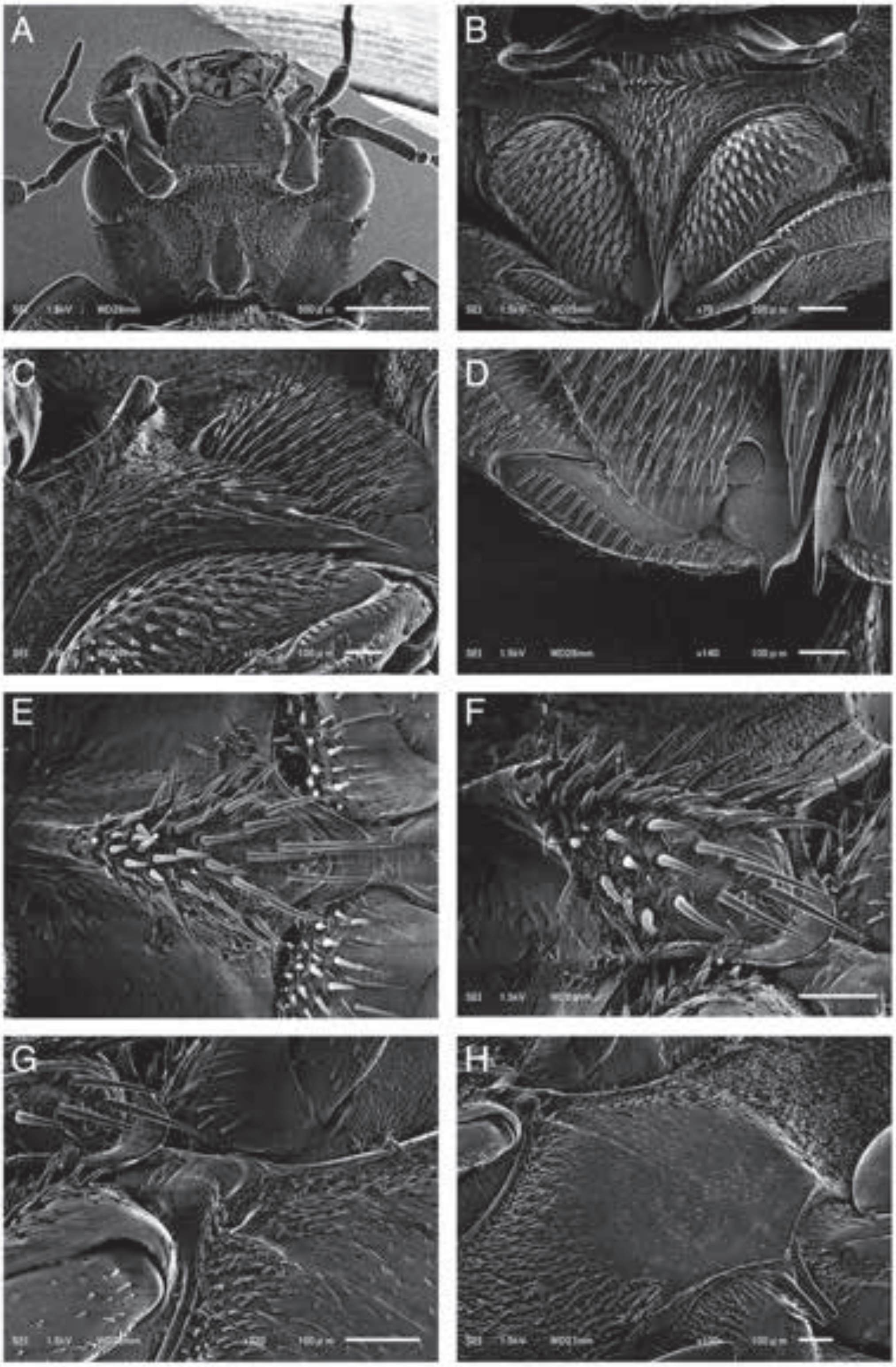

Figure 42. *Sphaeridium discolor*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

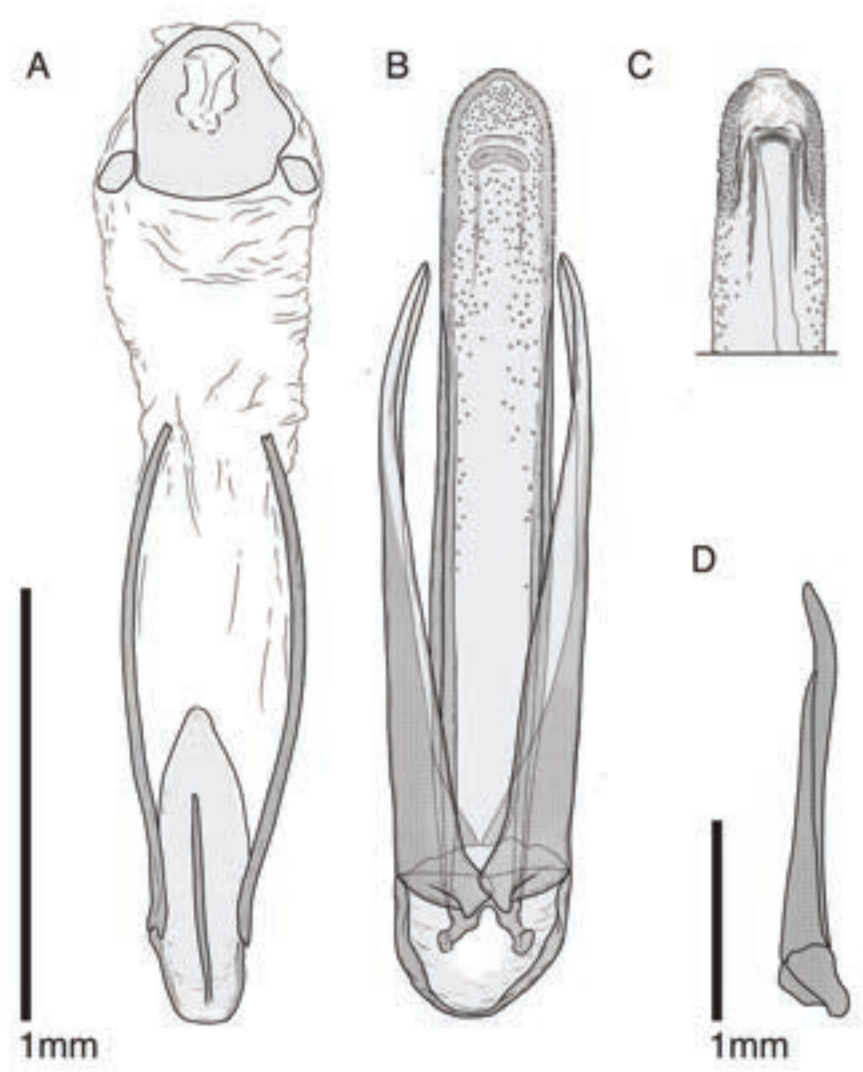

Figure 43. *Sphaeridium discolor*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

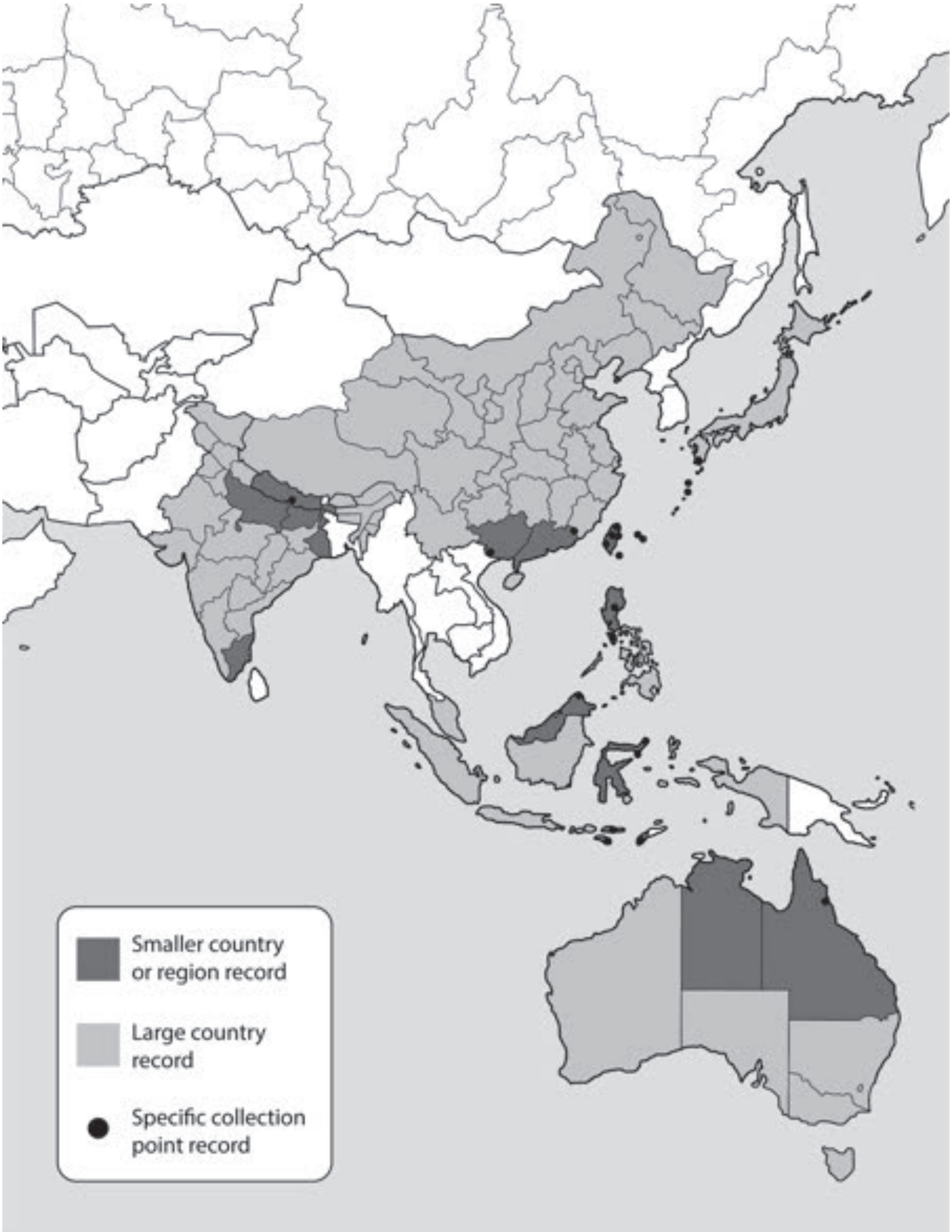

Figure 44. World distribution of *Sphaeridium discolor*.

Figure 45. World distribution of *Sphaeridium flavomaculatum*.

Figure 46. *Sphaeridium kolleri*, paratype, habitus. A–B) Female; A) Dorsal; B) Lateral; C) Male, dorsal, dissected with male genitalia. Photos by Arno van Berge Henegowen.

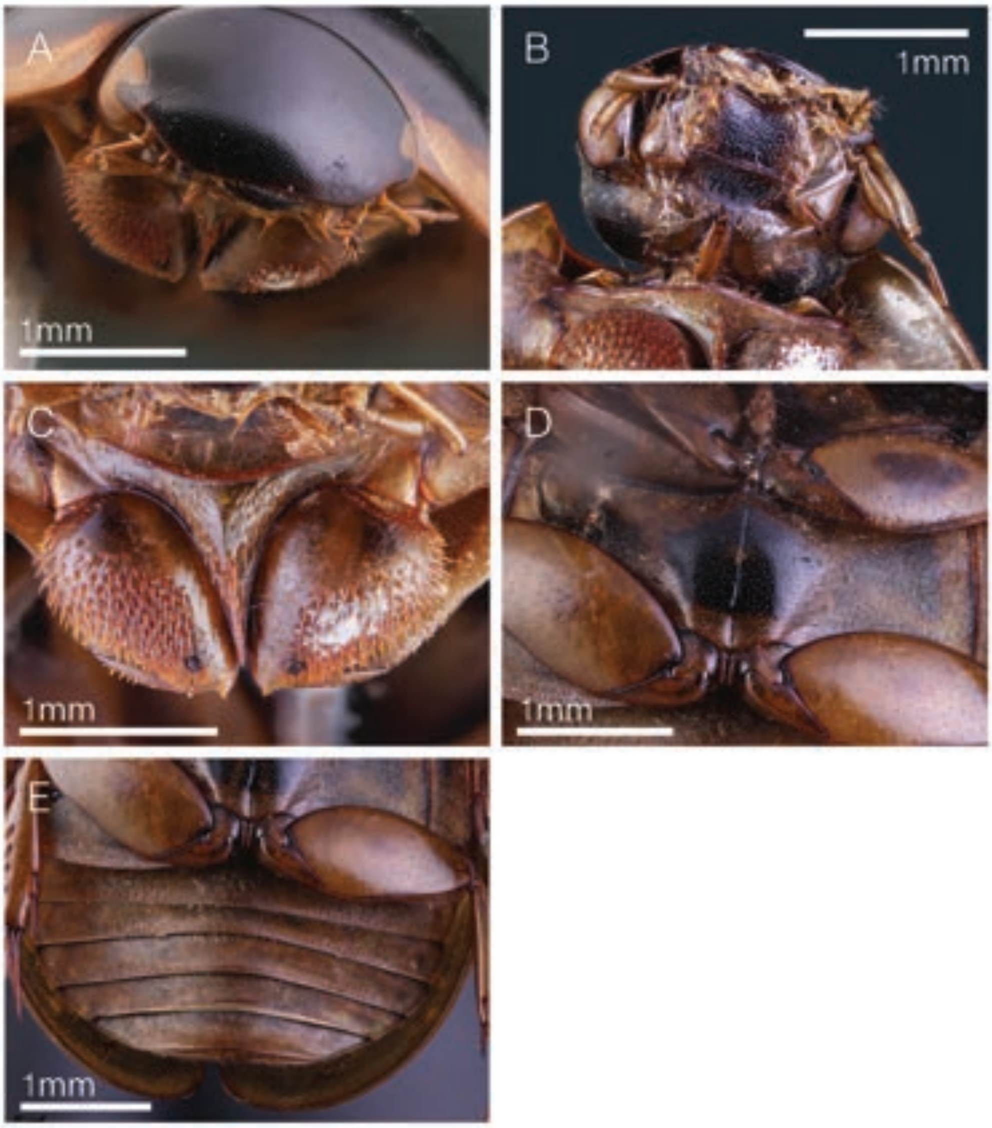

Figure 47. *Sphaeridium kolleri*, paratype, details. A) Head, anterodorsal; B) head and proventrite, ventral; C) proventrite and procoxae, anteroventral; D) metaventrite, ventral; E) abdomen, ventral. Photos by Arno van Berge Henegowen.

Figure 48. World distribution of *Sphaeridium kolleri*.

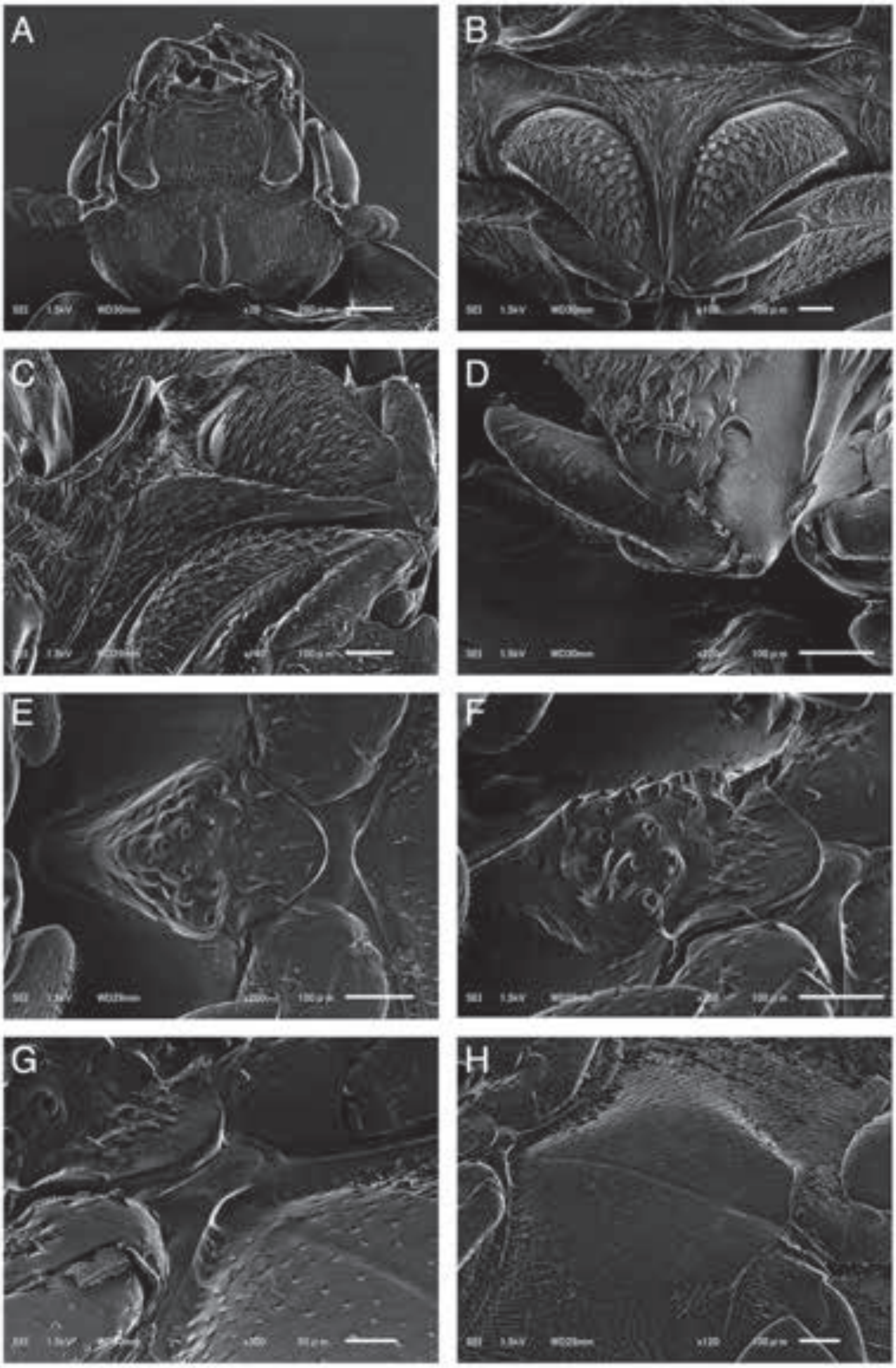

Figure 49. *Sphaeridium* sp.2, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

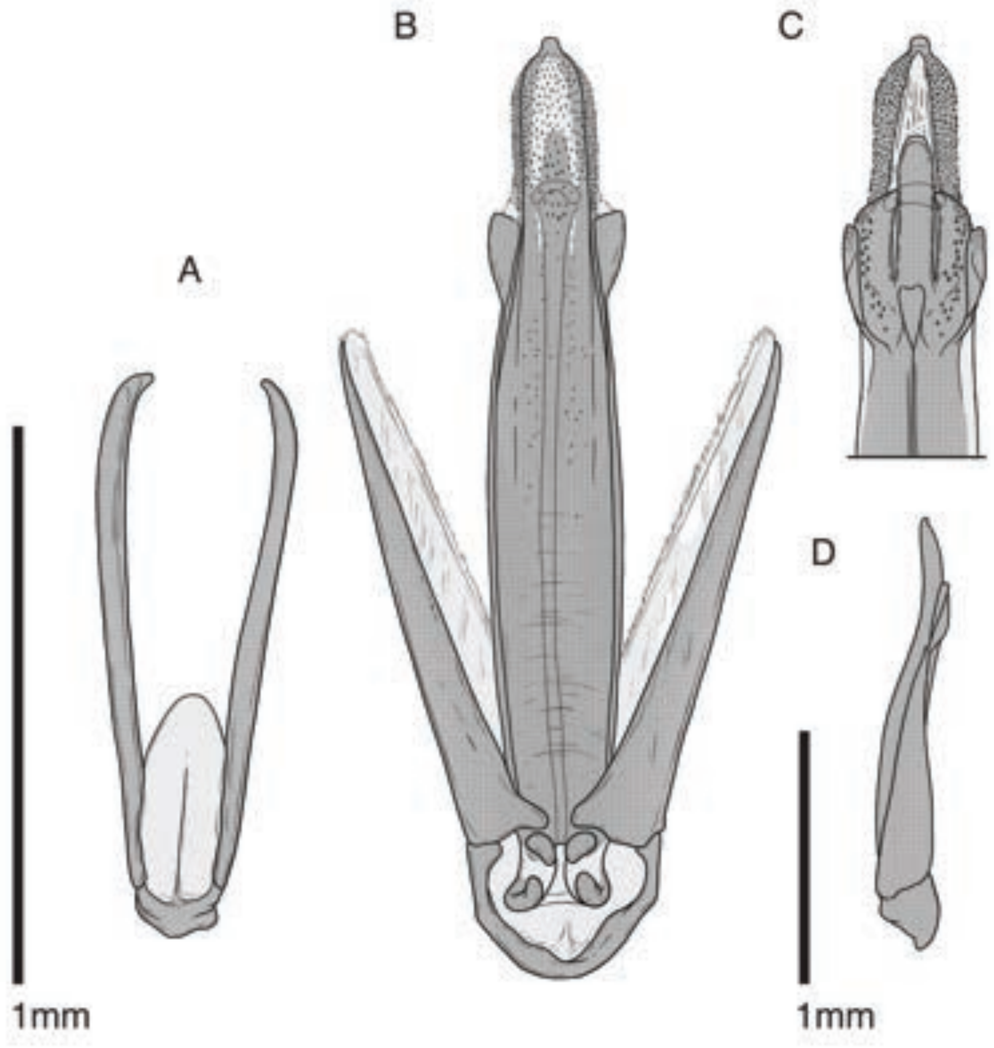

Figure 50. *Sphaeridium* sp.2, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

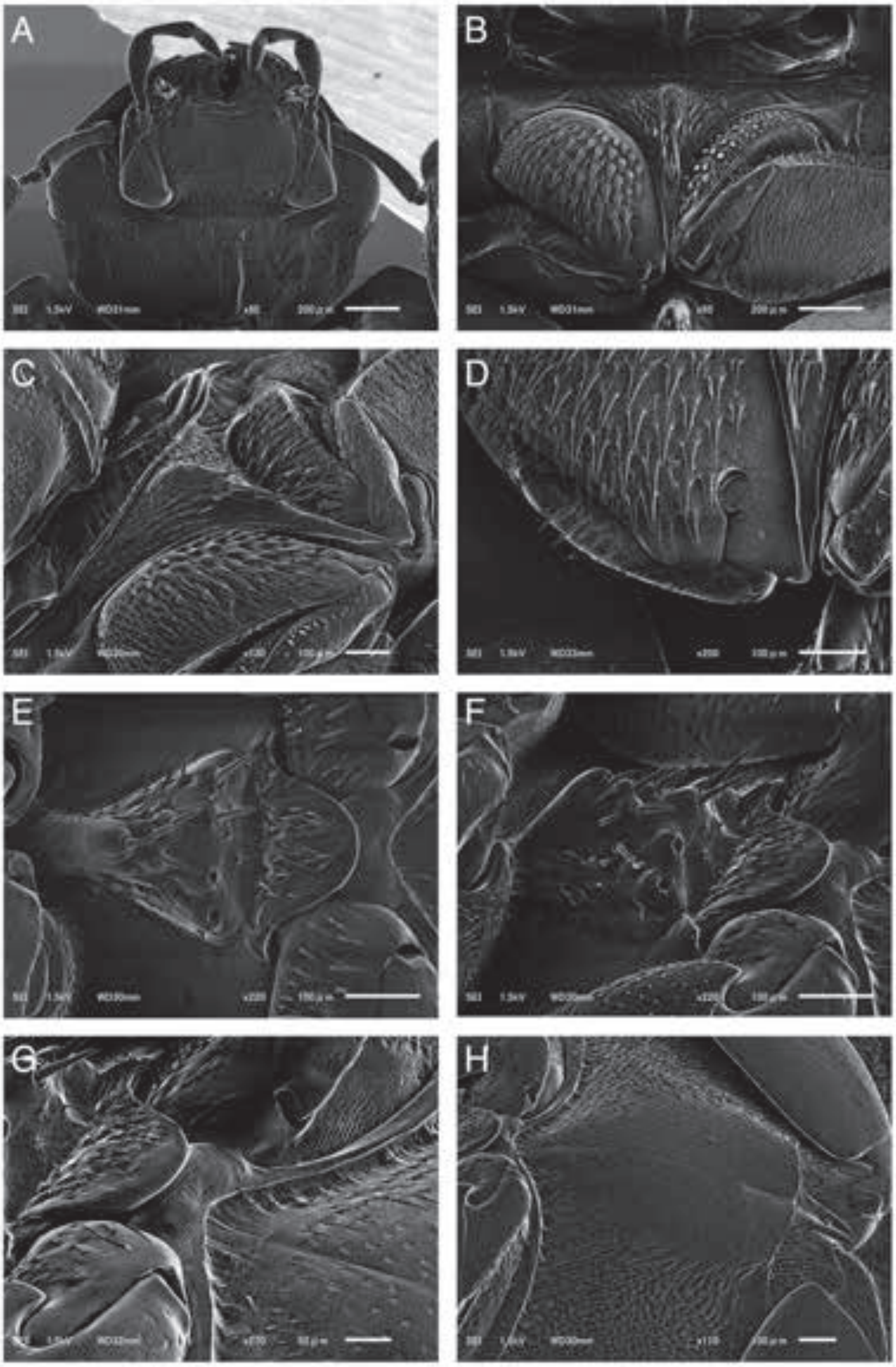

Figure 51. *Sphaeridium quinquemaculatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

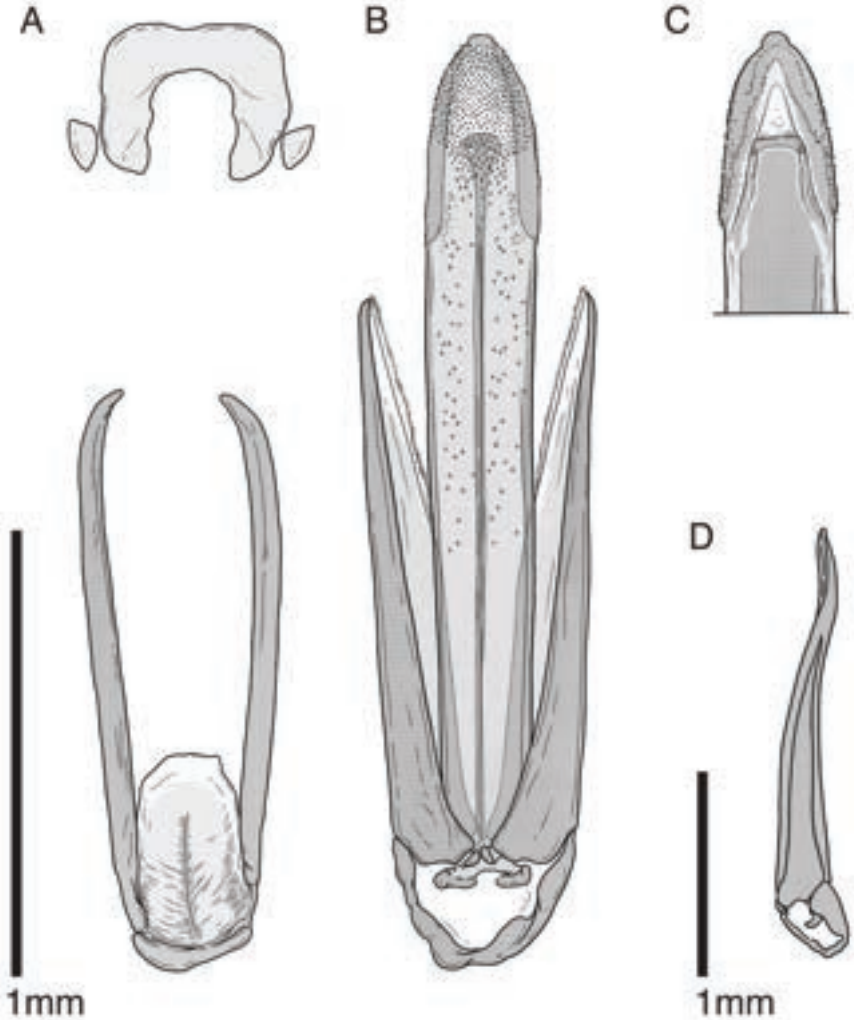

Figure 52. *Sphaeridium quinquemaculatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

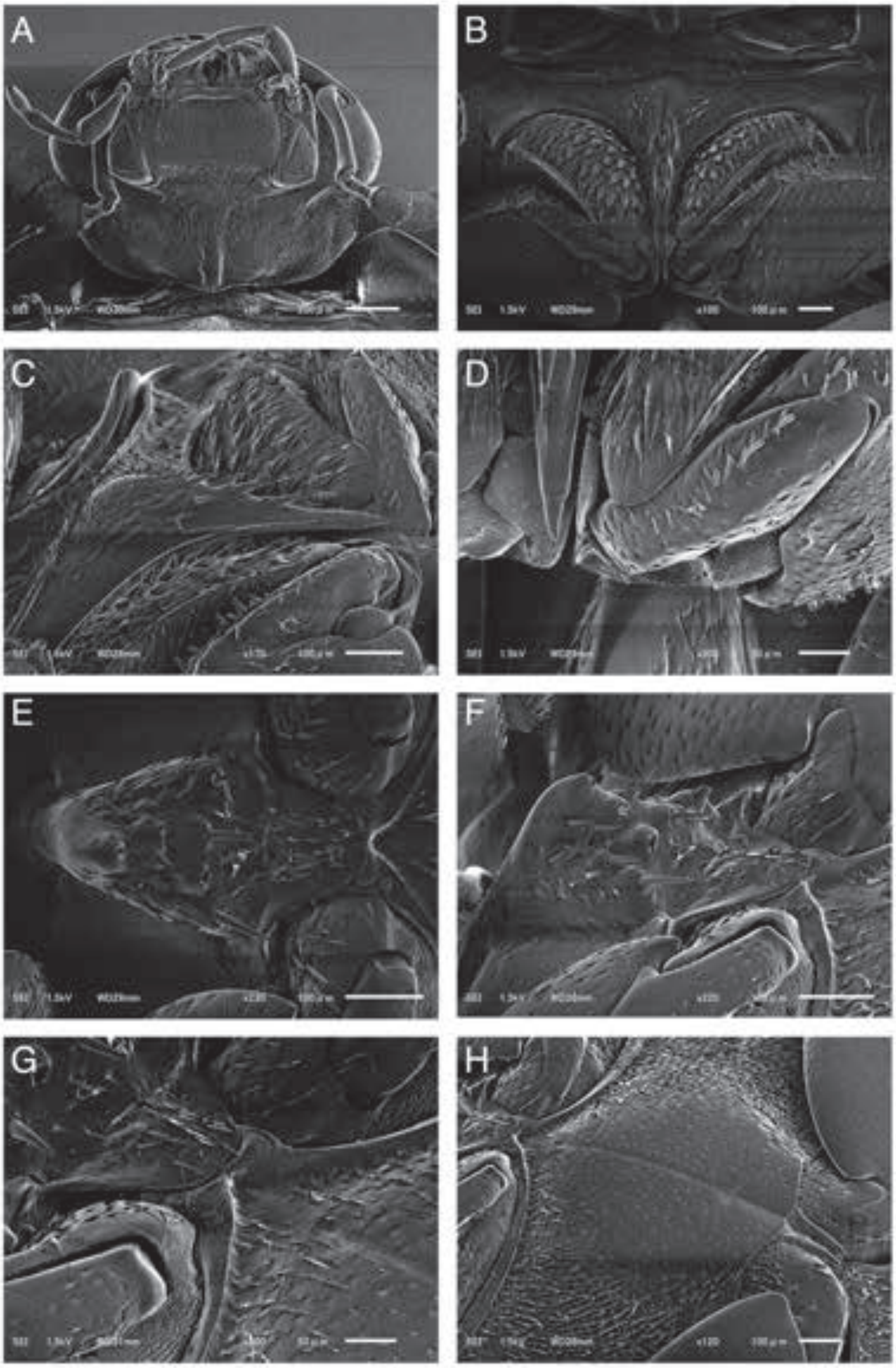

Figure 53. *Sphaeridium* sp.1, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

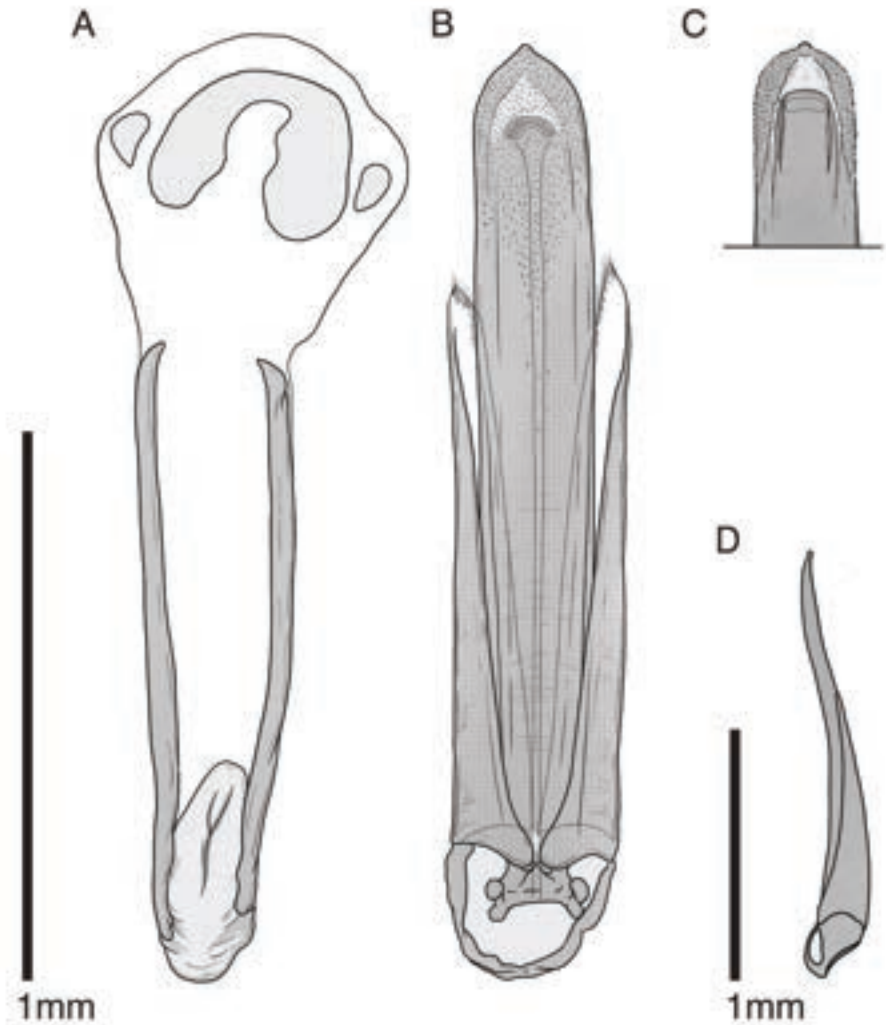

Figure 54. *Sphaeridium* sp.1, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

Figure 55. World distribution of *Sphaeridium* sp.2.

Figure 56. World distribution of *Sphaeridium quinquemaculatum*.

Figure 57. World distribution of *Sphaeridium* sp.1.

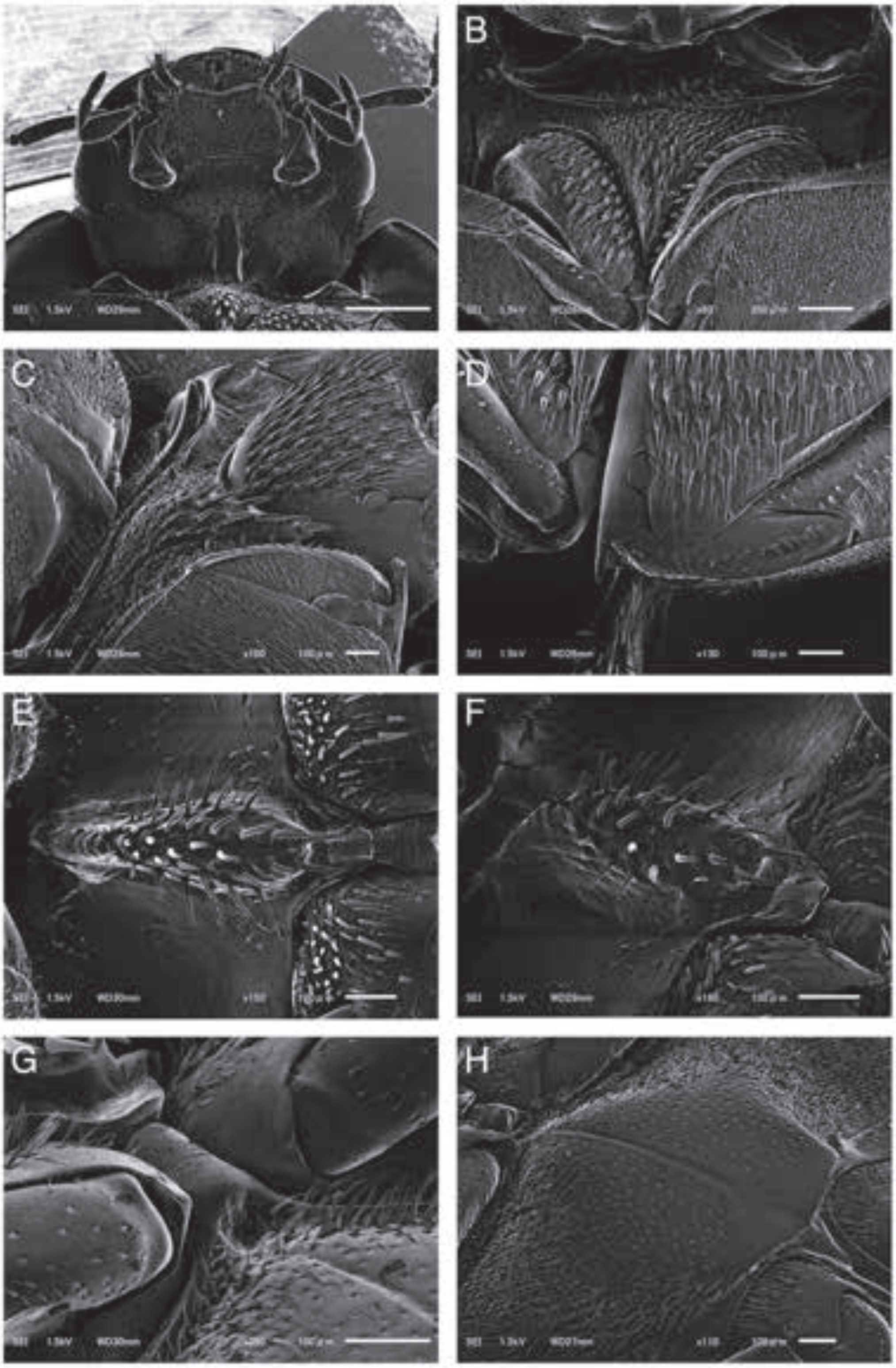

Figure 58. *Sphaeridium lunatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

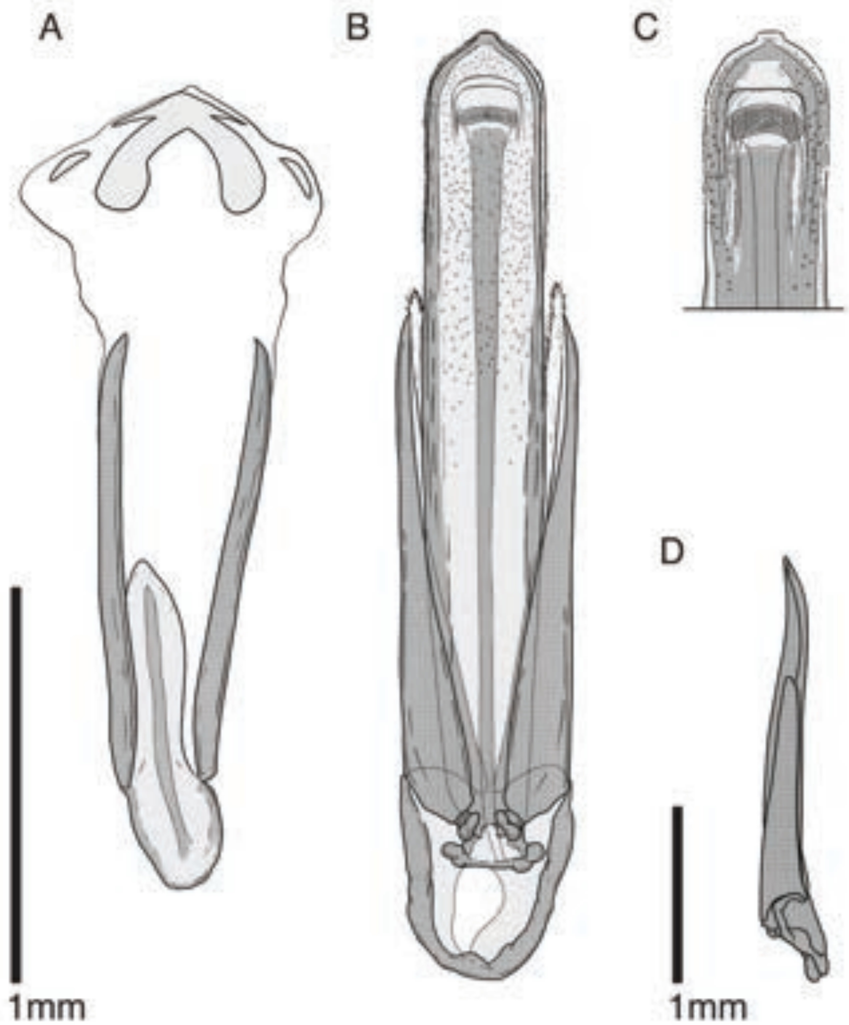

Figure 59. *Sphaeridium lunatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

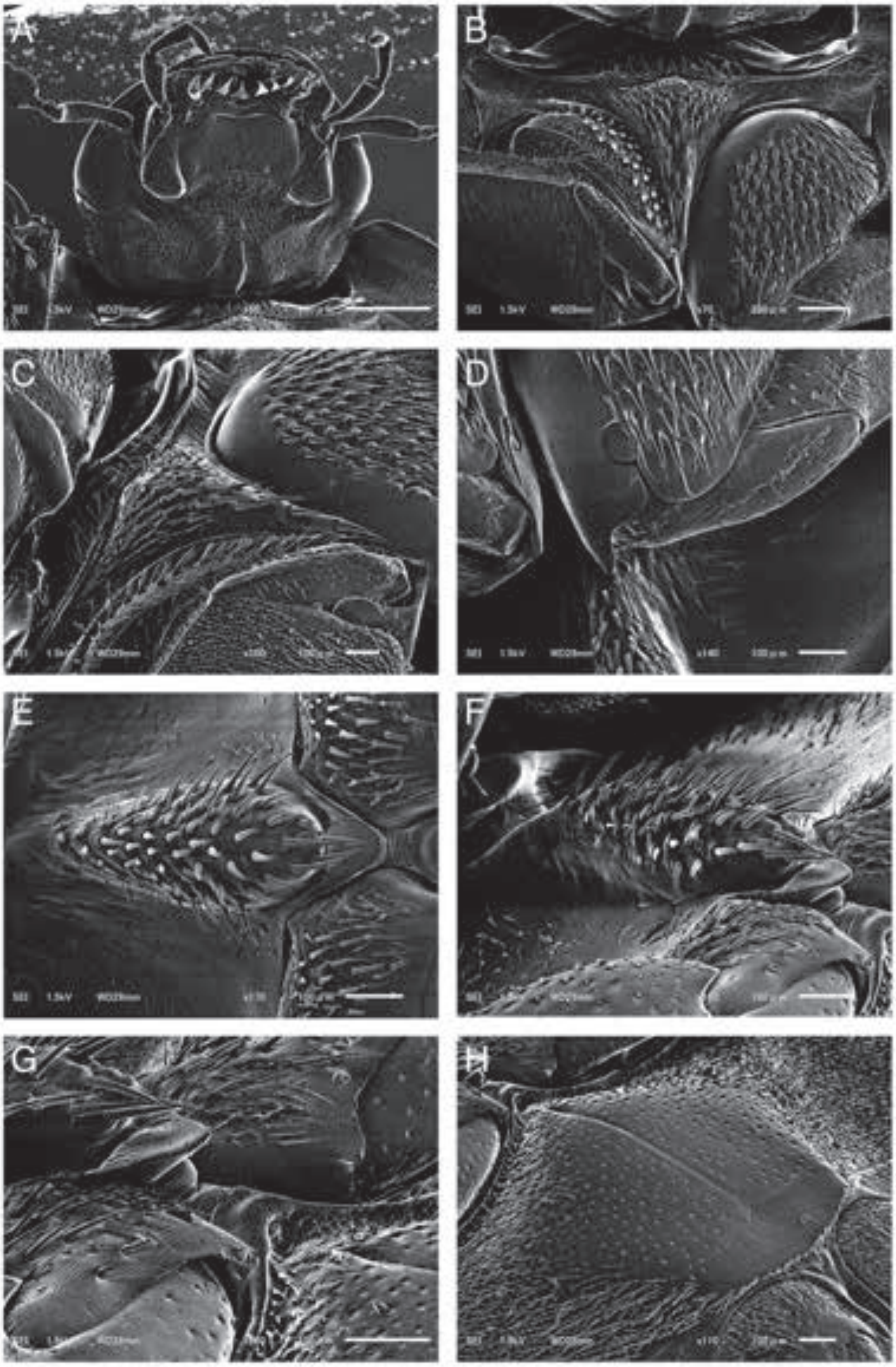

Figure 60. *Sphaeridium scarabaeoides*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

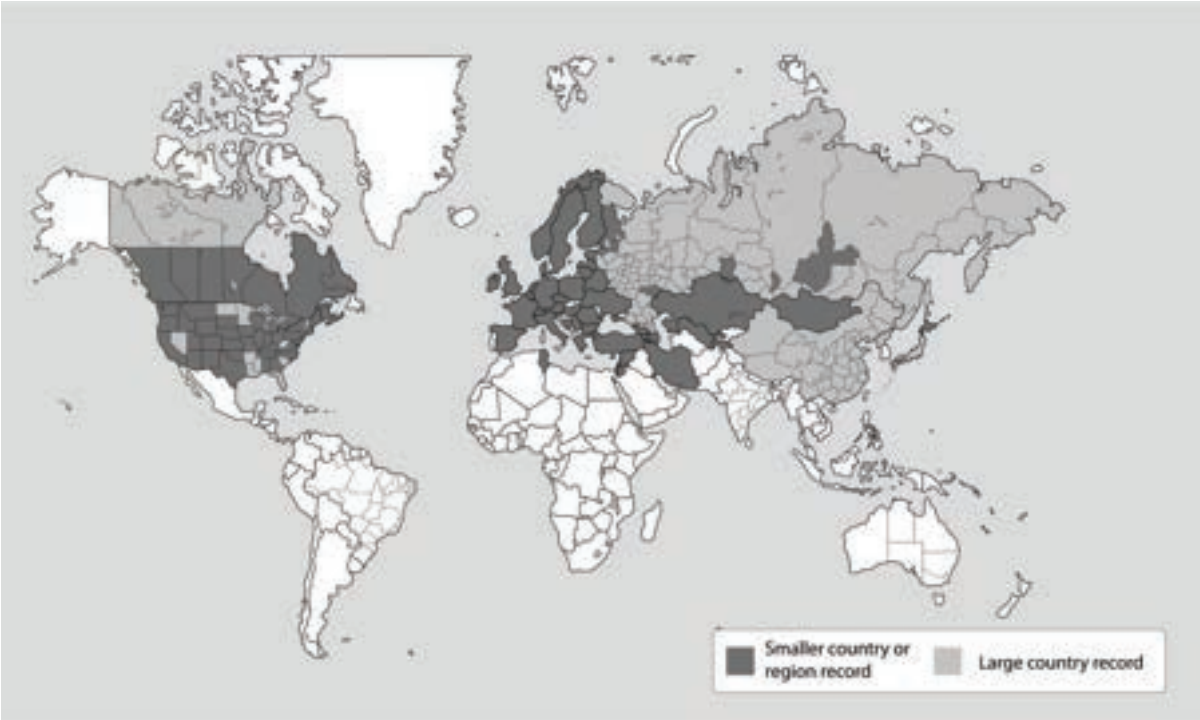

Figure 61. World distribution of *Sphaeridium lunatum*.

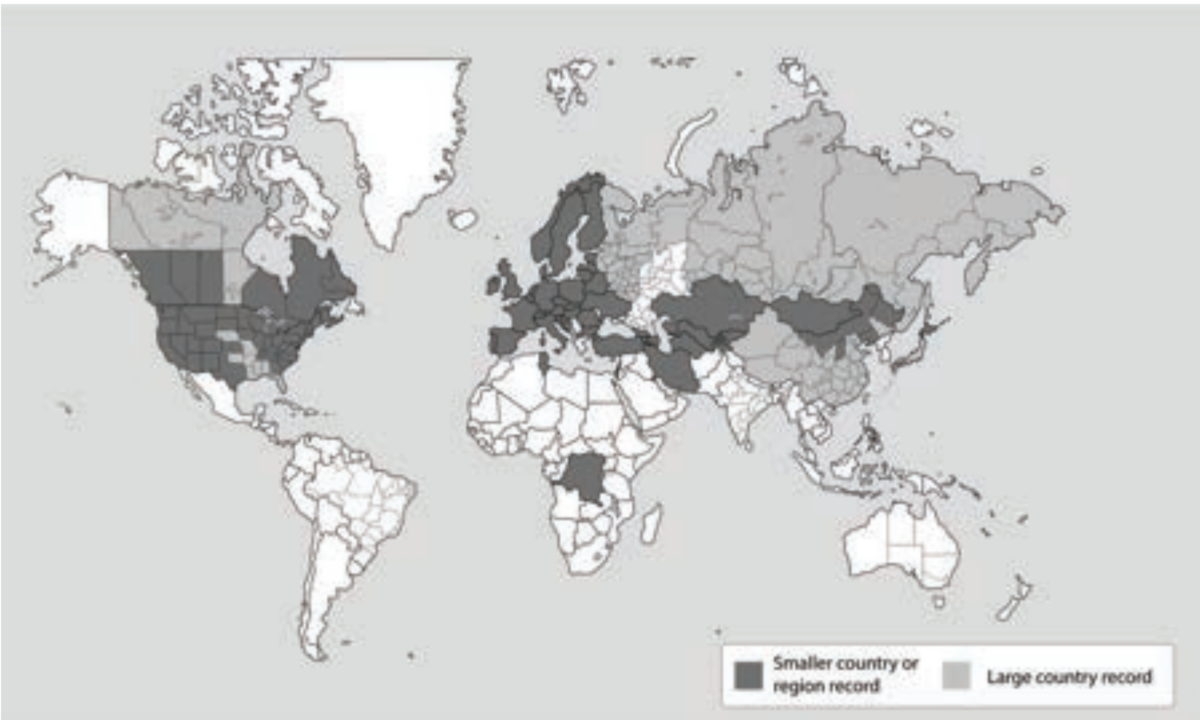

Figure 62. World distribution of *Sphaeridium scarabaeoides*.

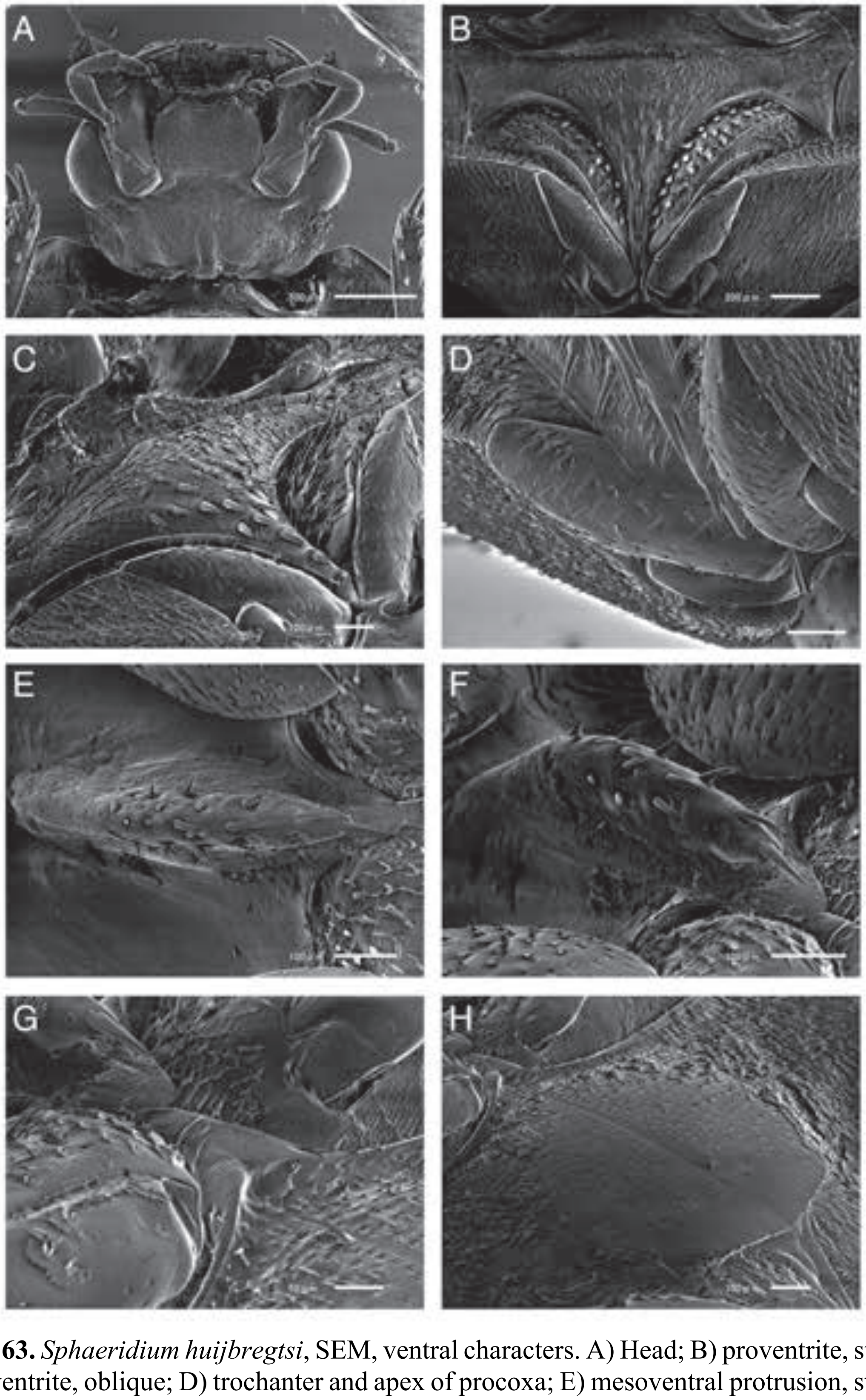

Figure 63. *Sphaeridium huijbregtsi*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

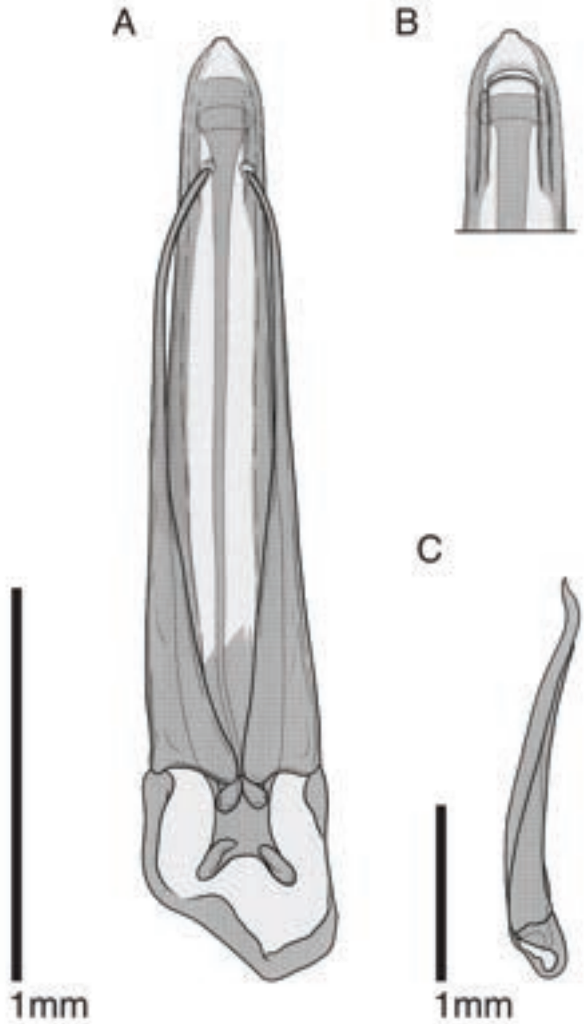

Figure 64. *Sphaeridium huijbregtsi*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

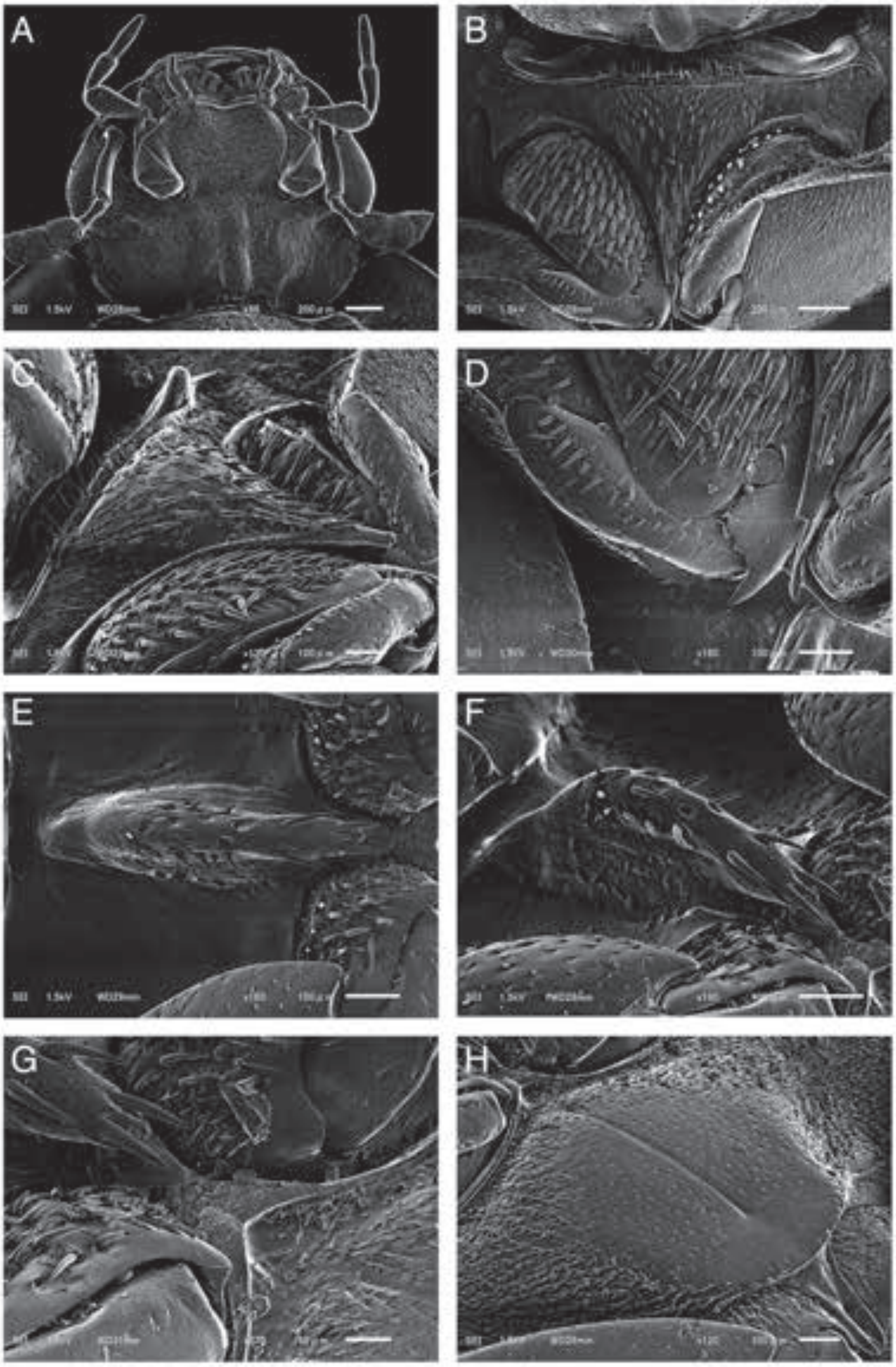

Figure 65. *Sphaeridium seriatum*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

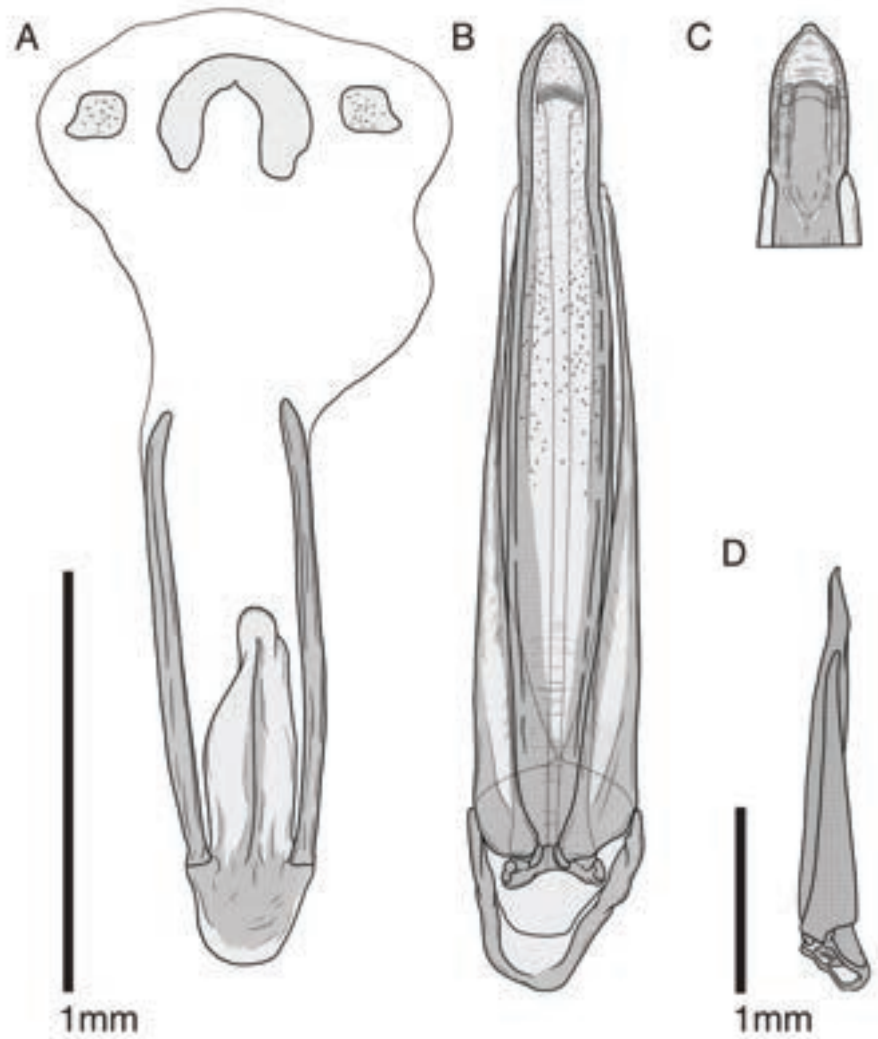

Figure 66. *Sphaeridium seriatum*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

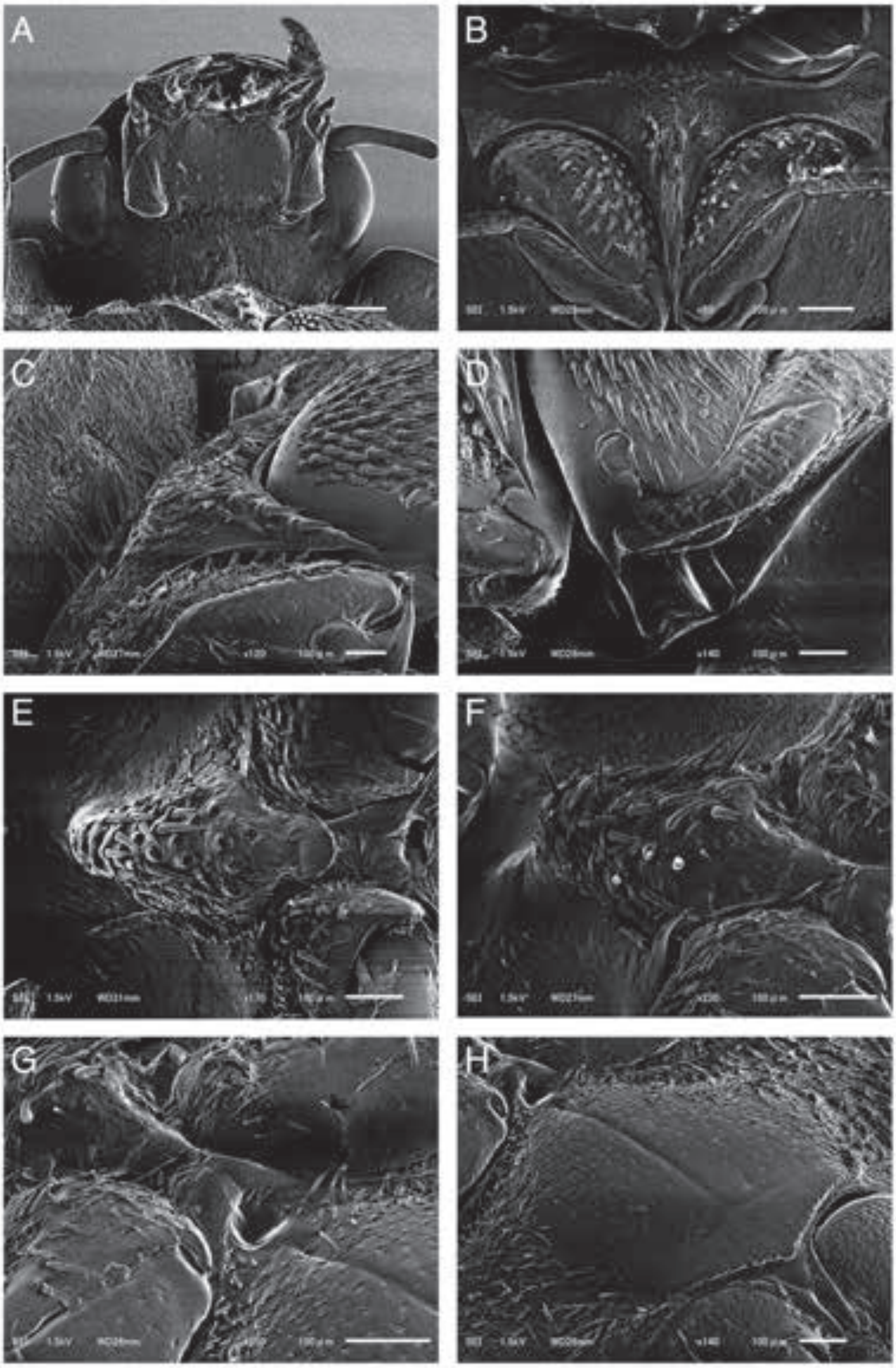

Figure 67. *Sphaeridium severini*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

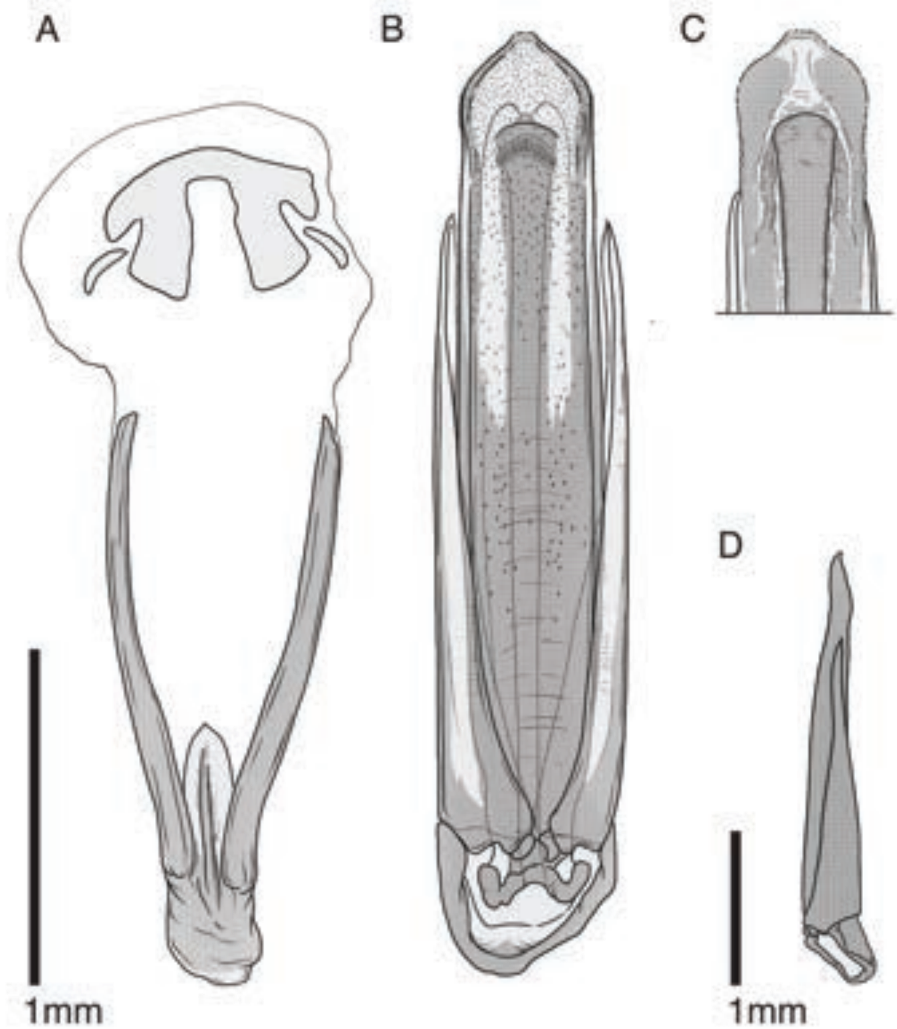

Figure 68. *Sphaeridium severini*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

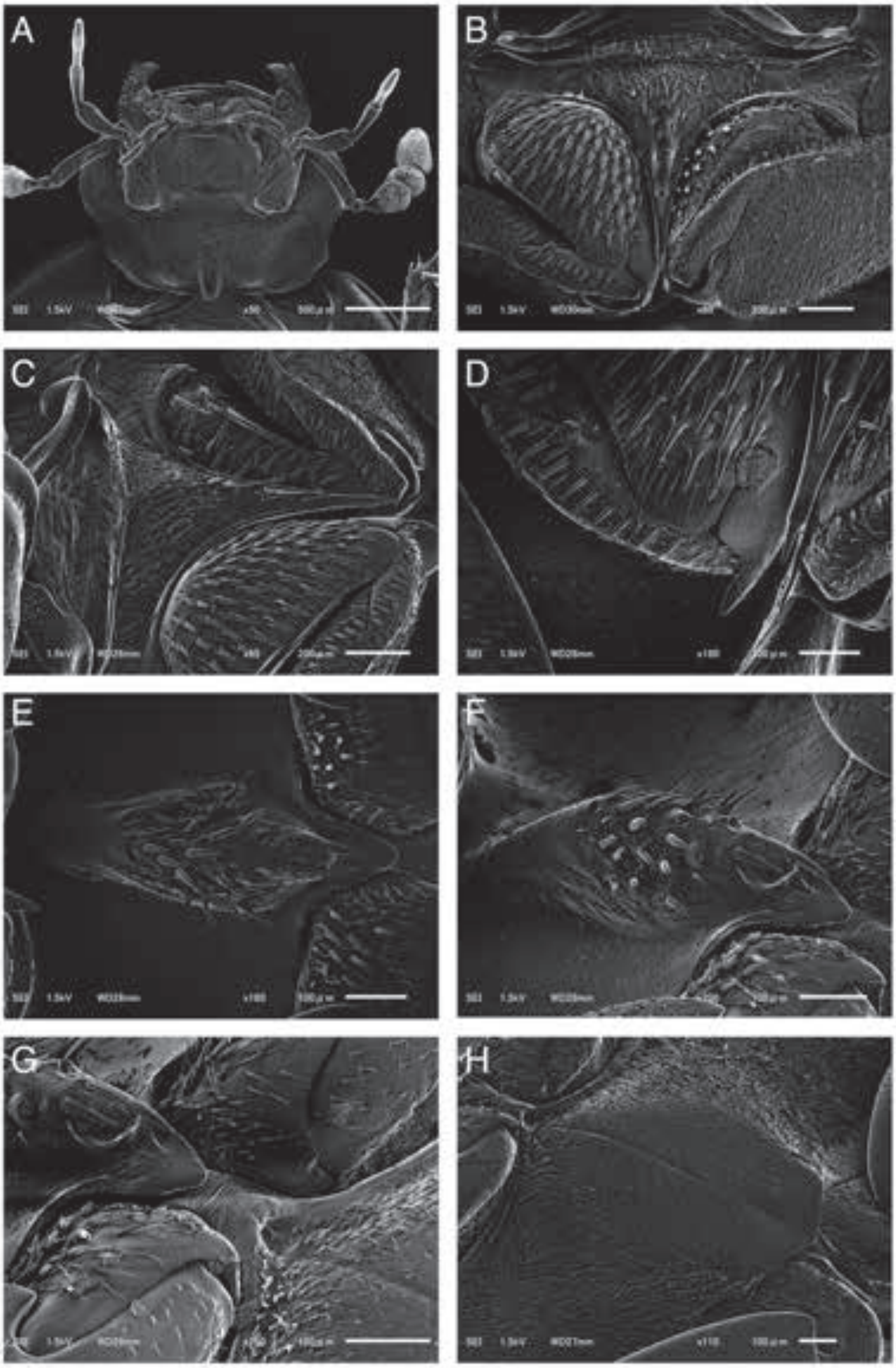

Figure 69. *Sphaeridium vitalisi*, SEM, ventral characters. A) Head; B) proventrite, straight; C) proventrite, oblique; D) trochanter and apex of procoxa; E) mesoventral protrusion, straight; F) mesoventral protrusion, oblique; G) median junction of posterior lip of mesoventral protrusion and anterior apex of metaventrite; H) metaventral disc.

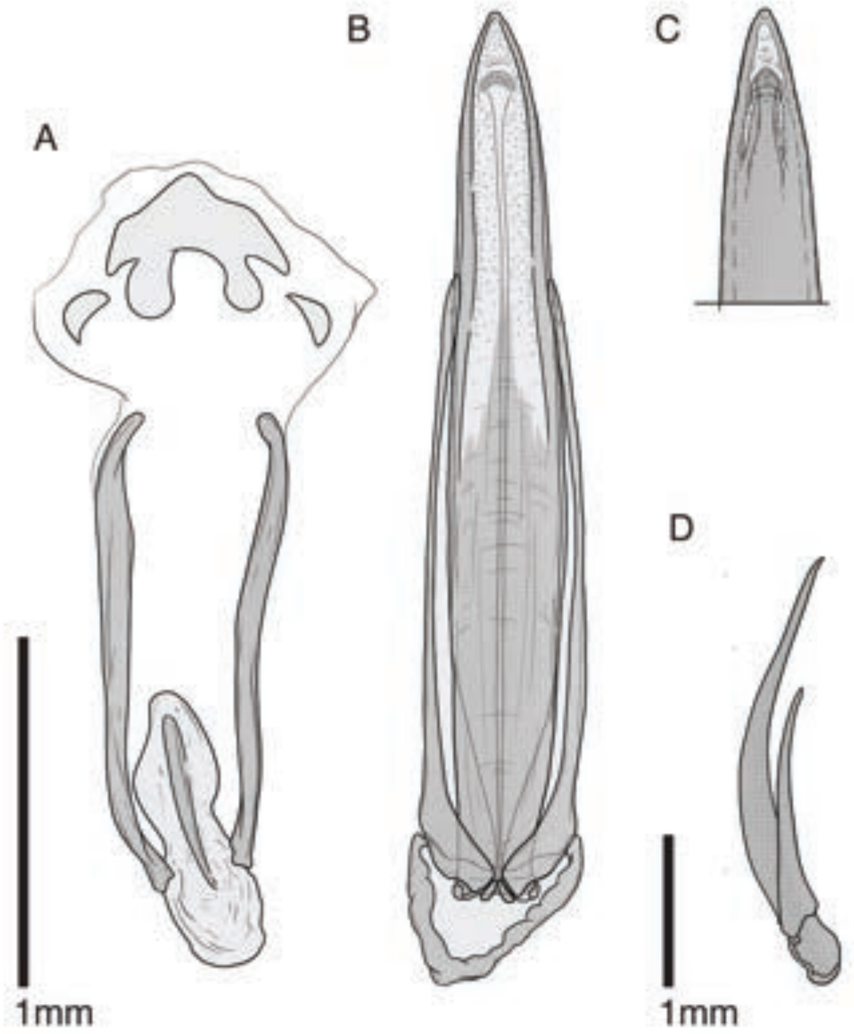

Figure 70. *Sphaeridium vitalisi*, male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

Figure 71. World distribution of *Sphaeridium huijbregtsi*.

Figure 72. World distribution of *Sphaeridium seriatum*.

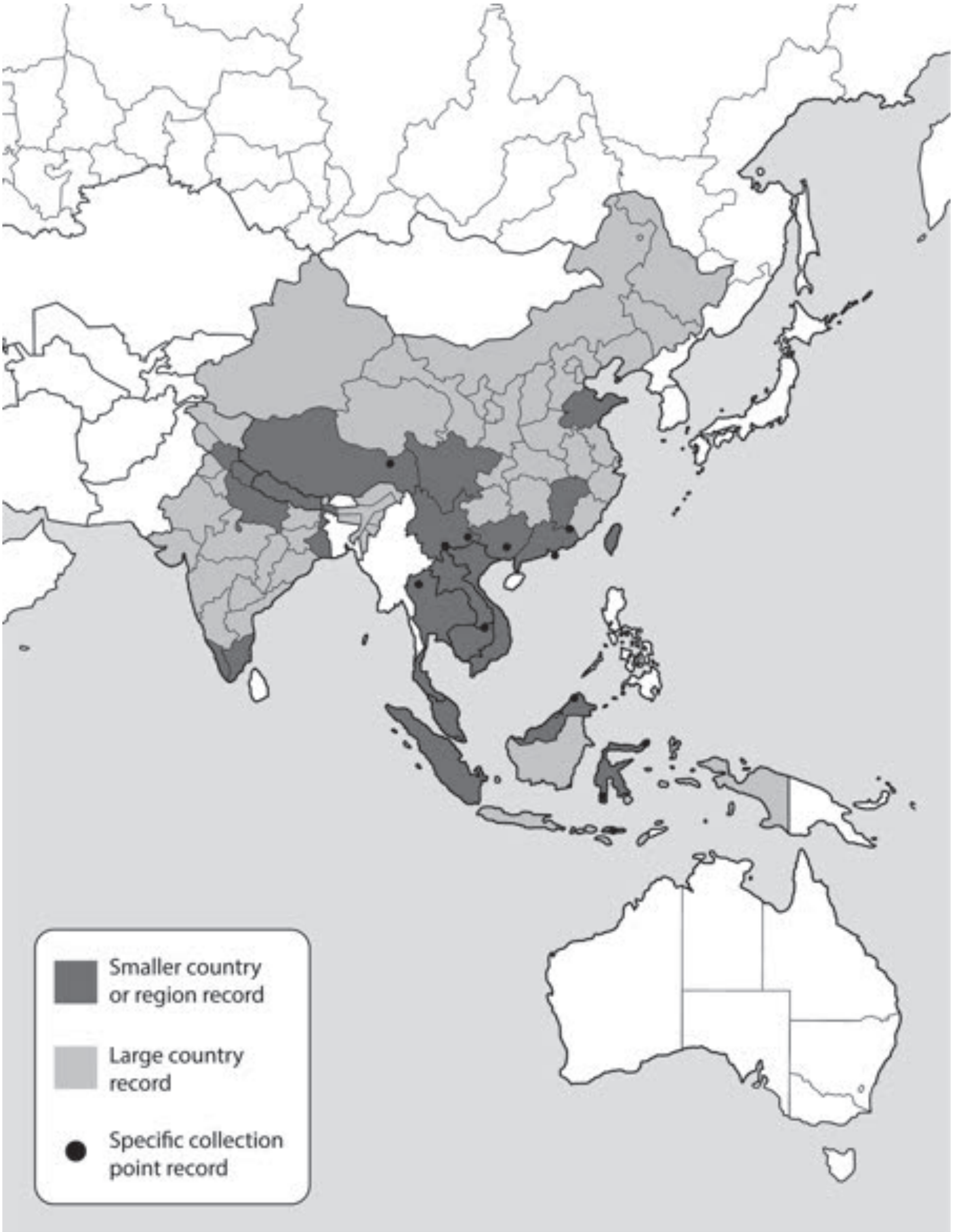

Figure 73. World distribution of *Sphaeridium severini*.

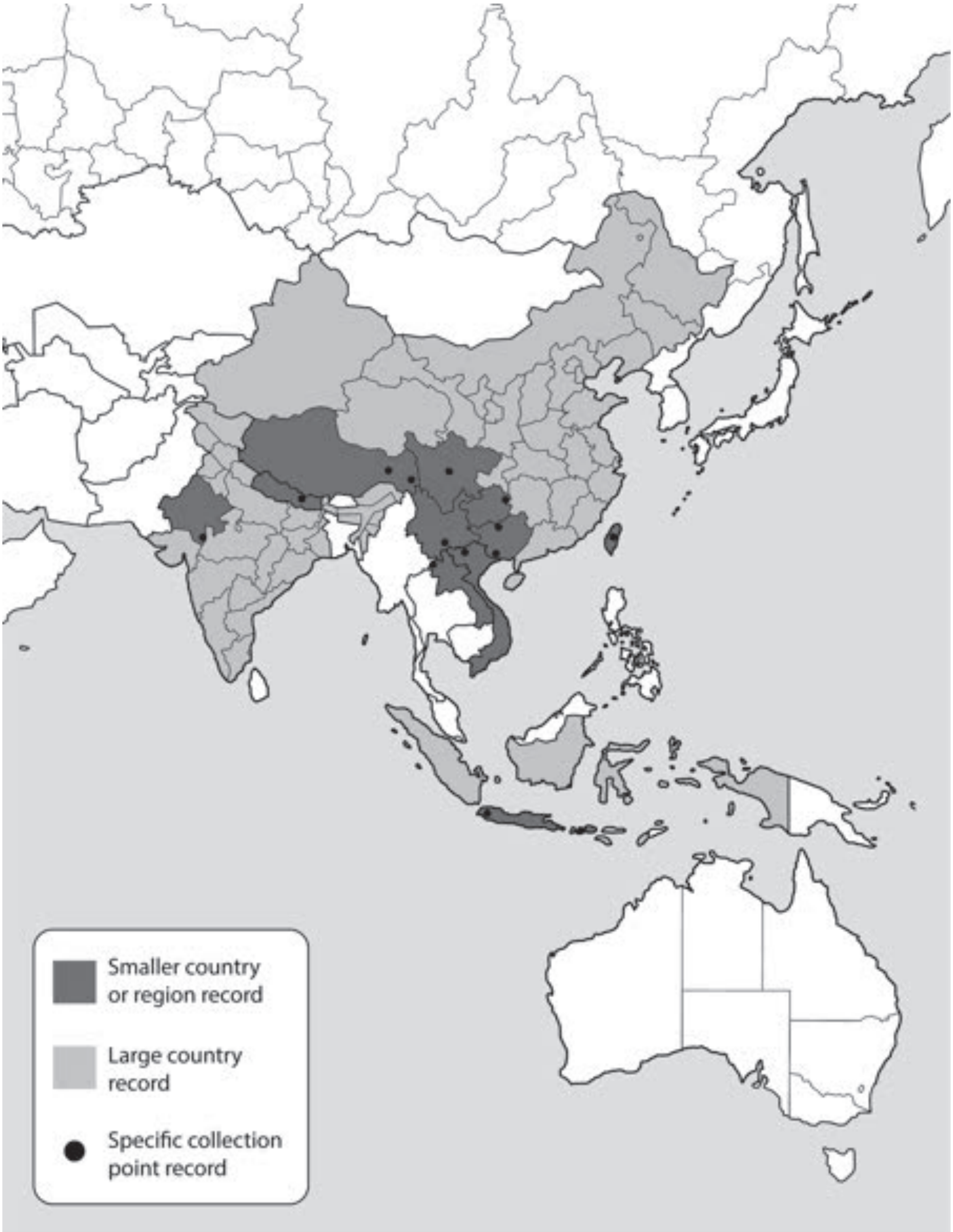

Figure 74. World distribution of *Sphaeridium vitalisi*.

Figure 75. *Sphaeridium sundense*, habitus. A) Dorsal; B) ventral; C) lateral; D) posterior. Photos by Arno van Berge Henegowen.

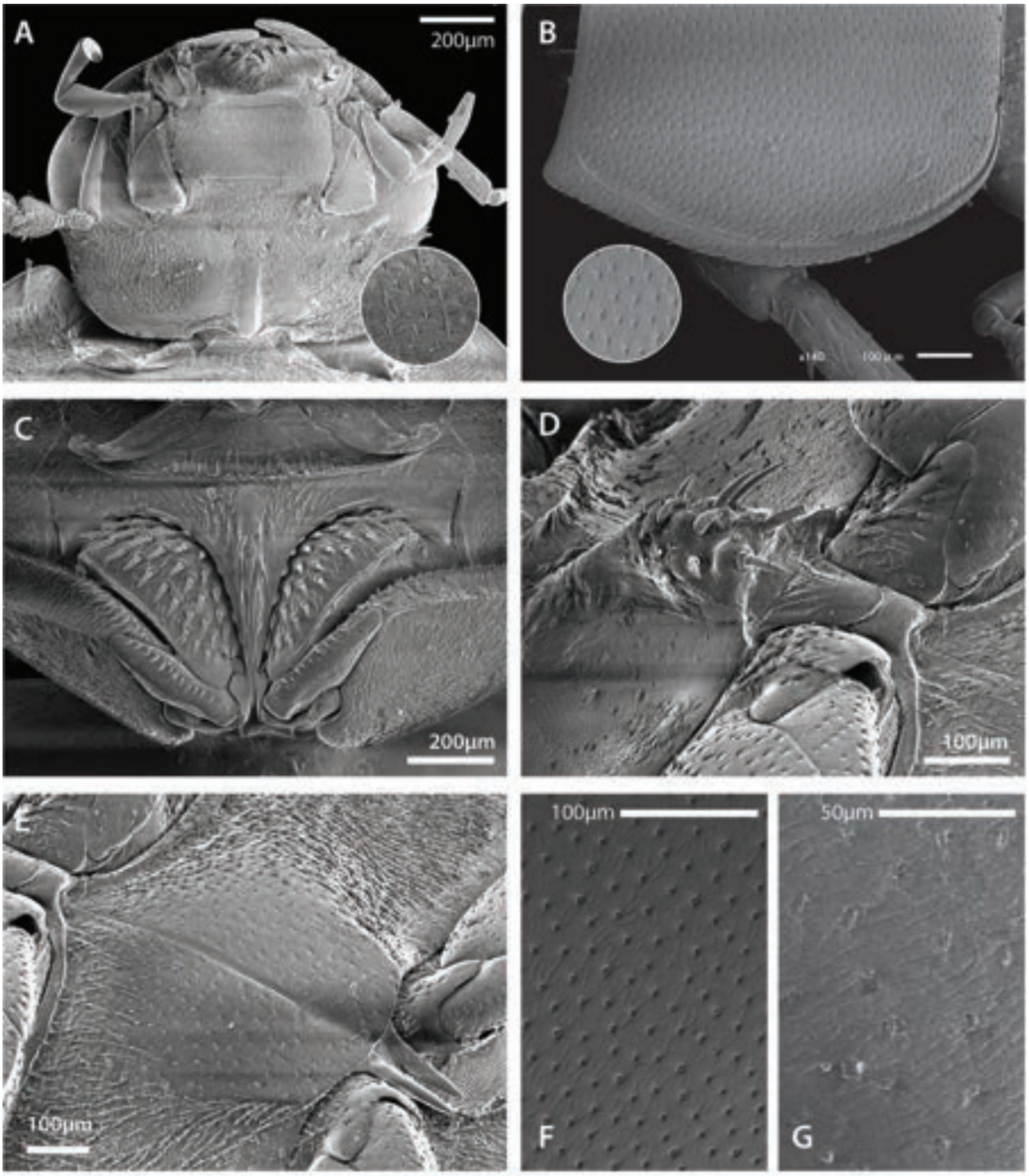

Figure 76. SEM of *Sphaeridium sundense*. A) Head, ventral, inset shows microrugae on surface of mentum; B) pronotum, dorsolateral, inset shows microsculpture on surface; C) proventrite; D) mesoventral keel, ventral oblique; E) metaventral field; F–G) detail of types of microsculpture: F) granulate microsculpture on pronotum, G) rugose microsculpture (microrugae) on metaventral field.

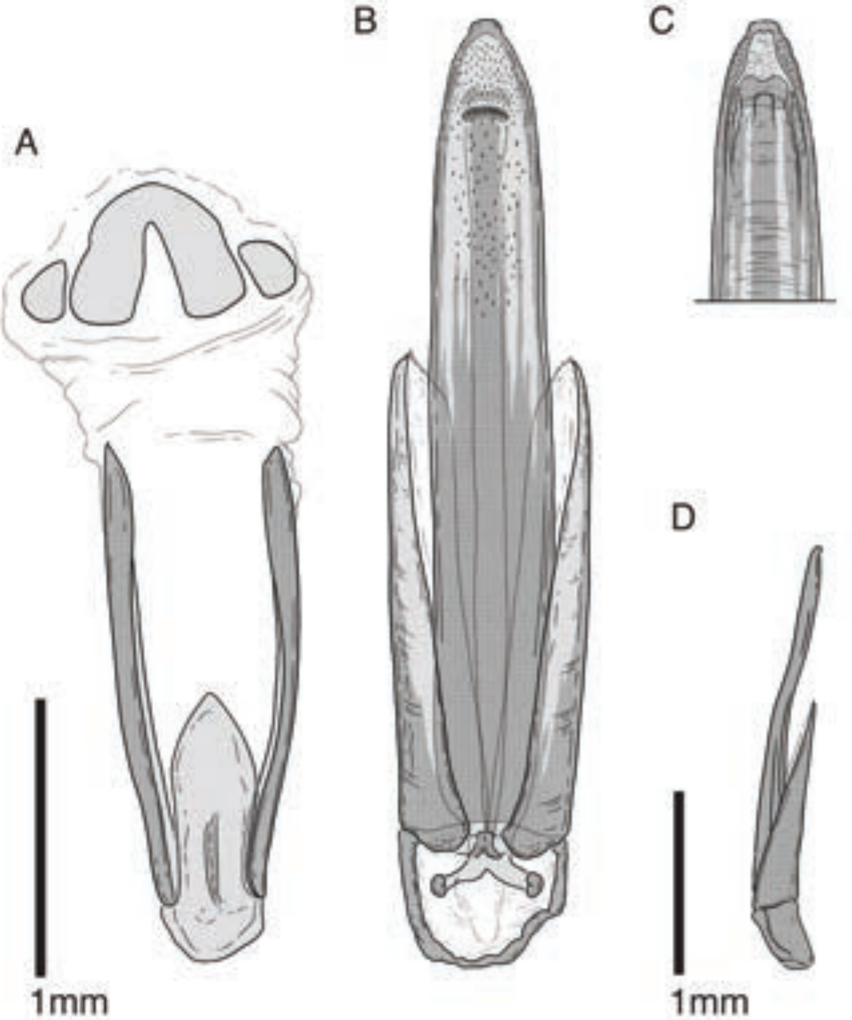

Figure 77. *Sphaeridium sundense* male genitalia. A) Abdominal tergite 9, dorsal; B) tegmen, dorsal; C) apex of median lobe, ventral; D) lateral profile.

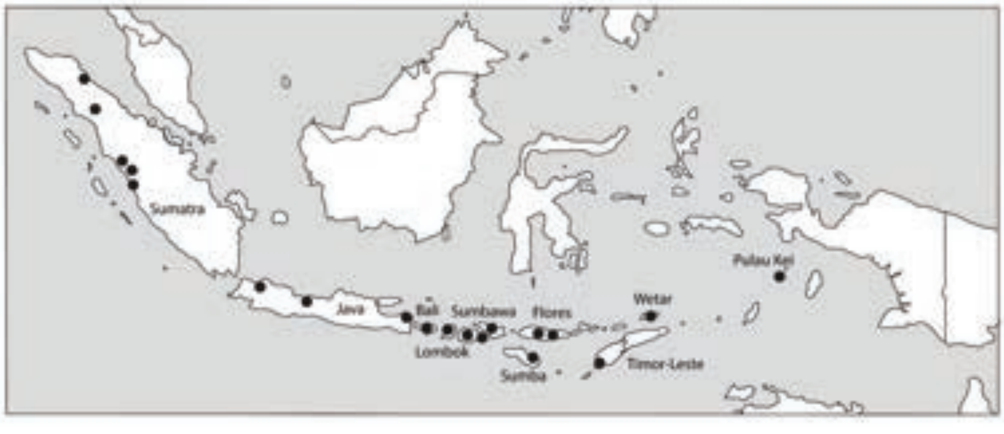

Figure 78. World distribution of *Sphaeridium sundense*.

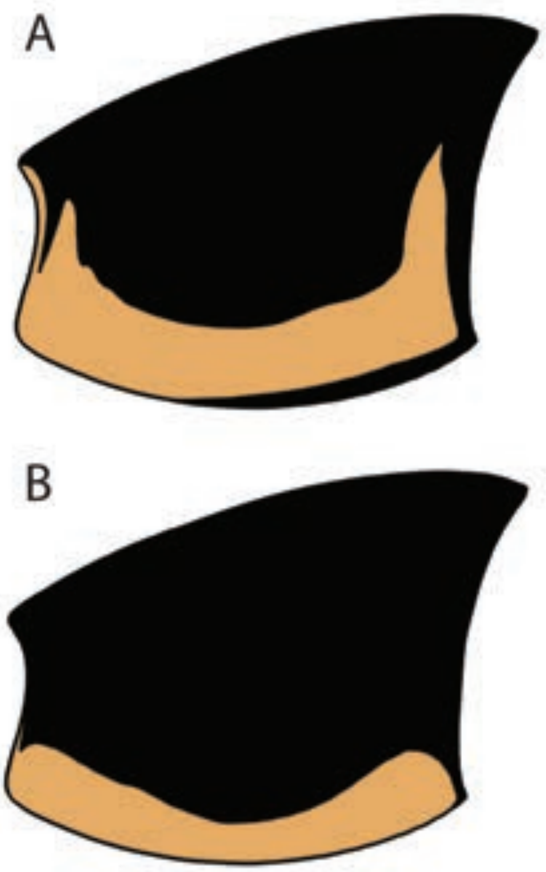

Figure 79. Pronotal coloration, left lateral view. A) *Sphaeridium sundense*; B) *S. quinquemaculatum*.

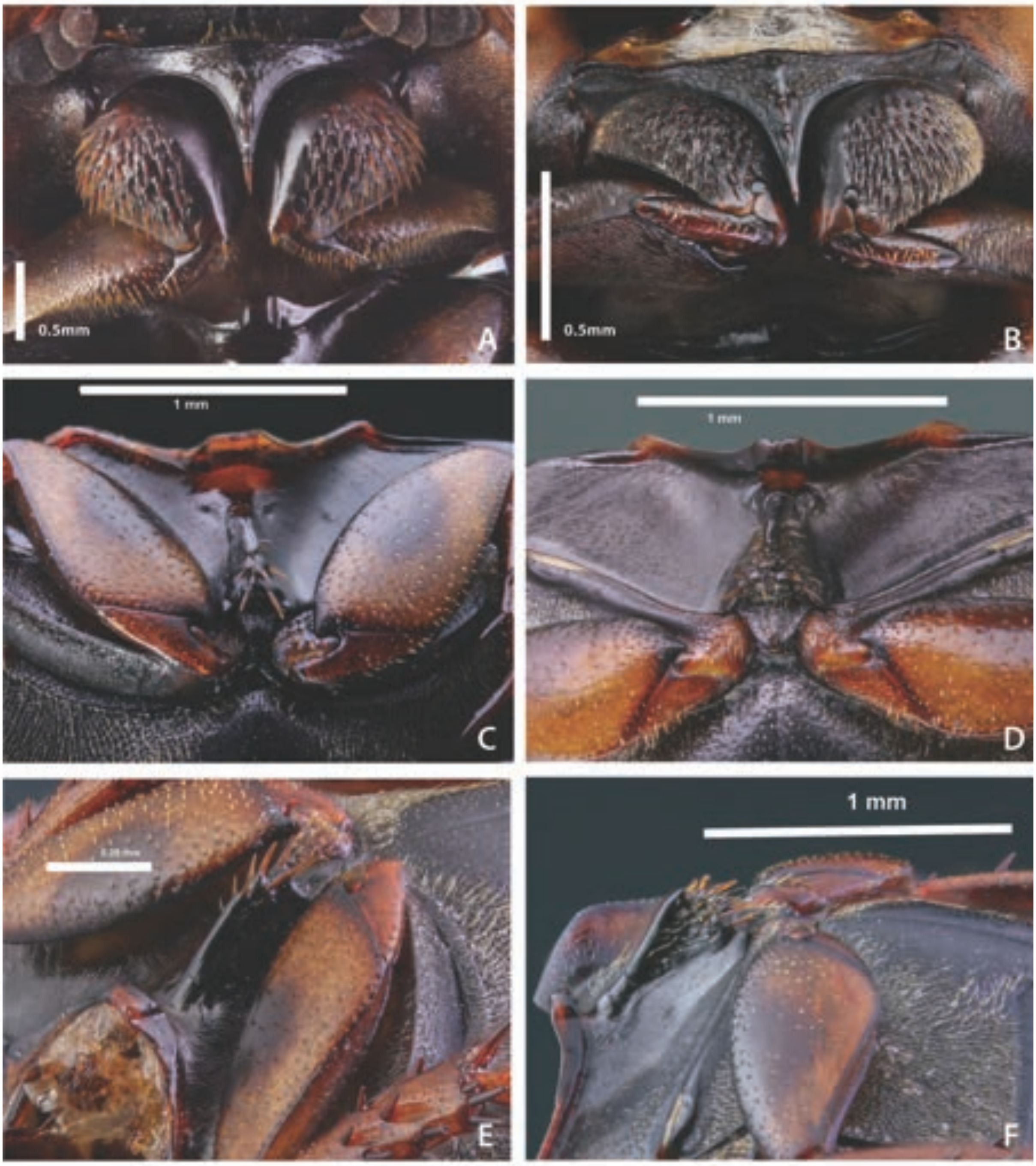

Figure 80. Morphology of *Sphaeridium* species. A, C, E) *Sphaeridium sundense*, B, D, F*) S. quinquemaculatum*. A–B) Procoxae, C–D) Mesoventral keel, ventral view, E–F) Mesoventral keel, oblique view. Photos by Arno van Berge Henegowen.

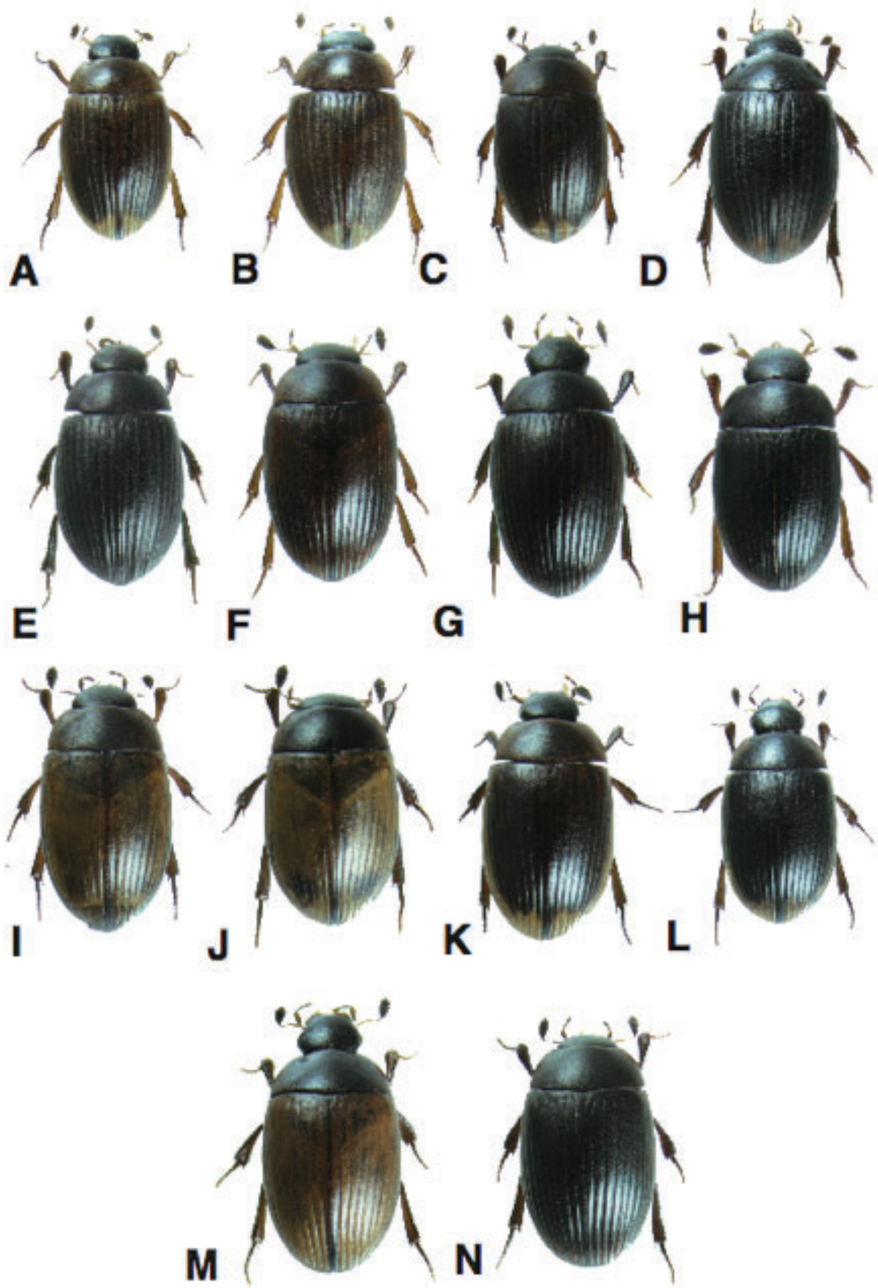

Figure 81. Habitus of beach-dwelling species of the genus *Cercyon (Cercyon)* spp. occurring in the Far East. A–E) *C. aptus*; F–G) *C. algarum*; H) *C. setulosus*; I–J) *C.* (*C.*) *numerosus*; K–L) *C. symbion*; M–N) *C. dux*.

Figure 82. *Cercyon* species. A, B) *C. whuljensis* (WA18AS-008). C, D) *C. dux* (WA16AS015). E, F) *C. fimbriatus* (WA17AS-004). G, H) *C. luniger* (WA17AS-008). I, J) *C. setulosus* (BC16MO-032). A, C, E, G) dorsal habitus; B, D, F, H) lateral habitus.

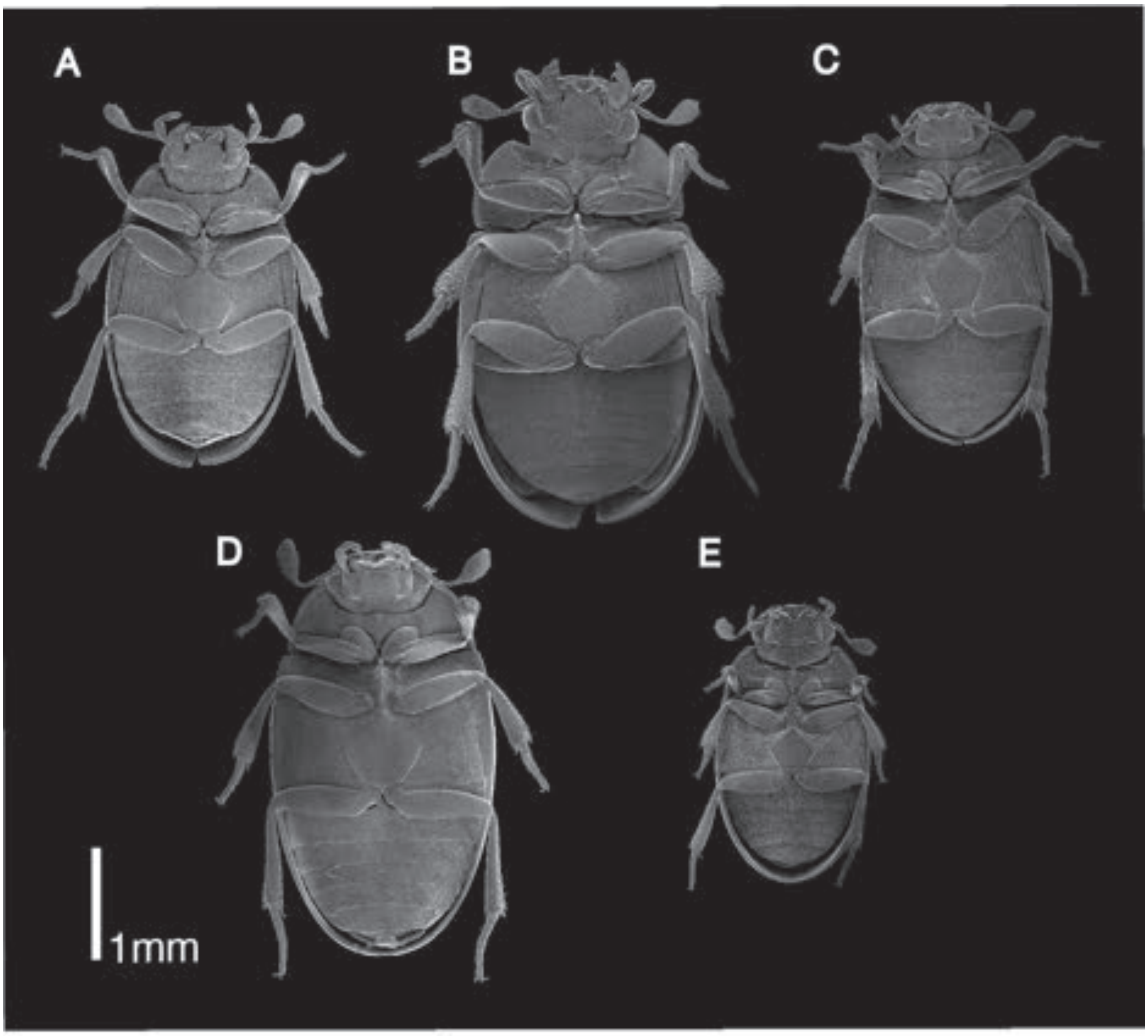

Figure 83. *Cercyon* (*Cercyon*) spp., ventral habitus SEM. A) *C. whuljensis* (BC14MO-008); B) *C. dux* (WA16AS-015); C) *C. fimbriatus* (WA13MO-039); D) *C. luniger* (WA18AS-008); E) *C. setulosus* (WA16AS-006).

Figure 84. Habitats in northwestern Washington State, USA. A–C) Sifting method of collecting as shown on sandy beach with kelp wrack (WA18AS-011). D–E) *Ulva* sp., *Zostera* sp., and kelp wrack on sandy beach (WA18AS-009). F–G) Kelp wrack on cobble beach (WA17AS-005). H–I) *Ulva* sp. wrack on pebble beach (WA18AS-005).

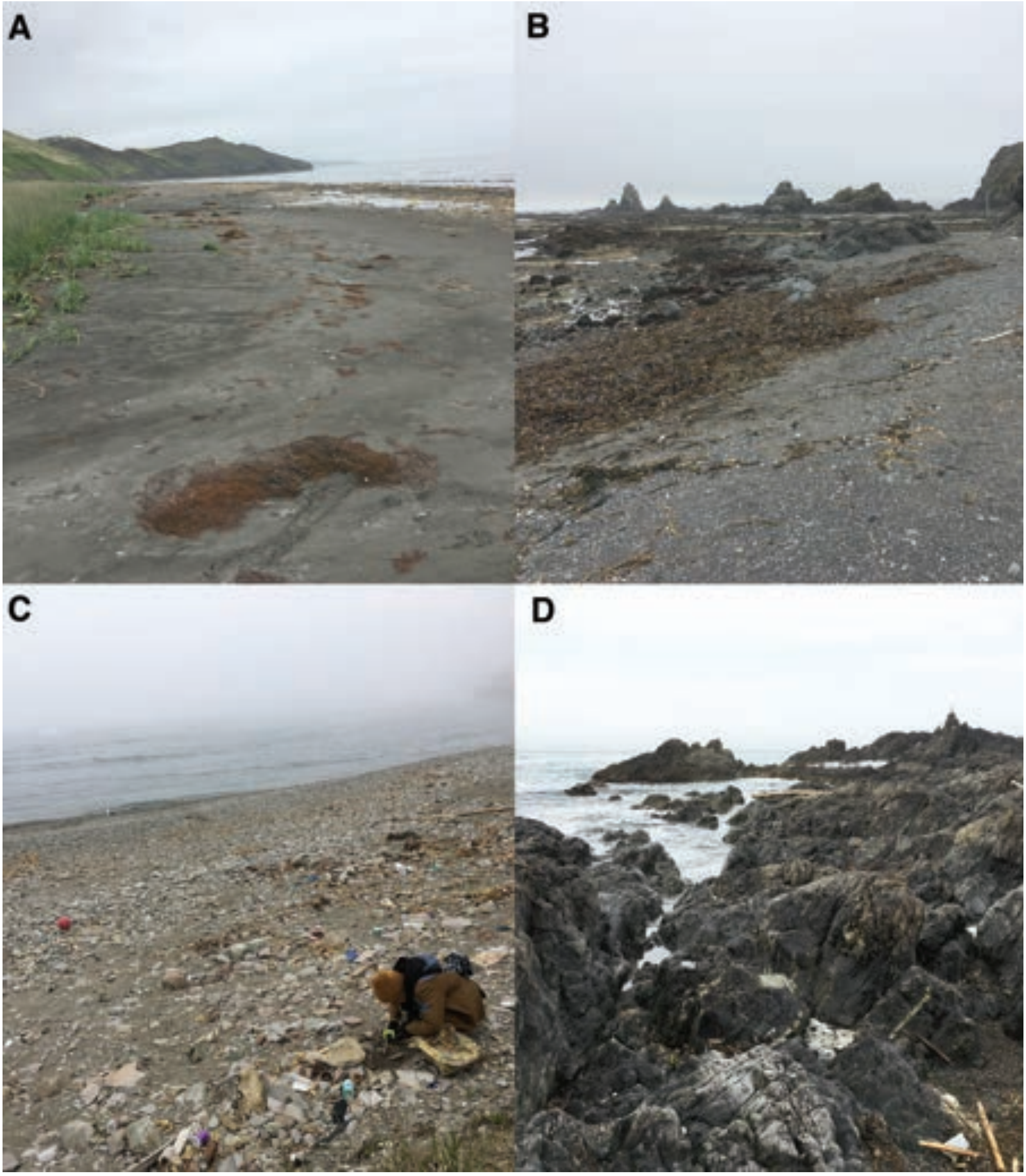

Figure 85. Landscape of beaches and shores. A) Sandy beach (SA); B) shingle beach (SH); C) cobble beach (CO); D) rocky shore.

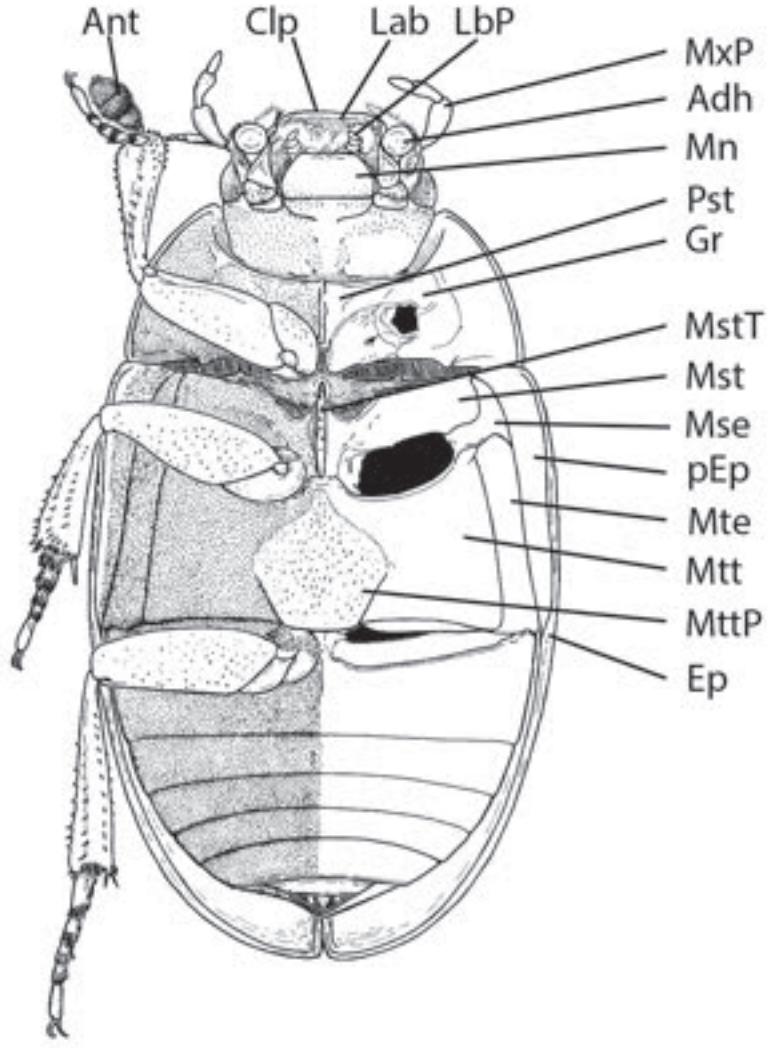

Figure 86. *Cercyon whuljensis*, male, ventral view.
Abbreviations: Adh = adhesion disc, Ant = antenna, Clp = clypeus, Ep = epipleuron, Gr = groove for reception of antenna, Lab = labrum, LbP = labial palp, Mn = mentum, Mse = mesepiventrite, Mst = mesoventrite, MstT = mesoventral tablet, Mte = metepiventrite, Mtt = metaventrite, MttP = raised plate of metaventrite, MxP = maxillary palp, pEp = pseudepipleuron, Pst = prosternum.

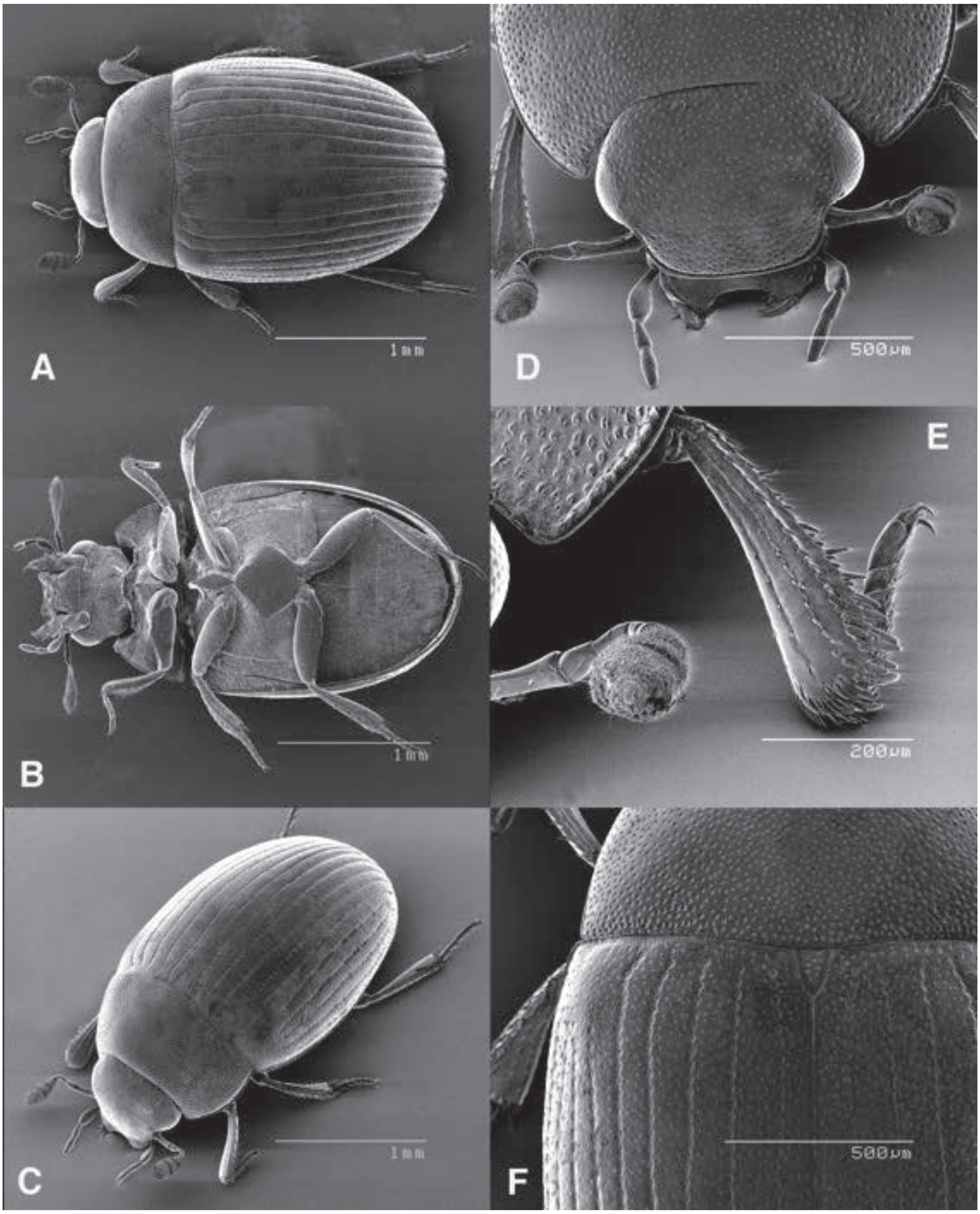

Figure 87. *Cercyon algarum*. A) Habitus, dorsal view; B) ditto, ventral view; C) ditto, oblique view; D) head, frontal view; E) left protibia, dorsal view; F) basal part of pronotum and left elytron [MO-09-014 from Hakodate, Hokkaido].

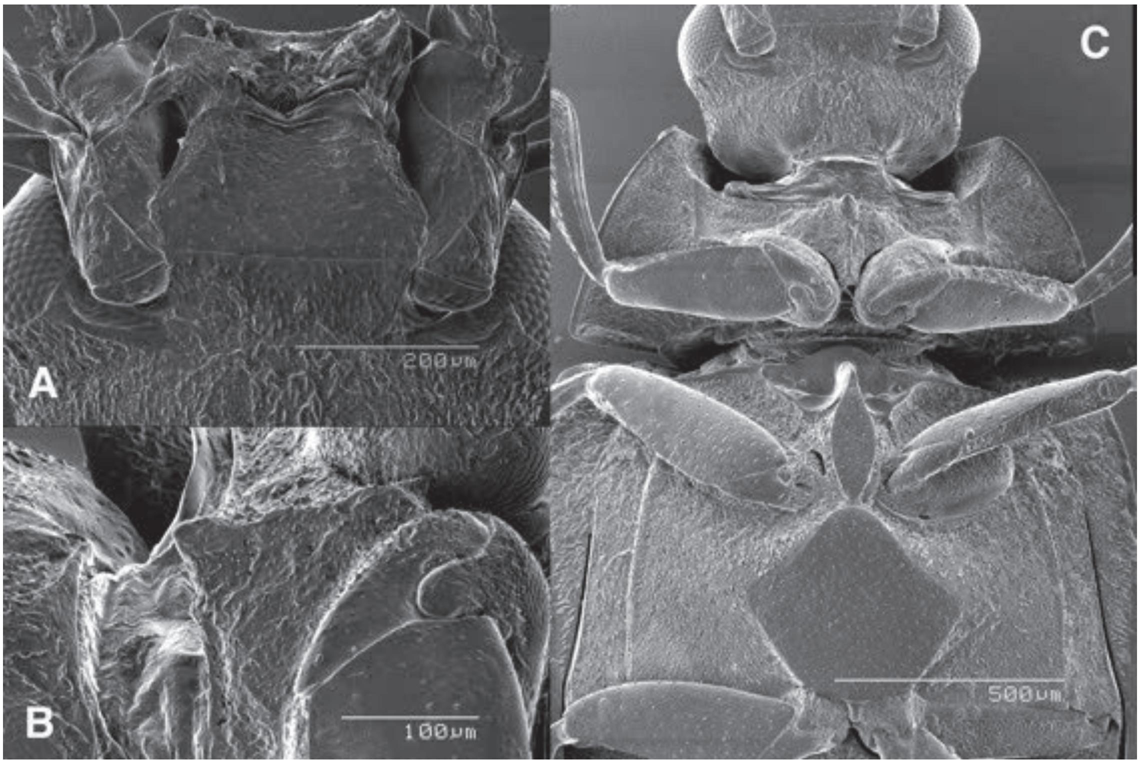

Figure 88. *Cercyon algarum*. A) Mouthparts, ventral view; B) prosternum, oblique view; C) Pro-, meso- and metasterna, ventral view [MO-09-014 from Hakodate, Hokkaido].

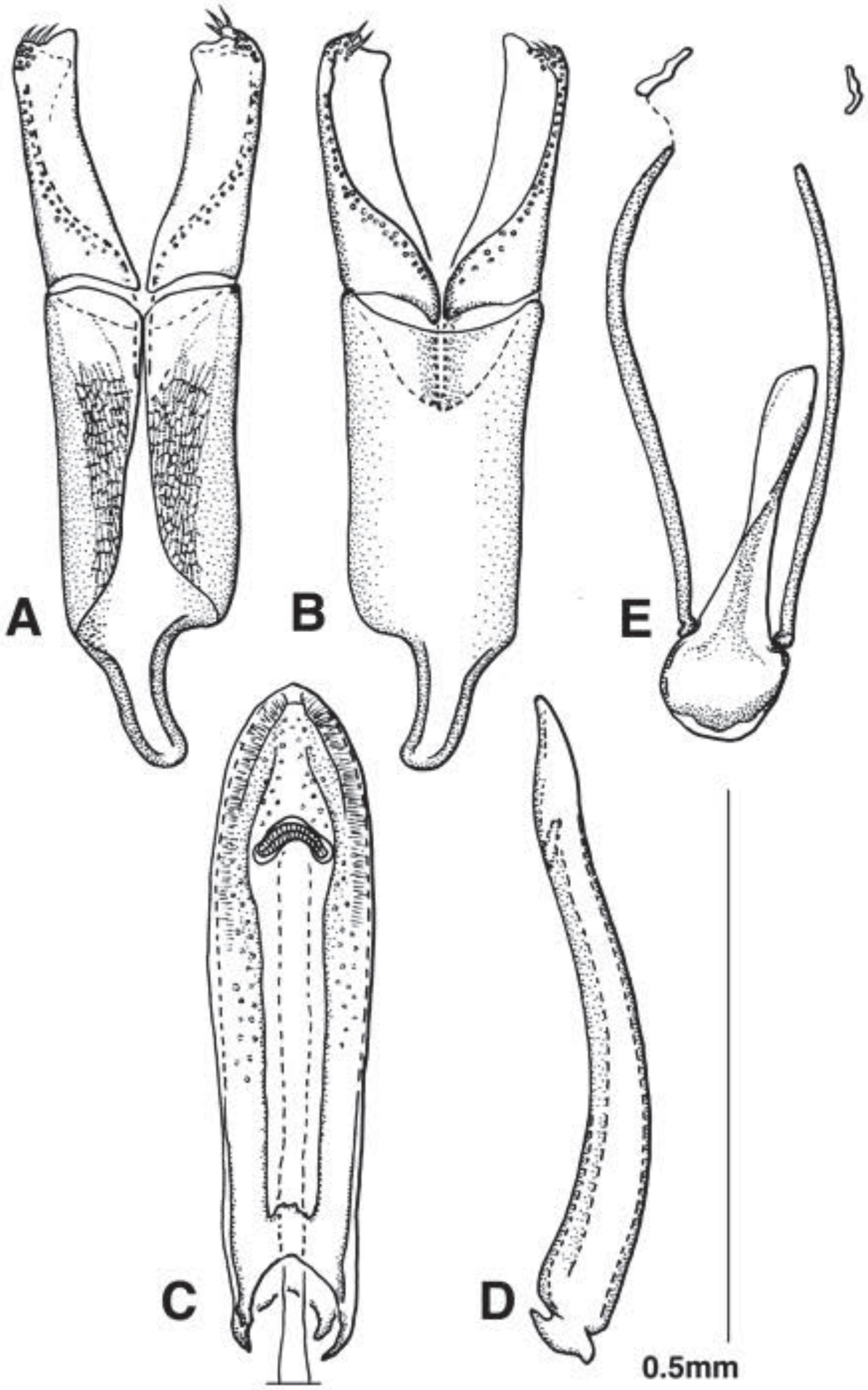

Figure 89. Male genitalia of *Cercyon algarum*. A) Tegmen, dorsal view; B) ditto, ventral view; C) median lobe, dorsal view; D, ditto, lateral view (right side); E, ninth sternum, dorsal view [MO-09-014 from Hakodate, Hokkaido]. Illustration by Masahiro Ôhara.

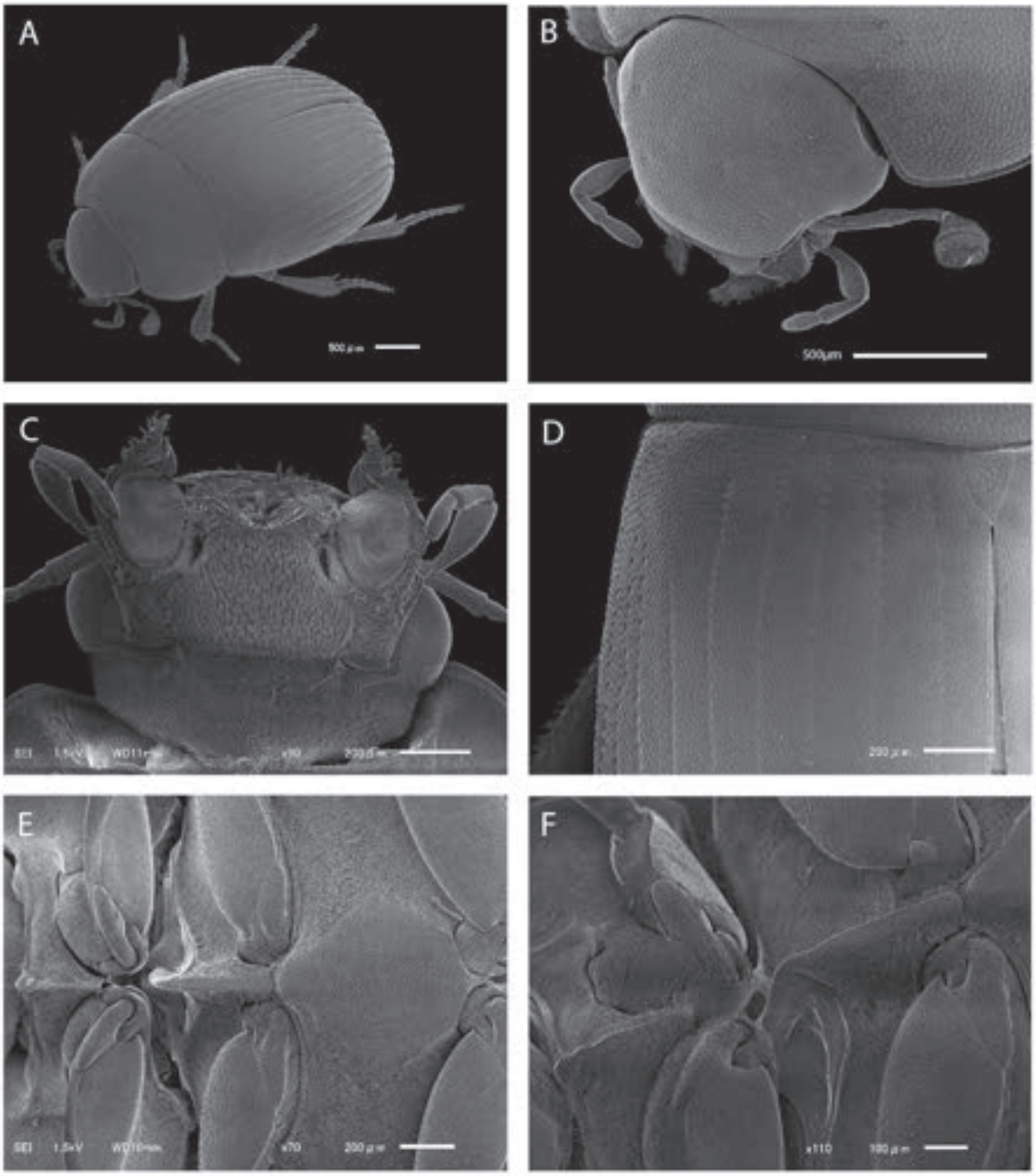

Figure 90. *Cercyon dux*, male (WA16AS-015). A) Habitus, oblique view; B) head, oblique view; C) head, ventral, showing adhesion discs; D) basal portion of left elytra; E) prosternum, meso-, and metaventrites, ventral view; F) pro- and mesoventrites, oblique ventral view.

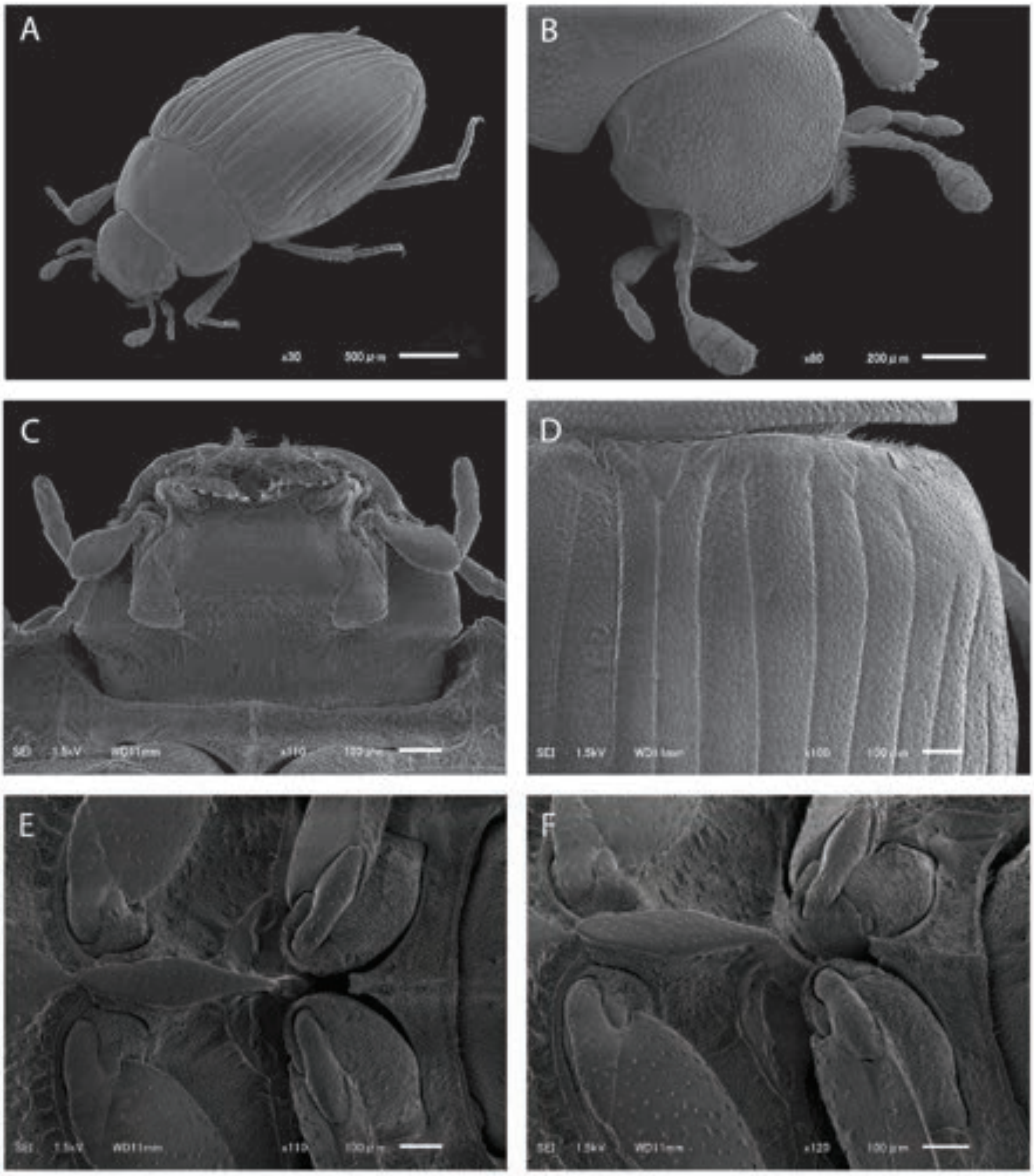

Figure 91. *Cercyon fimbriatus*, male (BC16MO-033). A) Habitus, oblique view; B) head, oblique view; C) head, ventral, showing adhesion discs; D) basal portion of left elytra; E) prosternum, meso-, and metaventrites, ventral view; F) prosternum and mesoventrites, oblique ventral view.

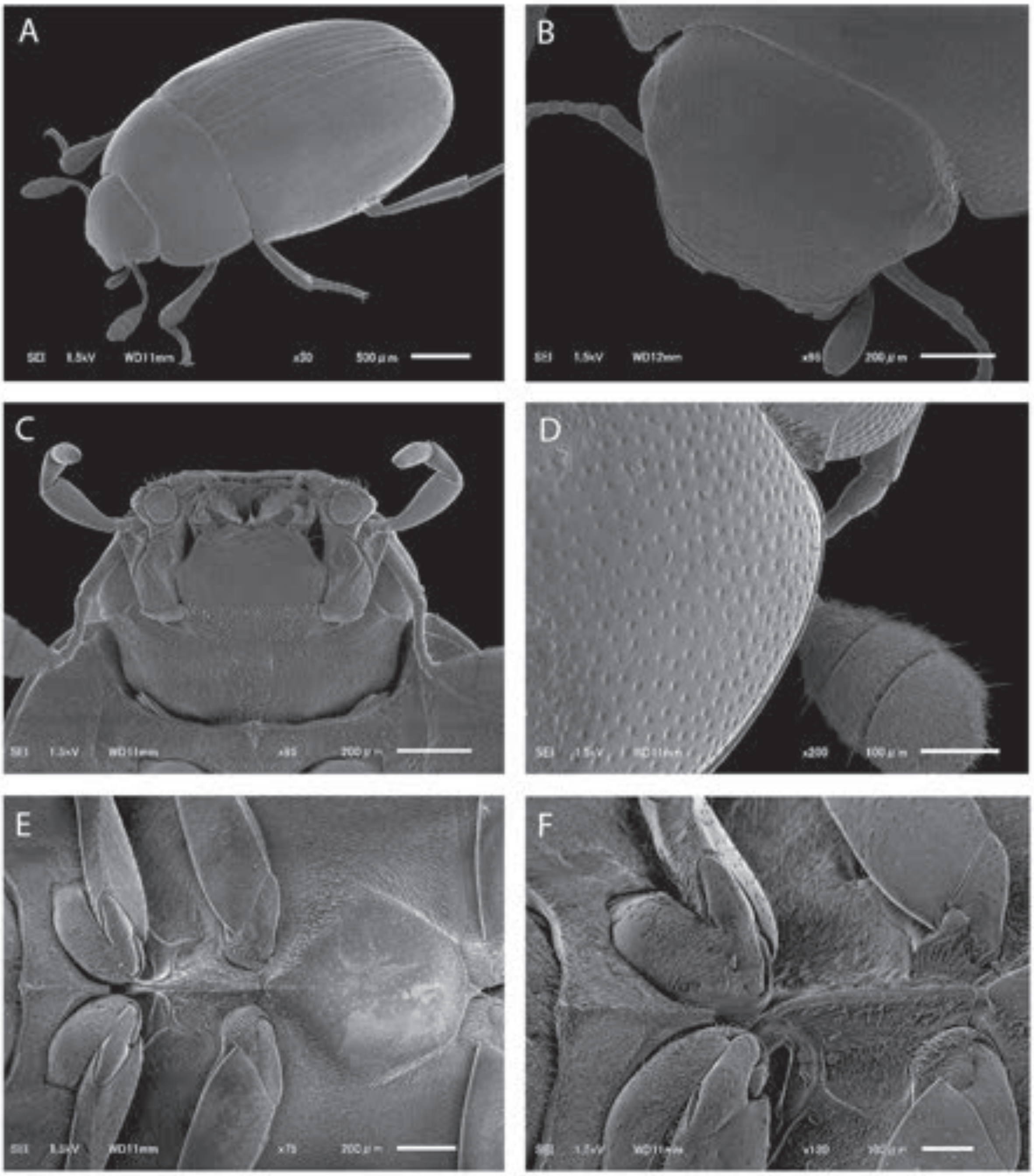

Figure 92. *Cercyon luniger*, male (WA18AS-008). A) Habitus, oblique view; B) head, oblique view; C) head, ventral, showing adhesion discs; D) basal portion of left elytra; E) prosternum, meso-, and metaventrites, ventral view; F) prosternum and mesoventrites, oblique ventral view.

Figure 93. *Cercyon luniger*, lectotype. A) Dorsal habitus; B) locality labels; C) lectotype label.

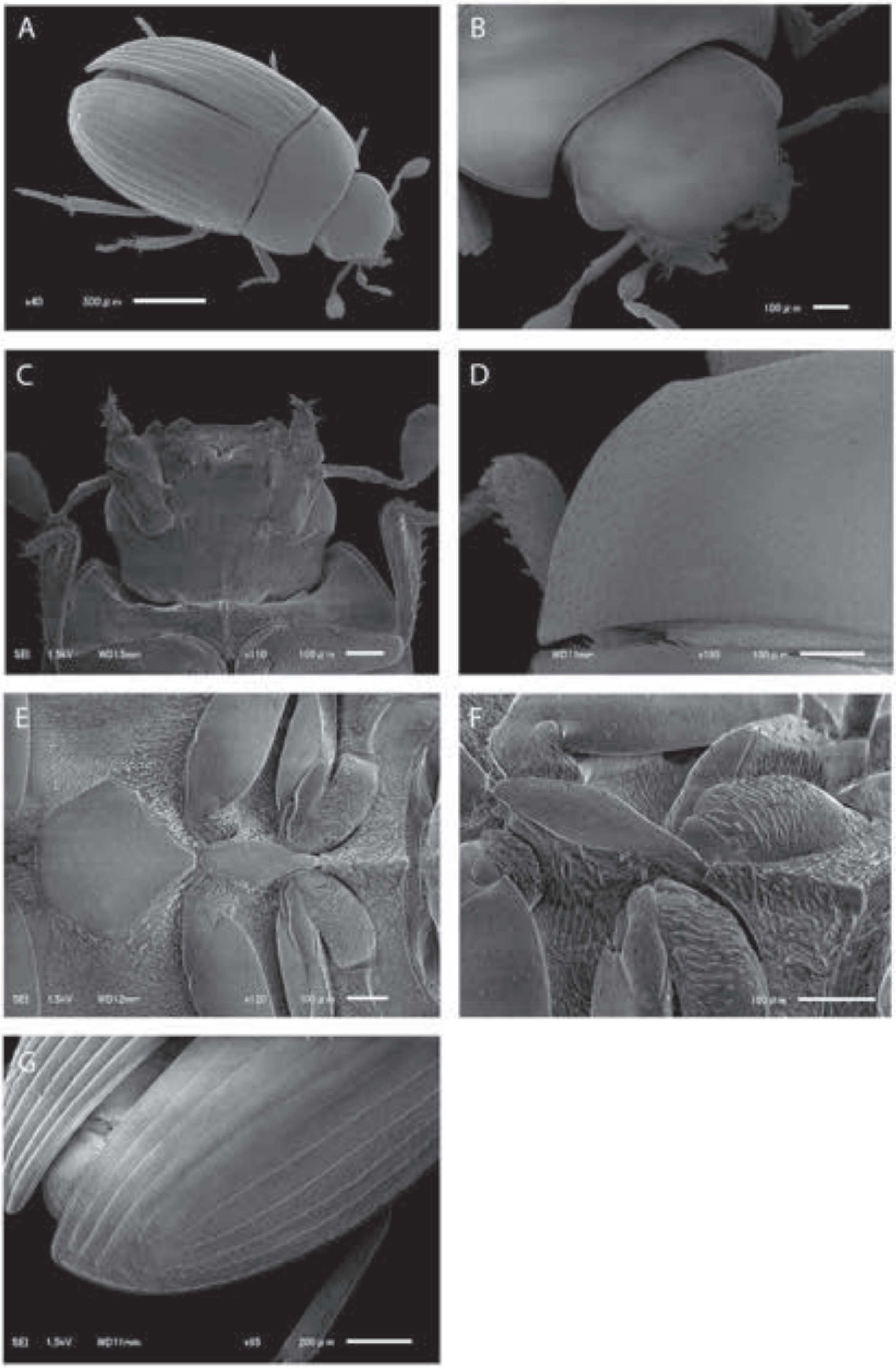

Figure 94. *Cercyon setulosus*, male (WA16AS-006). A) Habitus, oblique view; B) head, oblique view; C) head, ventral, showing adhesion discs; D) basal portion of left elytra; E) prosternum, meso-, and metaventrites, ventral view; F) prosternum and mesoventrites, oblique ventral view; G) apical portion of left elytra, oblique.

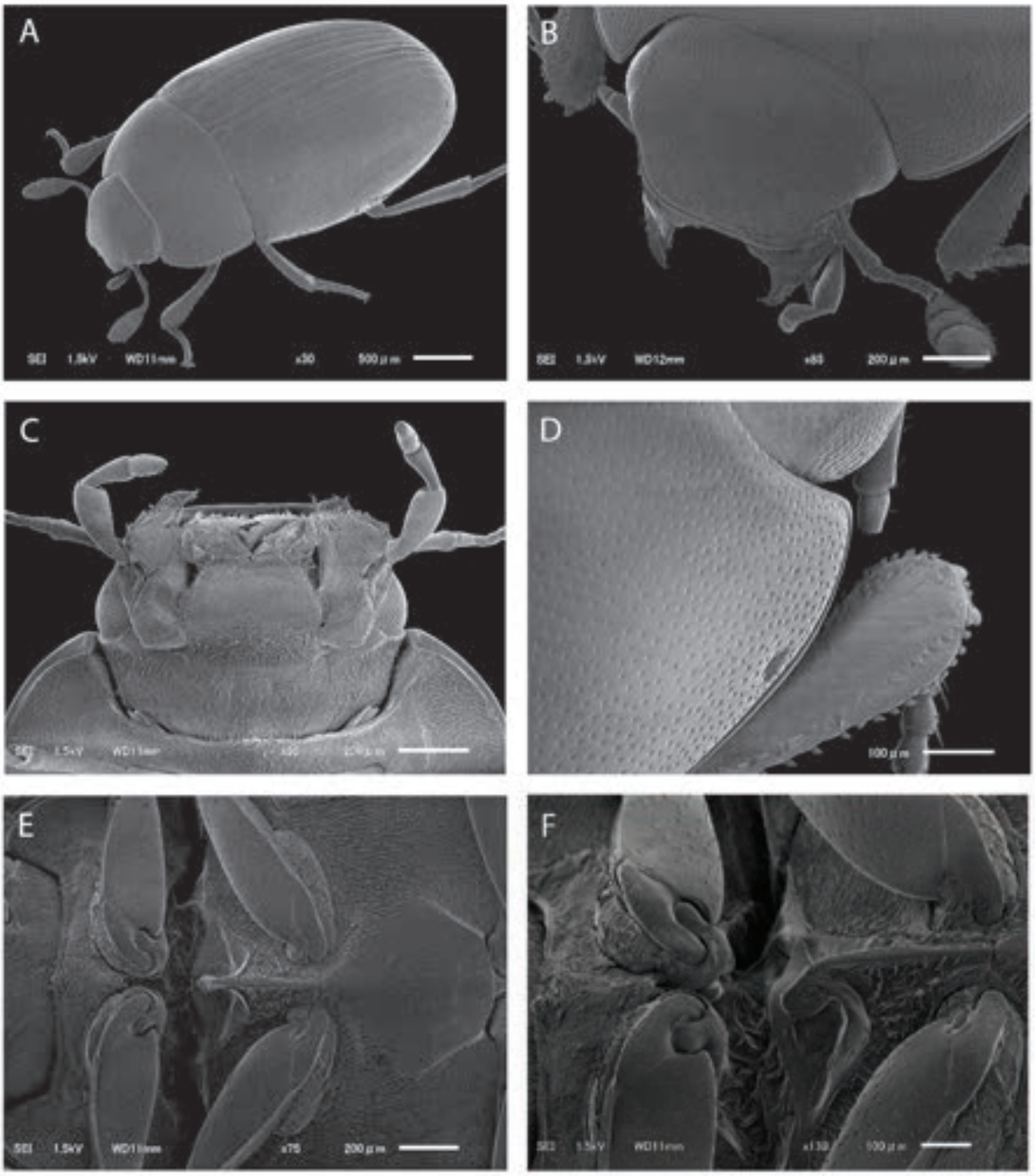

Figure 95. *Cercyon whuljensis*, male (BC14MO-008). A) Habitus, oblique view; B) head, oblique view; C) head, ventral, showing adhesion discs; D) basal portion of left elytra; E) prosternum, meso-, and metaventrites, ventral view; F) prosternum and mesoventrites, oblique ventral view.

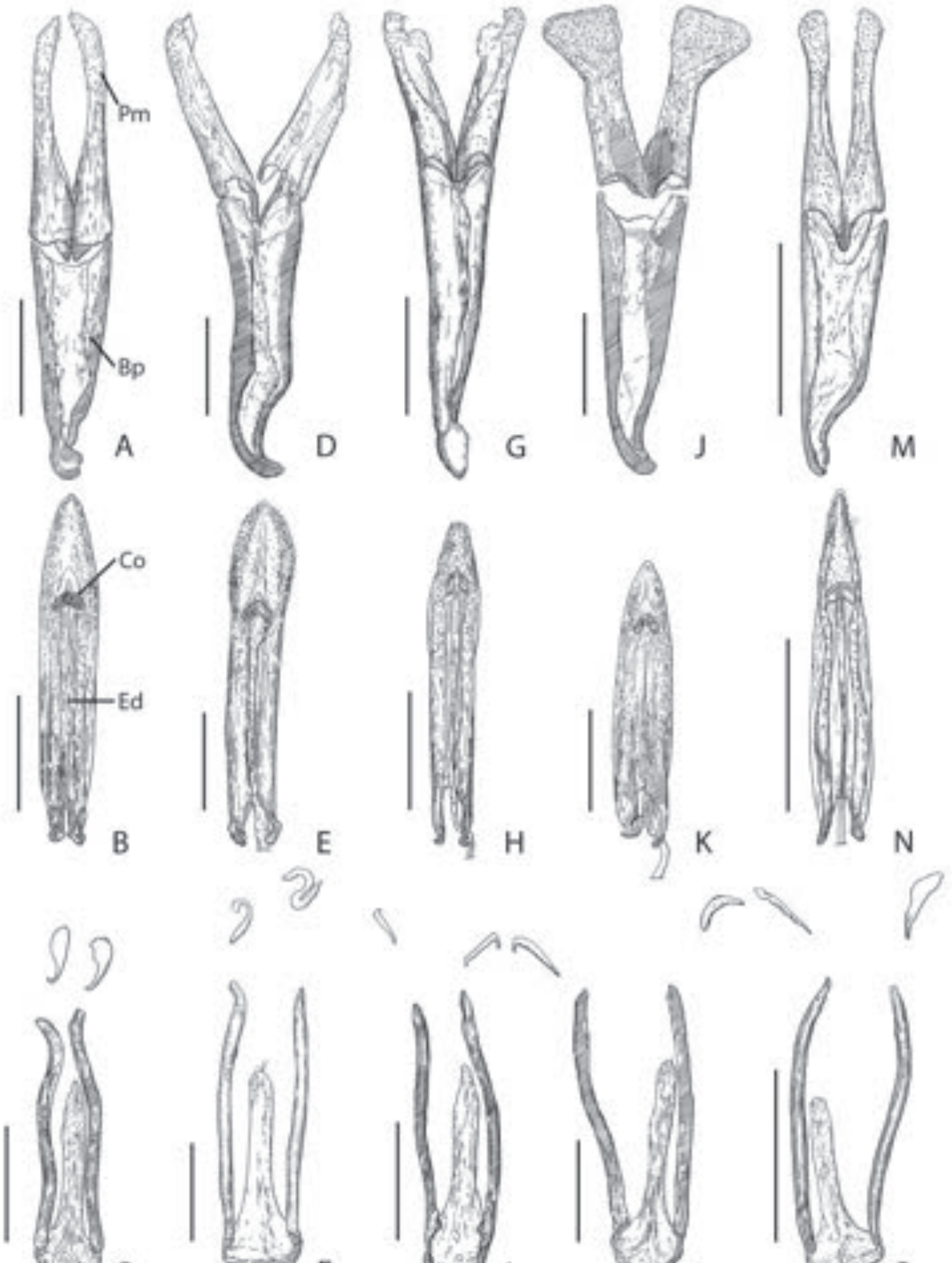

Figure 96. Male genitalia of beach-dwelling *Cercyon* occurring in Pacific North America. A, B, C) *C. whuljensis* (BC14MO-025); D, E, F) *C. dux* (BC14MO-030); G, H, I) *C. fimbriatus* (BC16MO-033); J, K, L) *C. luniger* (WA18AS-008); M, N, O) *C. setulosus* (WA16AS-006). A, D, G, J) parameres and basal piecel; B, E, H, K) median lobe. C, F, I, L) ninth ventrite. Abbreviations: Pm = parameres, Bp = basal piece, Co = corona, Ed = ejaculatory duct. Scale bars = 0.5 mm.

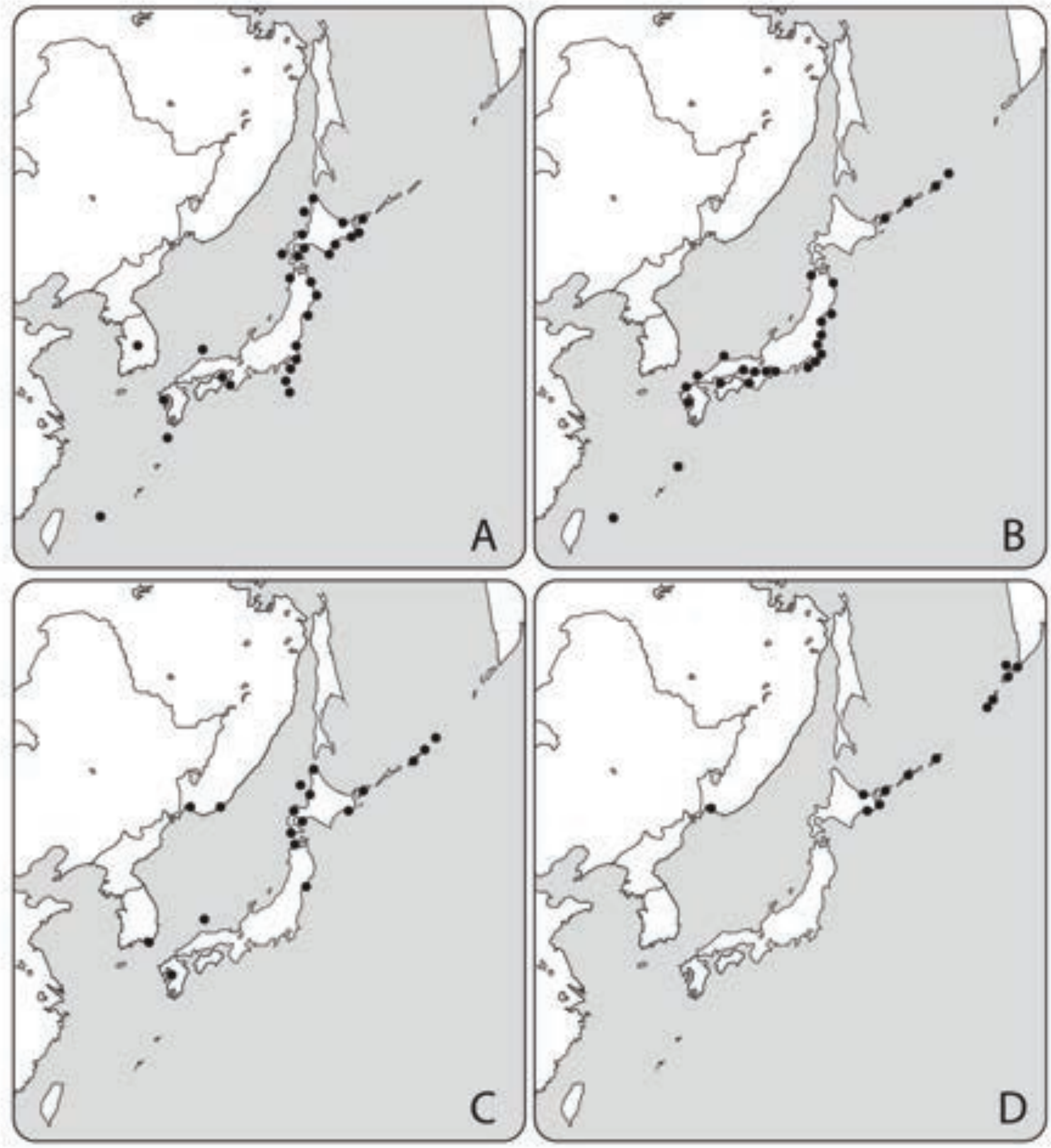

Figure 97. World distribution for the beach dwelling *Cercyon* (*Cercyon*) spp. occurring only in the Far East. A) *Cercyon* (*Cercyon*) *algarum*; B) *C.* (*C.*) *aptus*; C) *C.* (*C.*) *numerosus*; D) *C.* (*C.*) *symbion* (Ryndevitch 2003, Ôhara & Jia 2006, Ôhara, Yoo & Ahn 2013, Ôhara & Ogawa 2016).

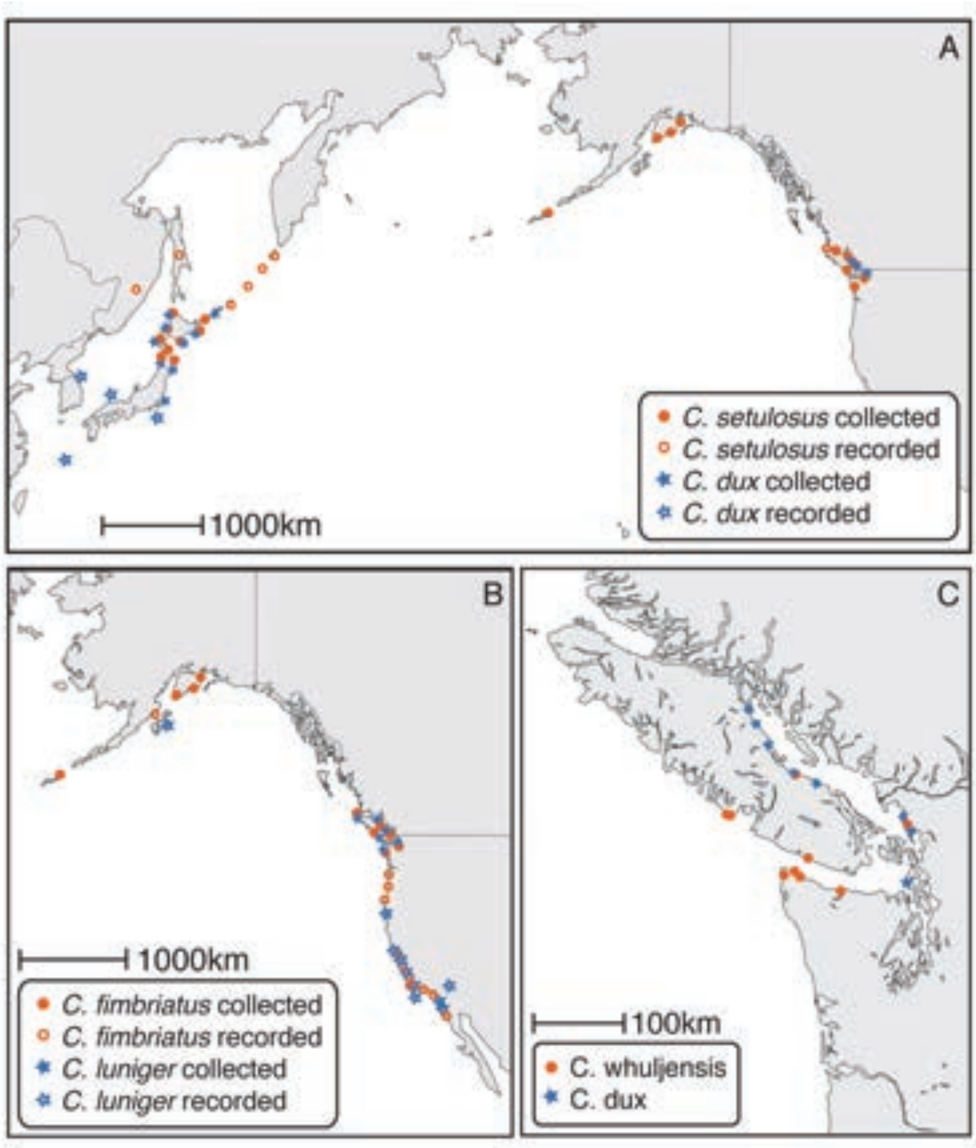

Figure 98. World distribution for A) *C. dux* and *C. setulosus* and B) *C. fimbriatus*, *C. luniger*, and *C. whuljensis* (Bousquet et al. 2013, Caterino 2009, Oh et al. 2013, Yoo et al. 2014).

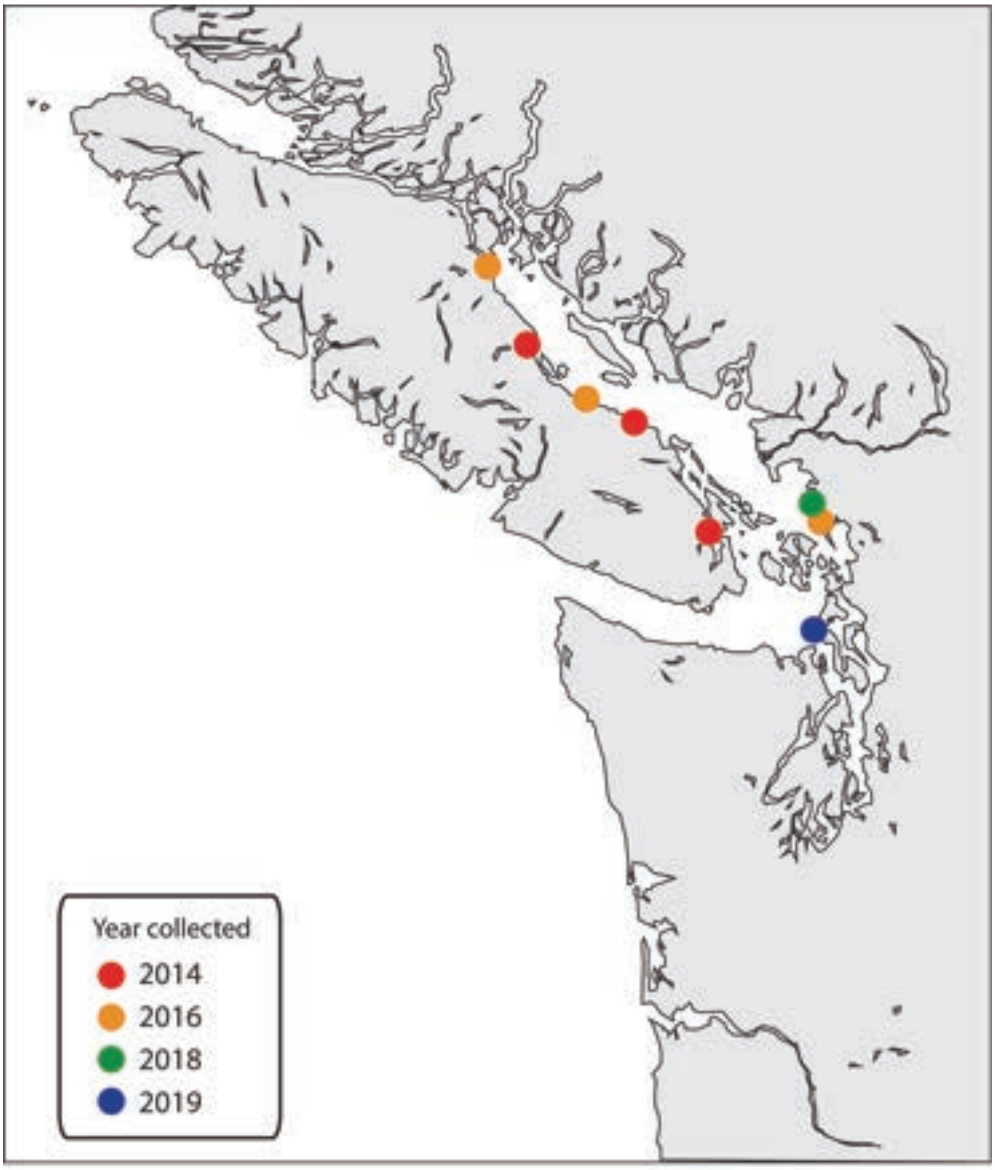

Figure 99. North America records for *Cercyon dux* by year collected.

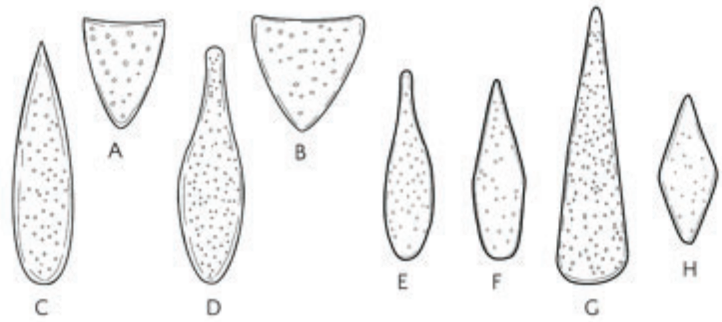

Figure 200. Scutellums (A–B) & mesoventral tablets (C–H). A, C,) *Cercyon numerosus*; B, D) *C. symbion*; E) *C. algarum*; F) *C. aptus*; G) *C. dux*; H) *C. setulosus*.

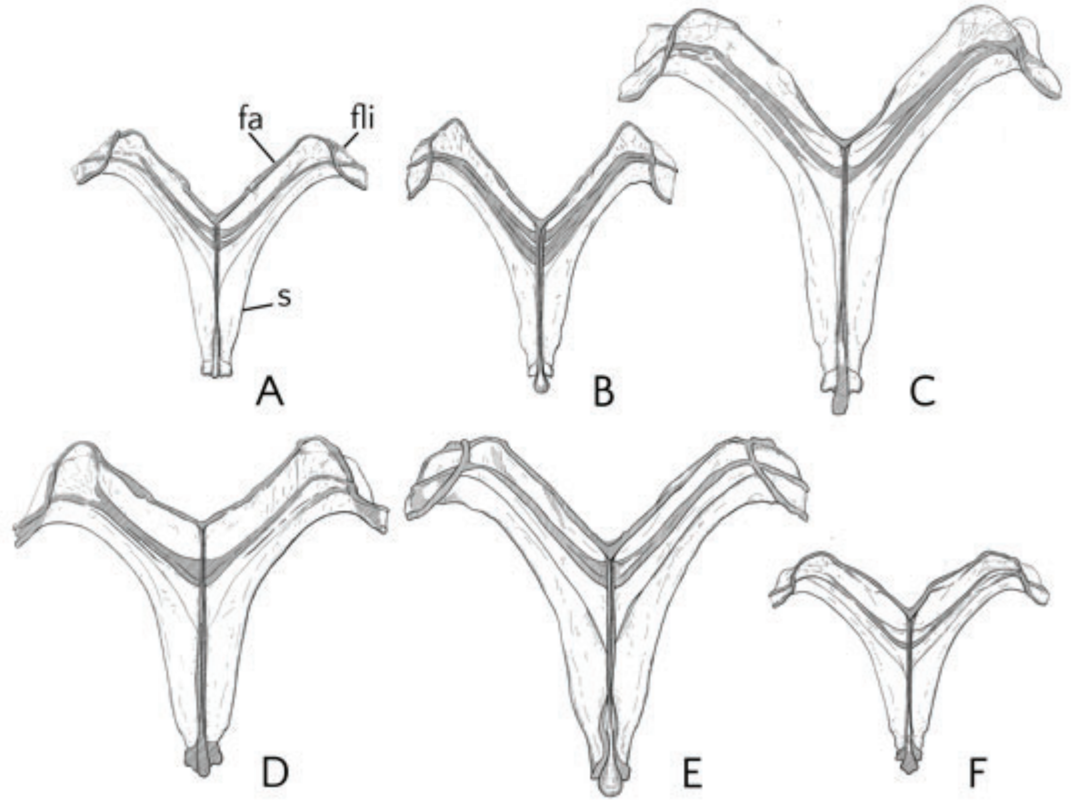

Figure 101. Metafurca. A) *Cercyon algarum*; B) *C. aptus*; C) *C. dux*; D) *C. numerosus*; E) *C. symbion*; F) *C. setulosus*.
Abbreviations: fa – furcal arm, fli – lateral extension of furcal arm, s – stem.

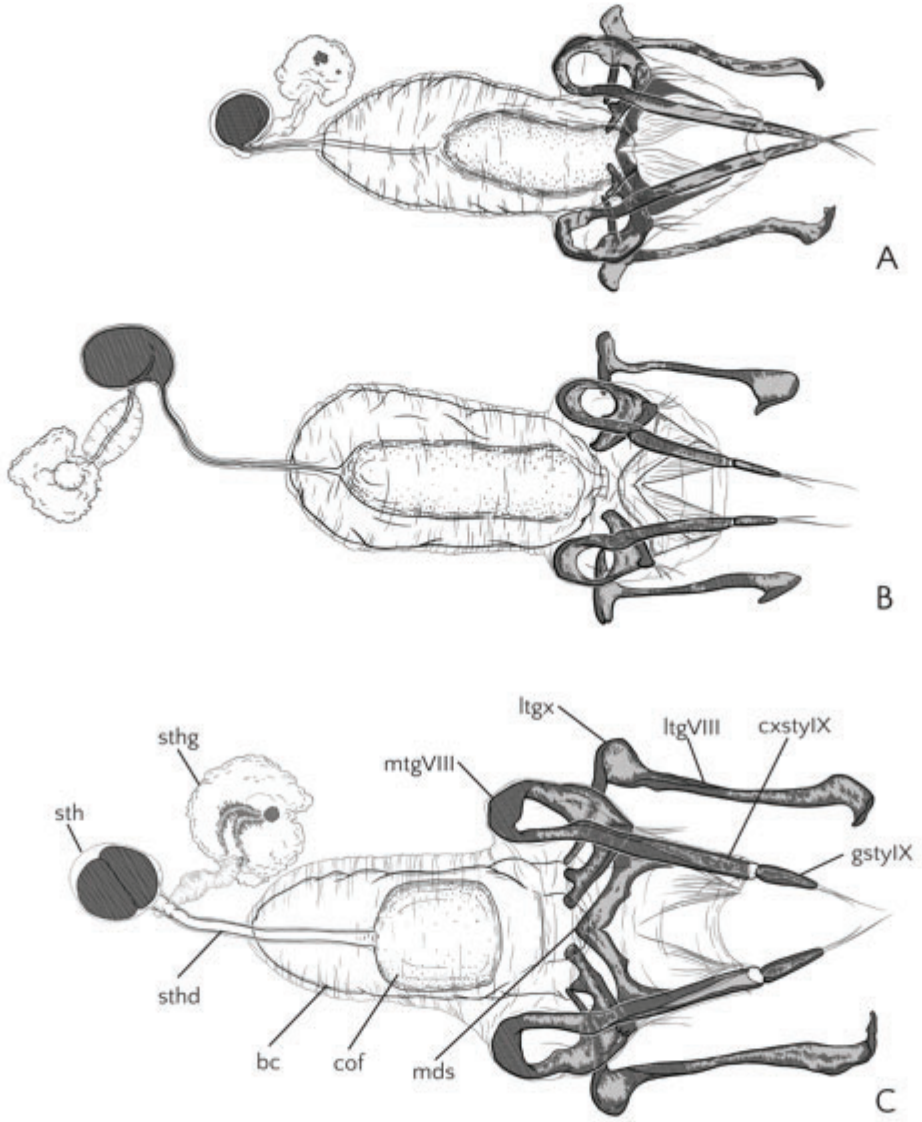

Figure 102. Female genitalia. A) *Cercyon algarum*; B) *C. aptus*; C) *C. dux*.
Abbreviations: bc, bursa copulatrix; cof, canal of fecundation; cxstyIX, coxostylus 9; gstyIX, gonostylus 9; ltgVIII, laterotergite 8; ltgx, lateral extension of laterotergite 8; mds, median sclerite; mtgVIII, mediotergite 8; sth, spermatheca;, sthd, spermathecal duct; sthg, spermathecal gland.

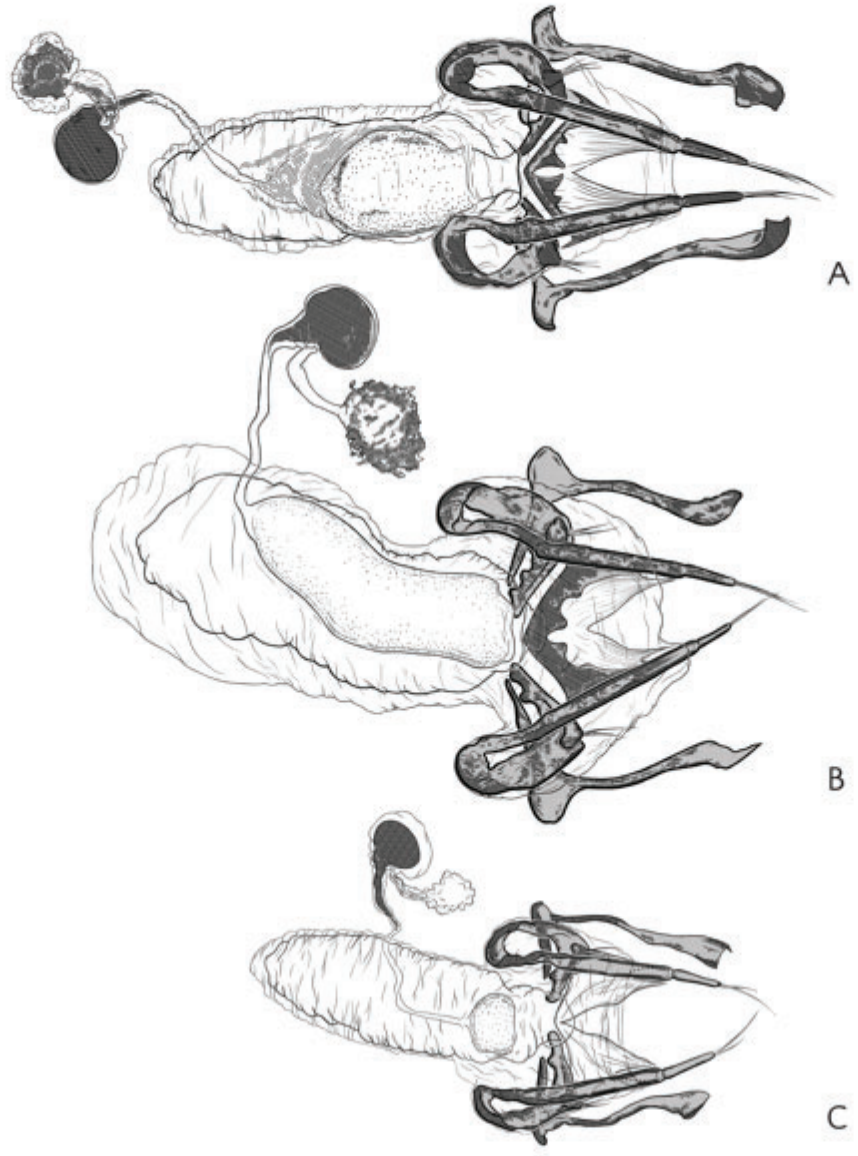

Figure 103. Female genitalia. A) *Cercyon numerosus*; B) *C. symbion*; C) *C. setulosus*.

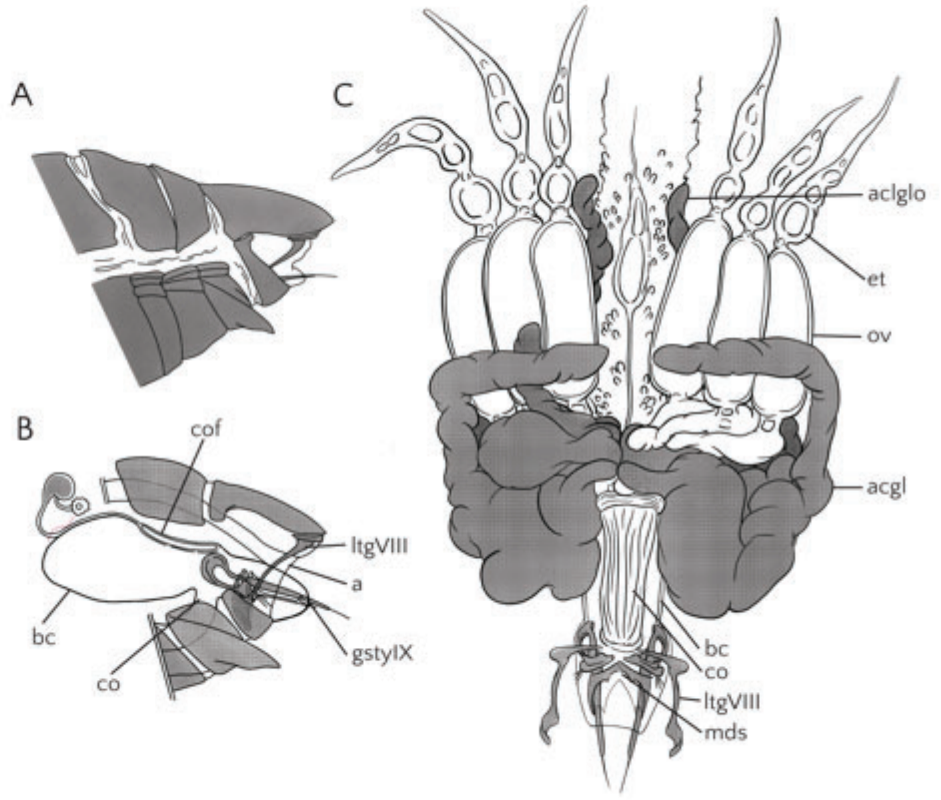

Figure 104. *Cercyon aptus*, terminal segments and internal female genitalia. A) Terminal segment, lateral; B) lateral structure of terminal segments and bursa copulatrix; C) internal female genitalia, ventral.

Abbreviations: a, anus; acgl, accessory colleterial gland; acglo, ovariole-derived accessory colleterial gland; bc, bursa copulatrix; co, common oviduct; cof, canal of fecundation; et, egg tube; gstylIX, gonostylus; ltgVIII, laterotergite VIII; mds, median sclerite.

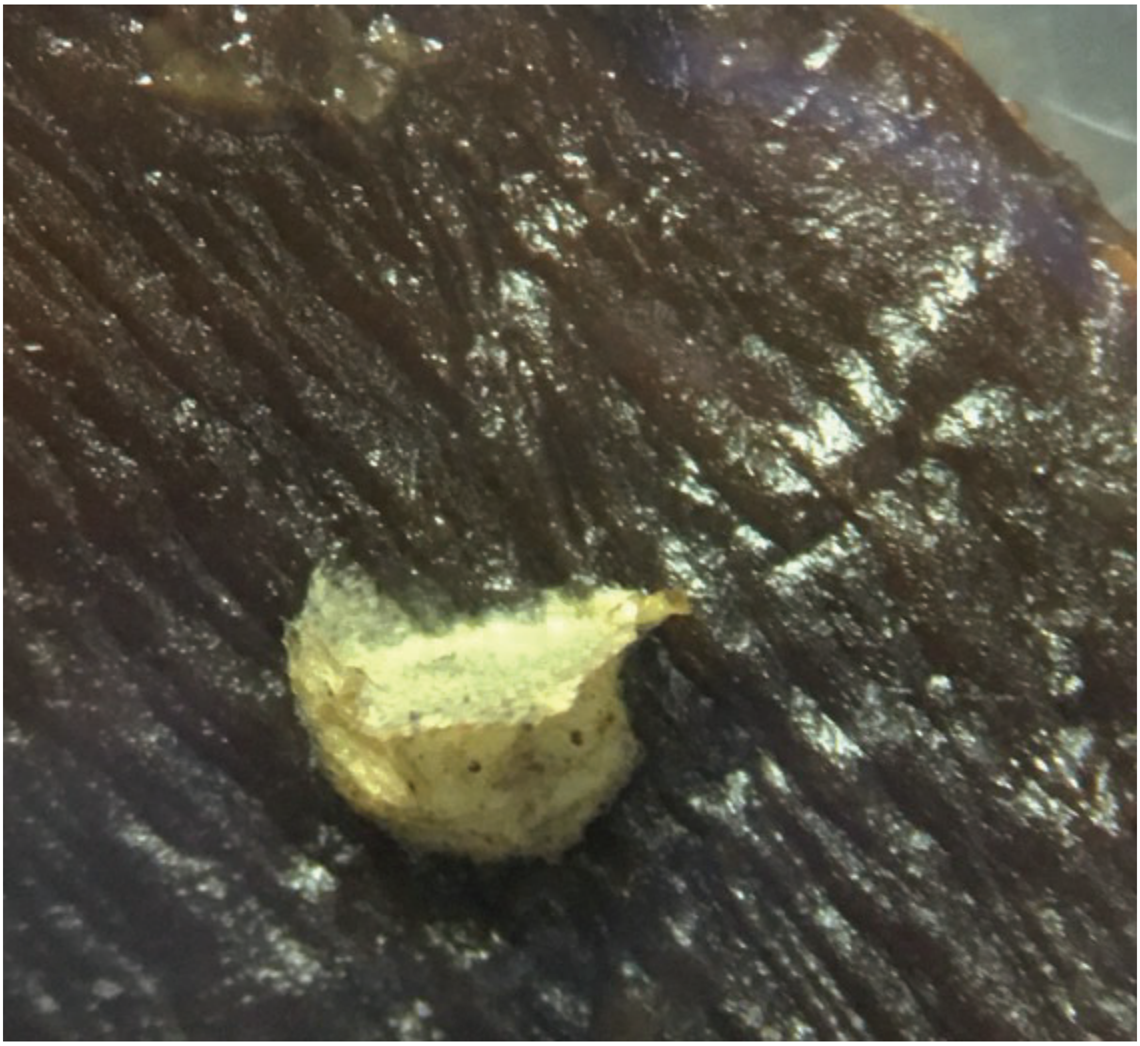

Figure 105. Silk egg case of *Cercyon aptus* on laminaria kelp.

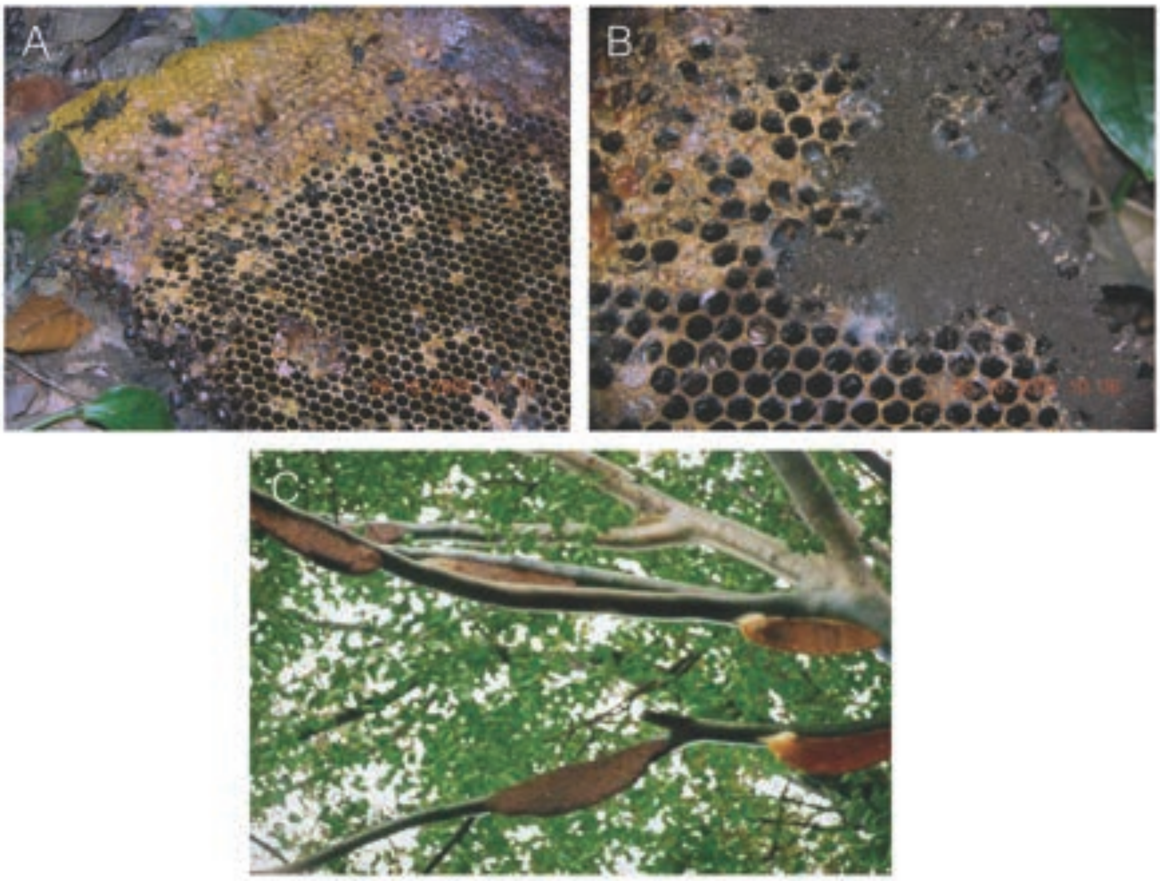

Figure 106. Nest of *Apis dorsata dorsata*. A–B) The fallen nest from which beetles were collected; C) intact nests in tree.

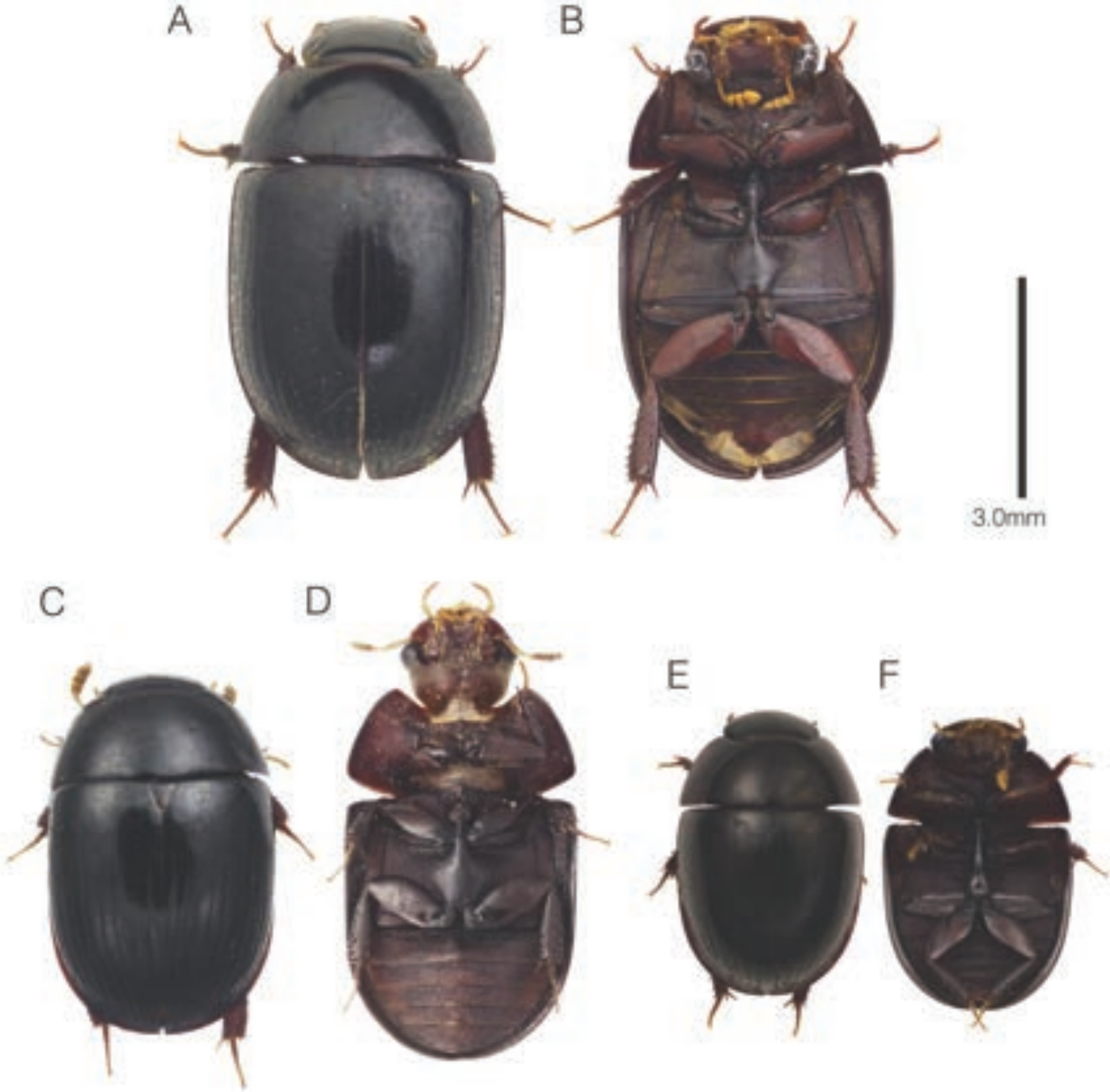

Figure 107. *Dactylosternum* spp., habitus. A–B) *D. hydrophiloides*; C–D) *D. abdominale*; E–F) *D. seriatum*.

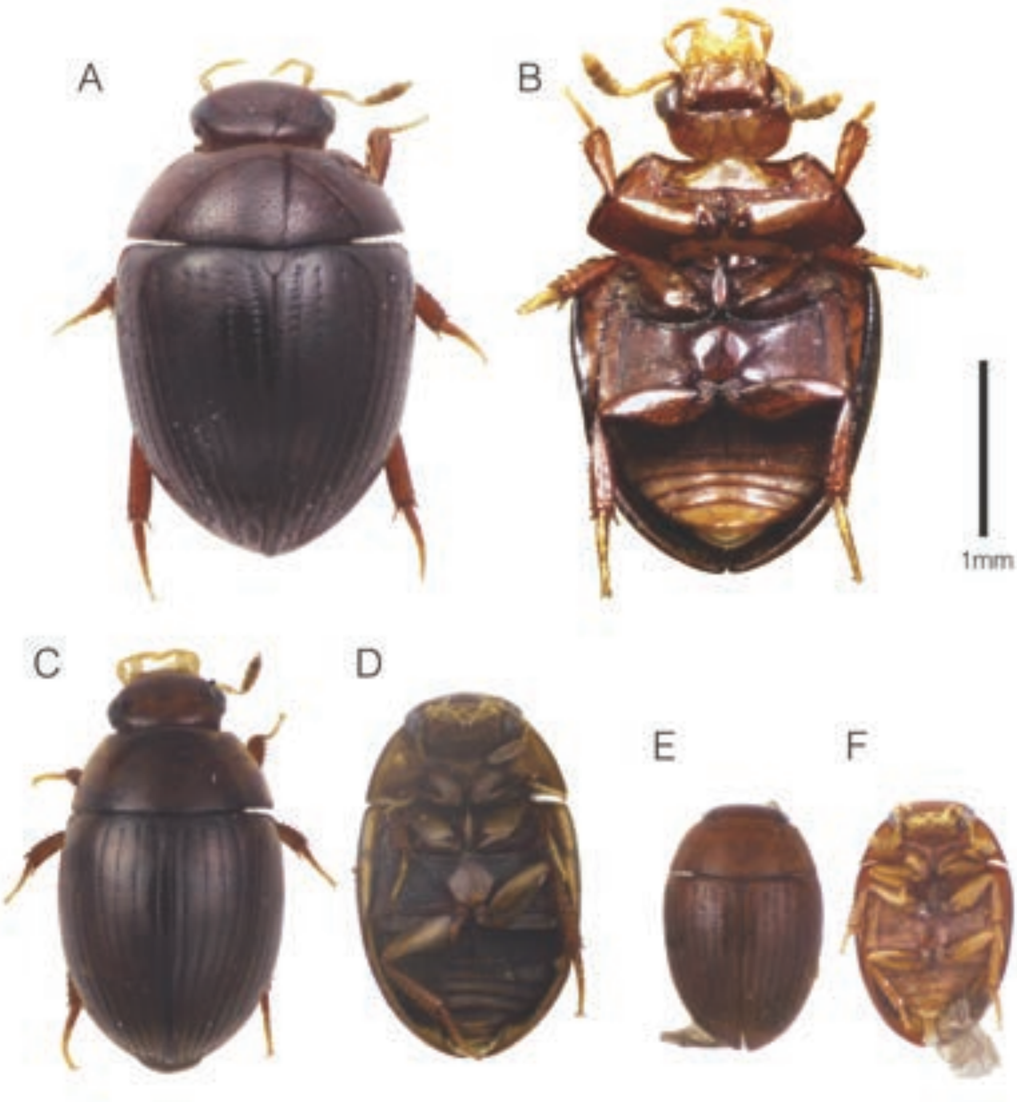

Figure 108. *Cercyon* spp., habitus. A–B) *Cercyon* (*Clinocercyon*) sp.1; C–D) *Cercyon* (*Cercyon*) sp.2; E–F) *Cercyon* (*Cercyon*) sp.3.

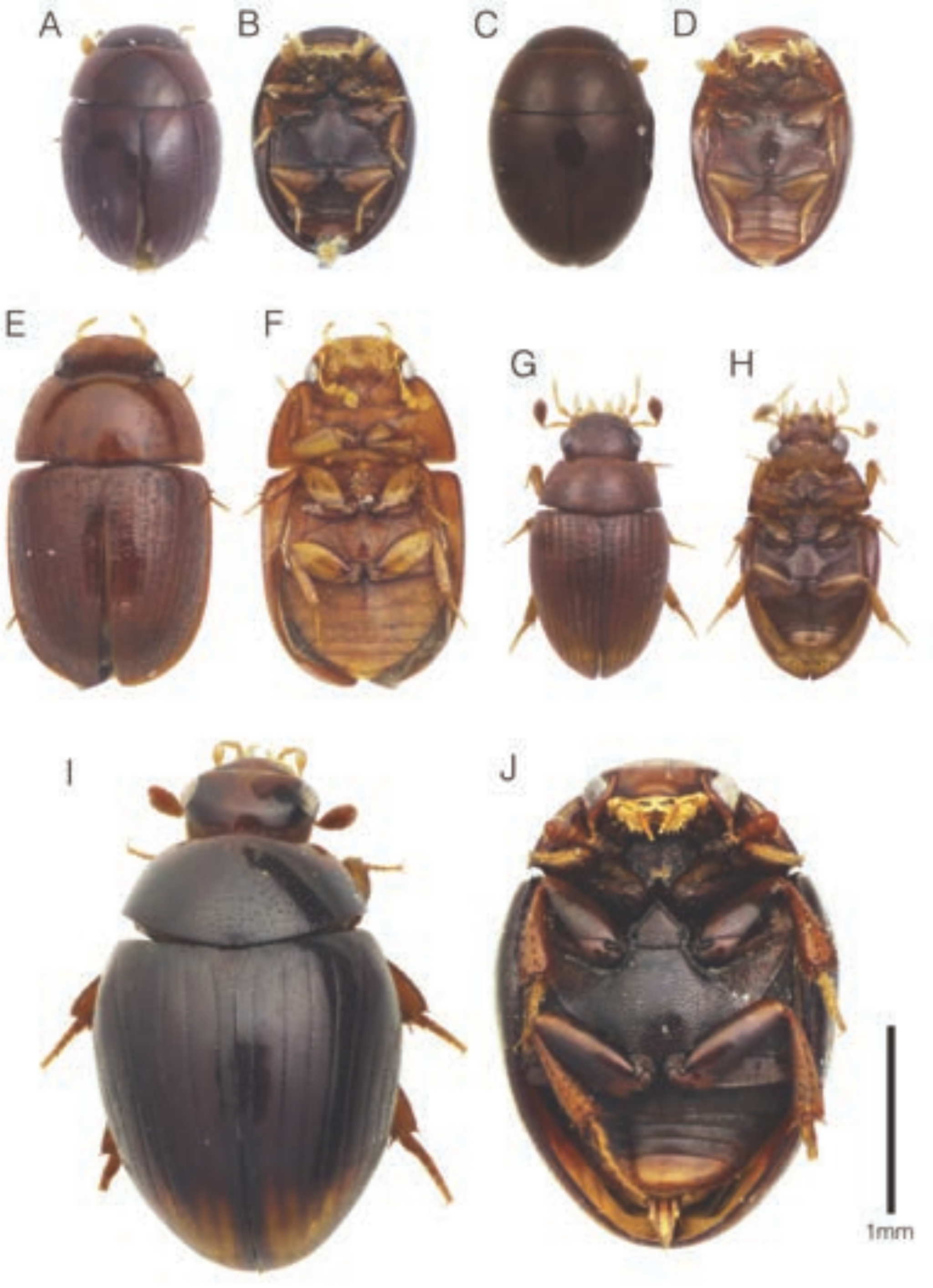

Figure 109. Other species habitus. A–B) *Noteropagus obliquus*; C–D) *N. occlusus*; E–F) *Protosternum hainanensis*; G–H) *Paroosternum saundersi*; I–J) *Pachysternum apicalis*.

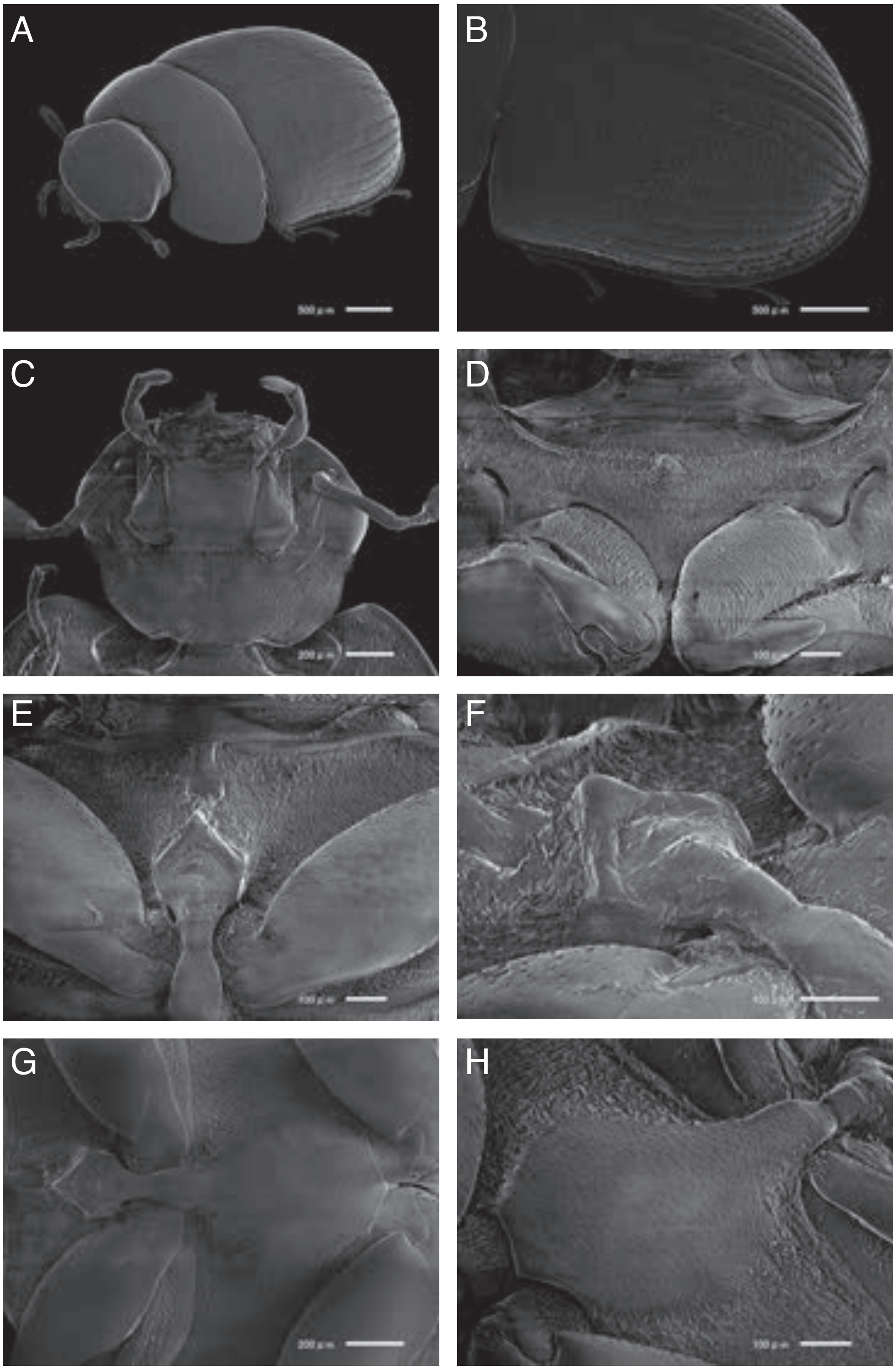

Figure 110. SEM images of *Dactylosternum abdominale*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) mesoventral process, oblique; G) meso- and metaventrites; H) metaventrite, oblique.

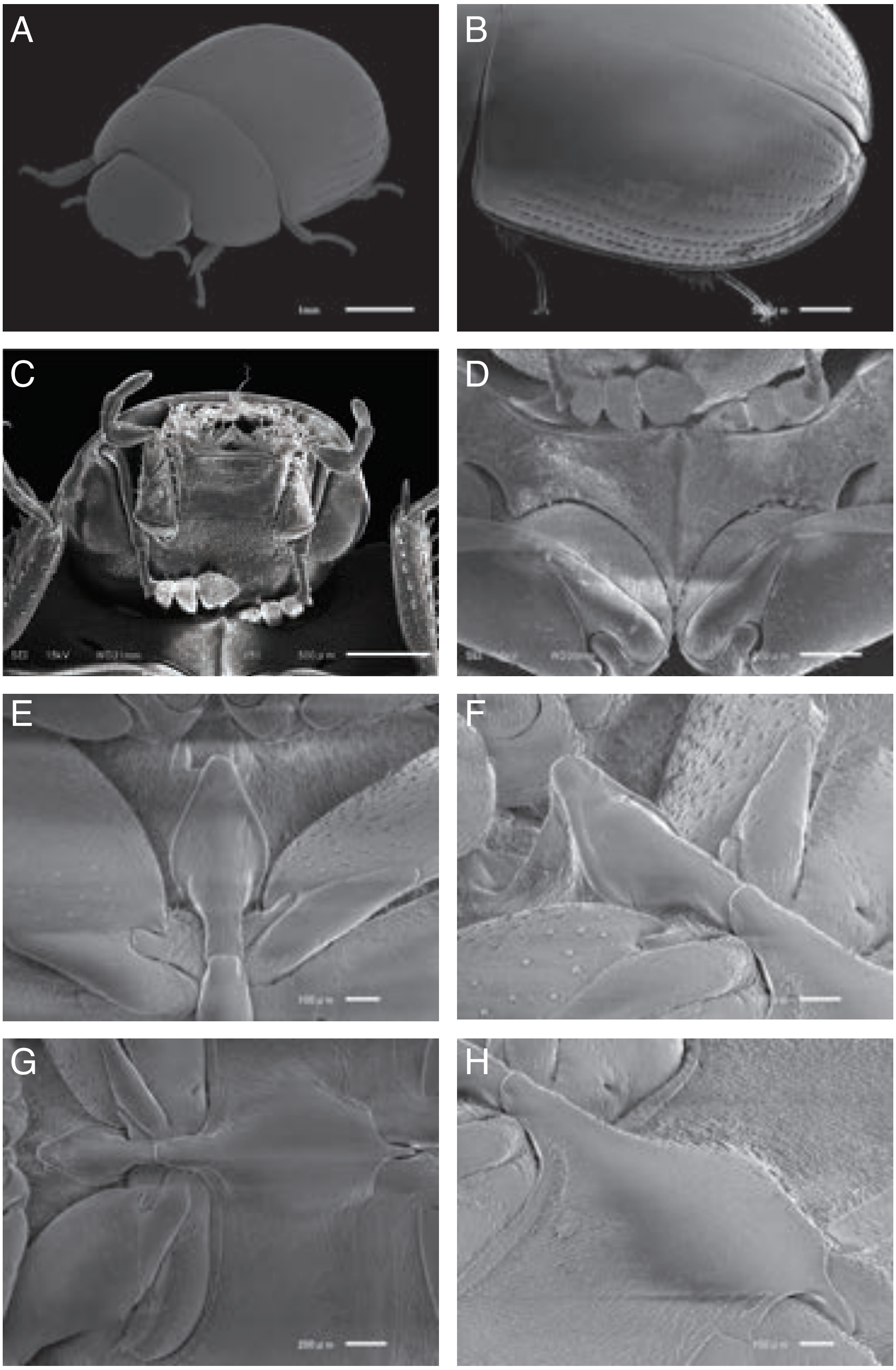

Figure 111. SEM images of *Dactylosternum hydrophiloides*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) mesoventral process, oblique; G) meso- and metaventrites; H) metaventrite, oblique.

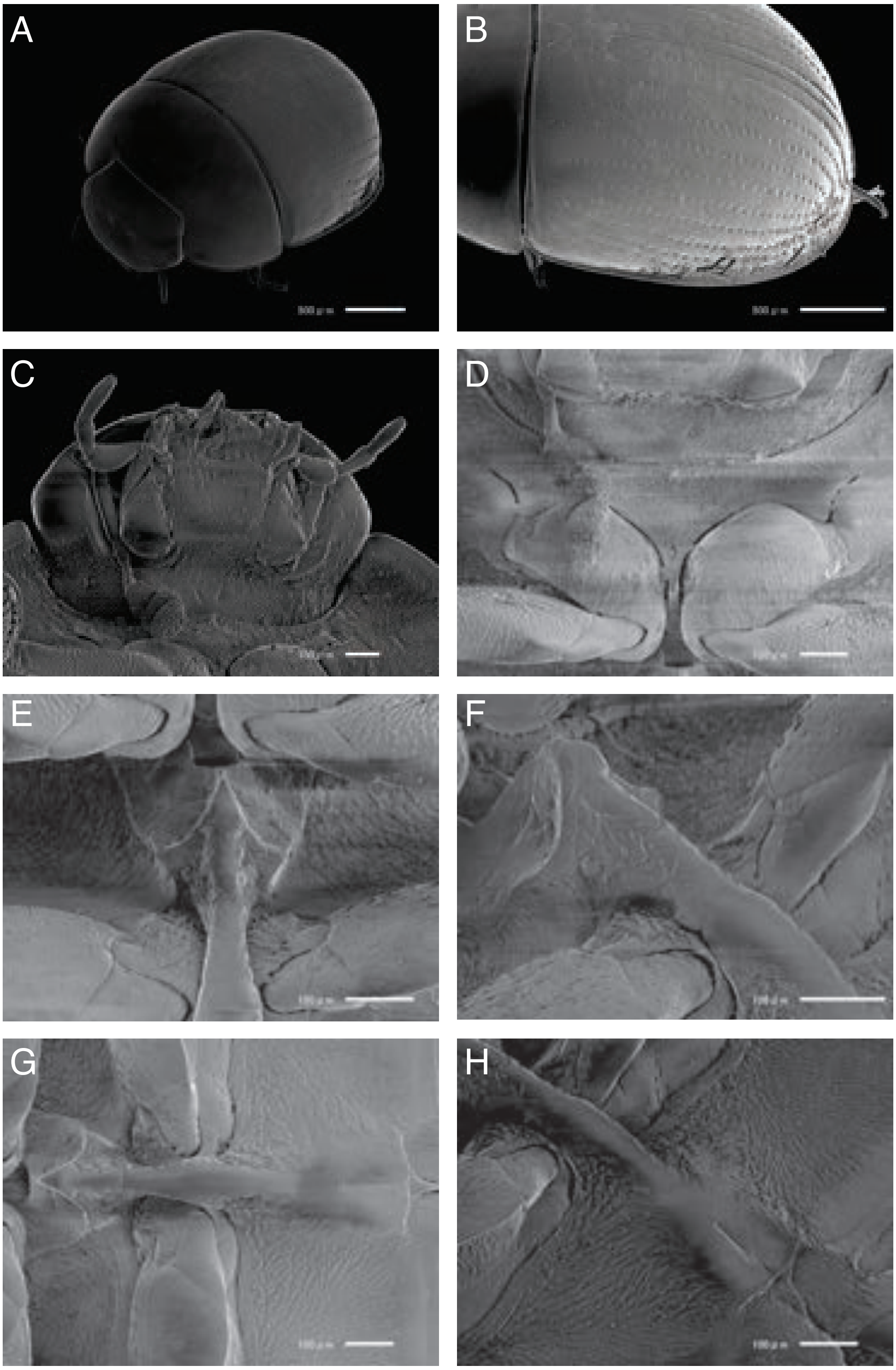

Figure 112. SEM images of *Dactylosternum grouvellei*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) mesoventral process, oblique; G) meso- and metaventrites; H) metaventrite, oblique.

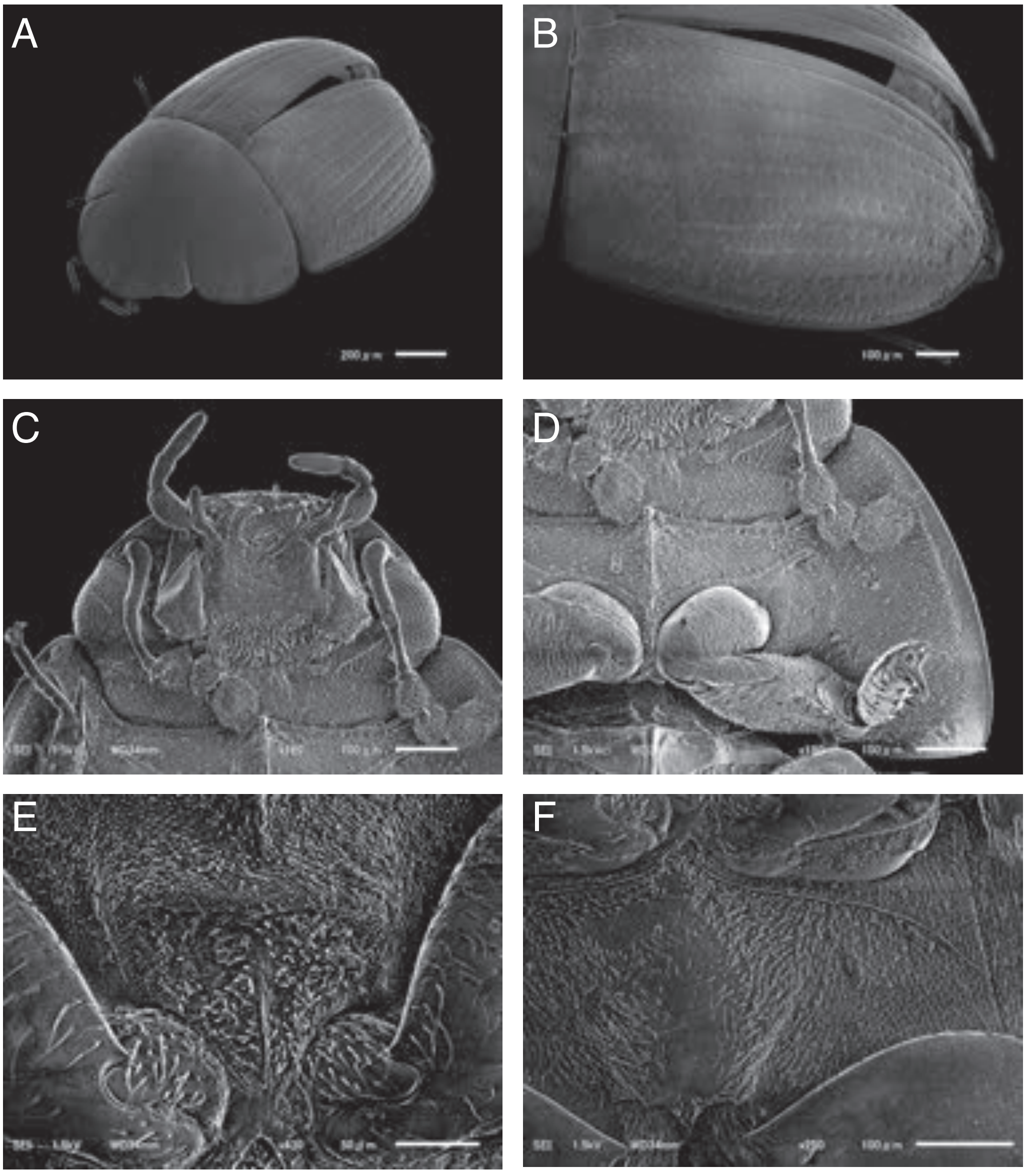

Figure 113. SEM images of *Protosternum hainanensis*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

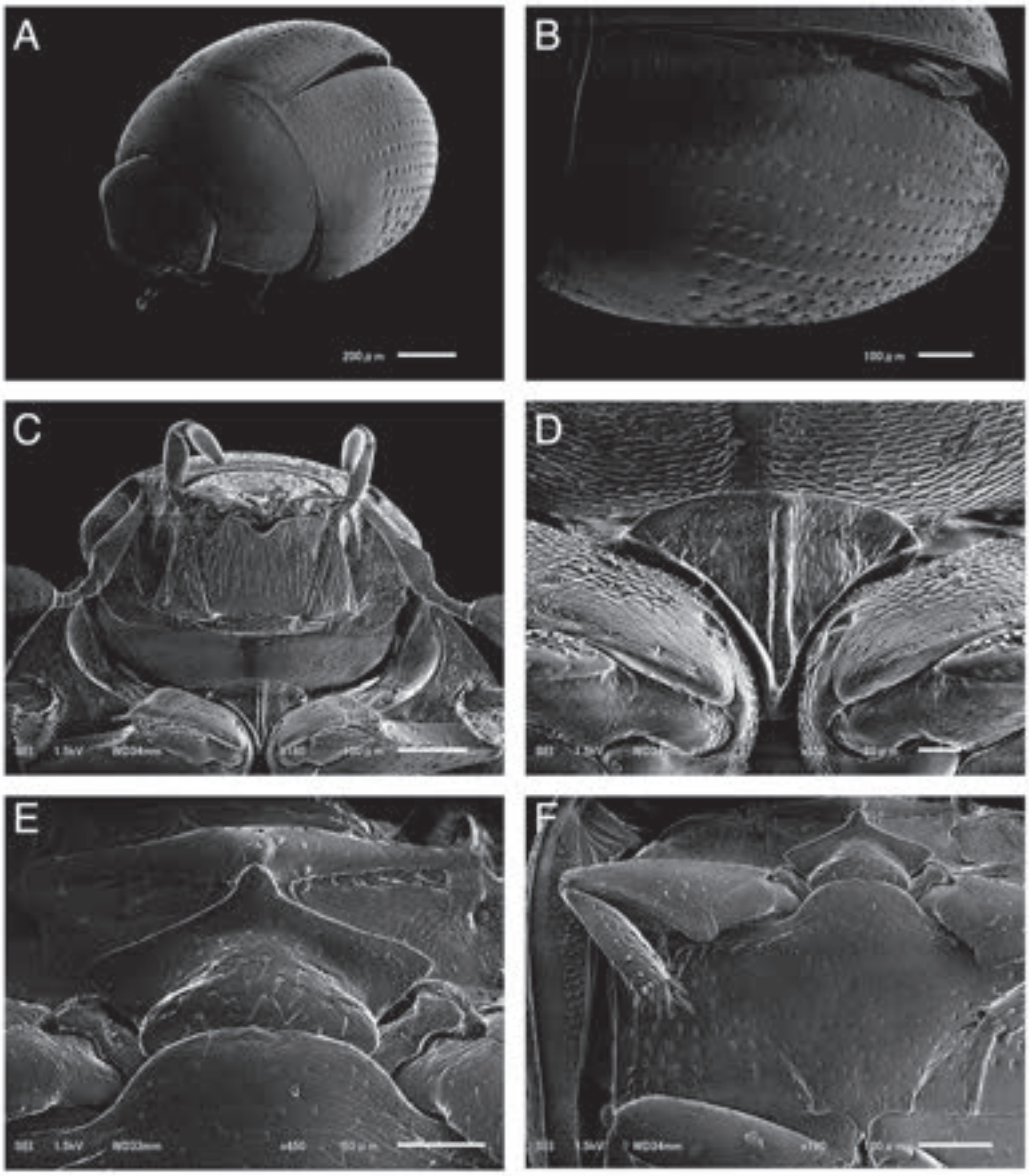

Figure 114. SEM images of *Noteropagus obliquus*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

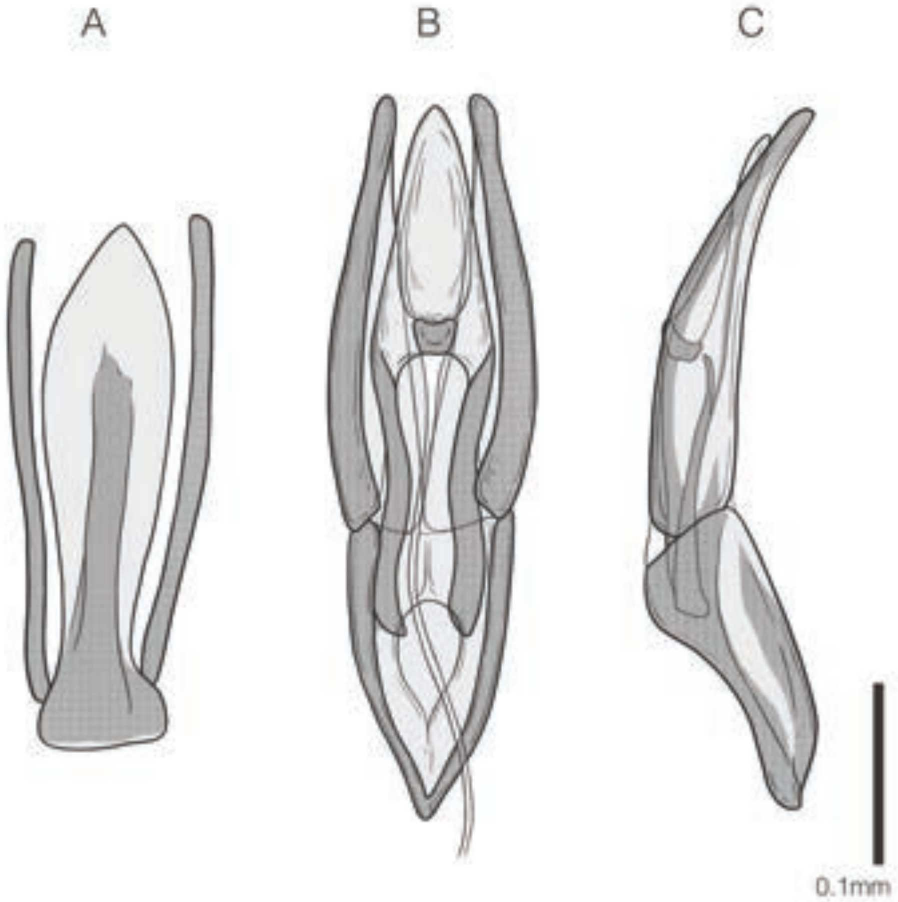

Figure 115. *Noteropagus obliquus*, male genitalia. A) 9th tergite; B) aedeagus, dorsal view; C) aedeagus, lateral view.

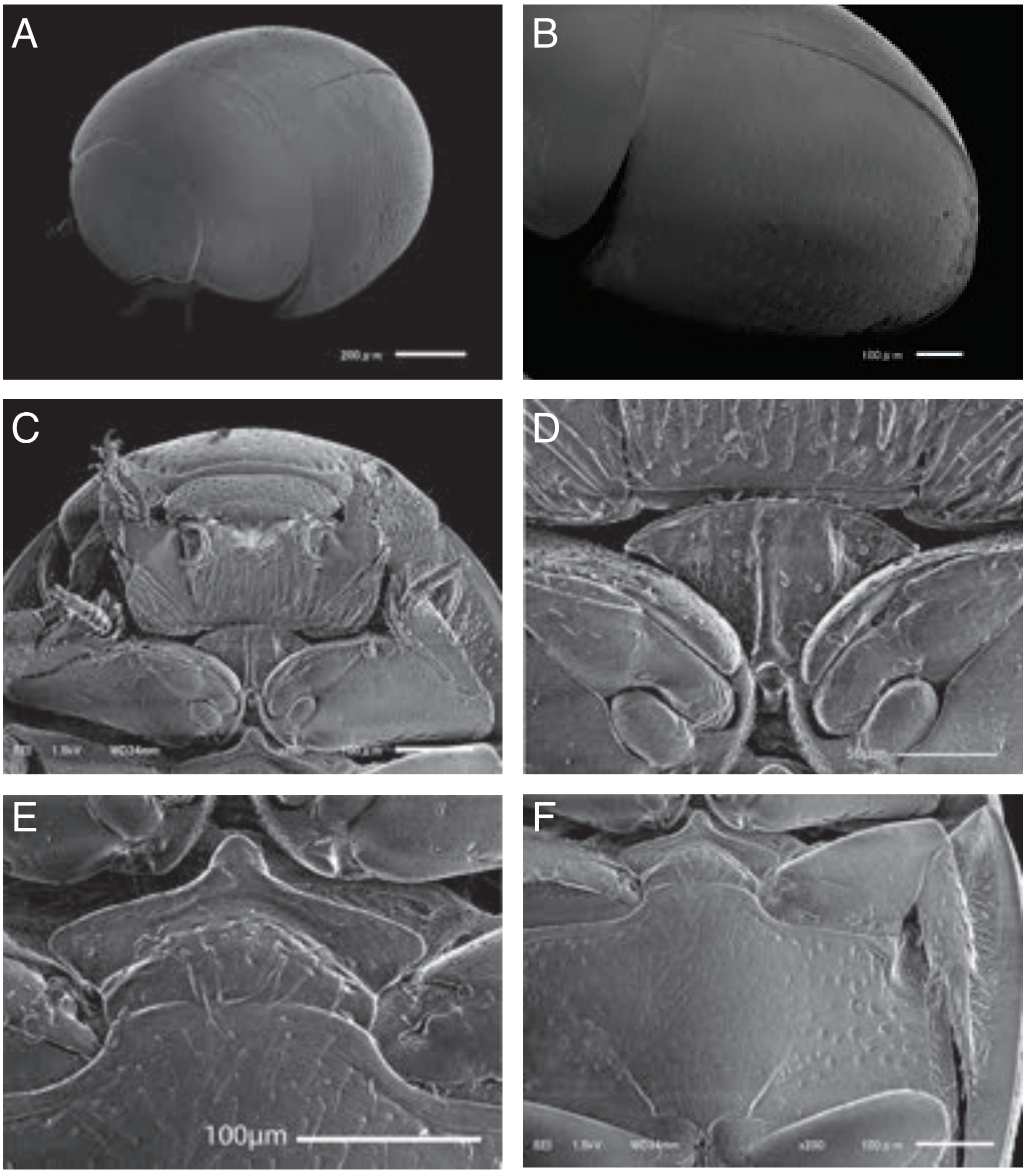

Figure 116. SEM images of *Noteropagus occlusus*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

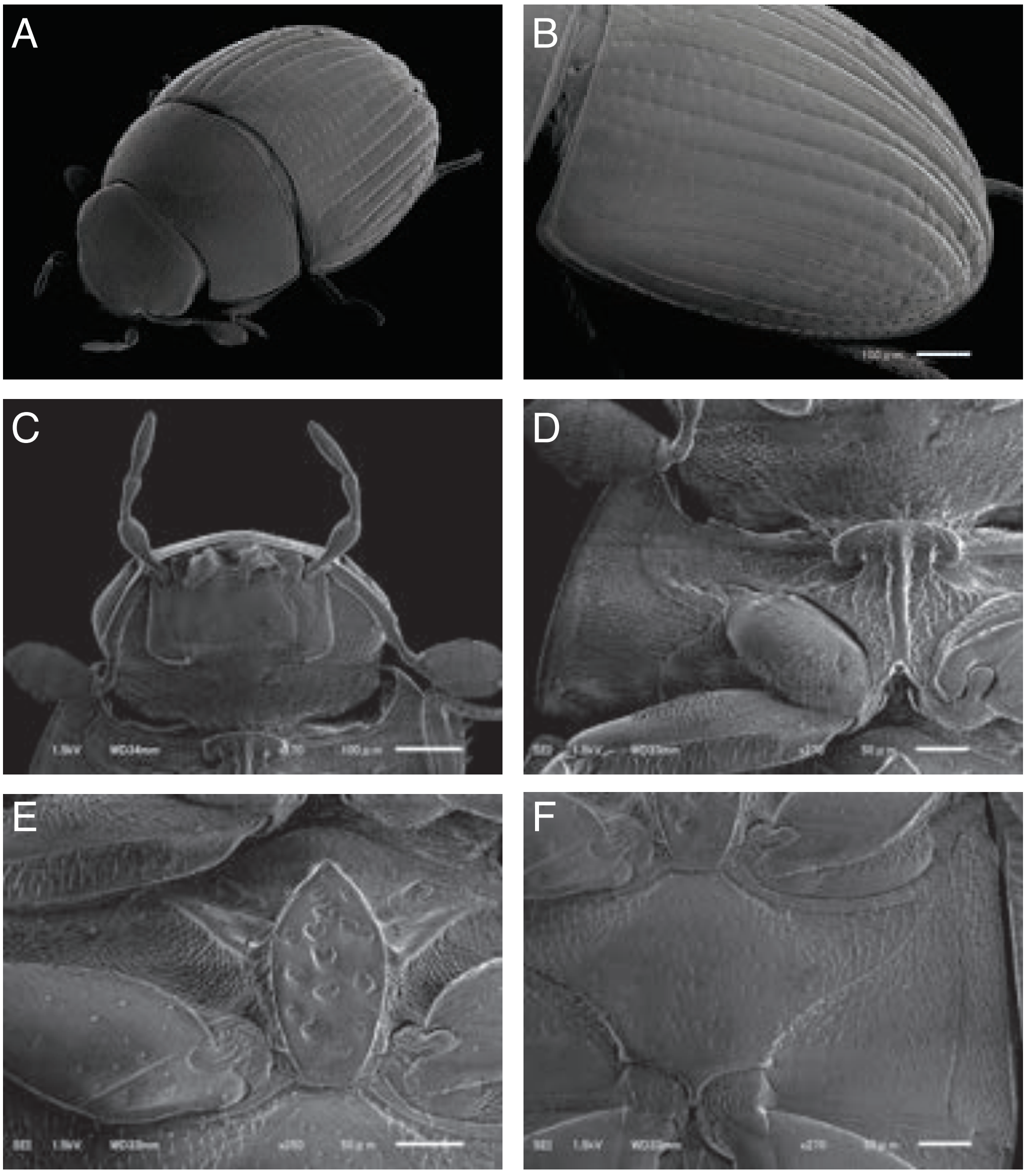

Figure 117. SEM images of *Paroosternum saundersi*. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

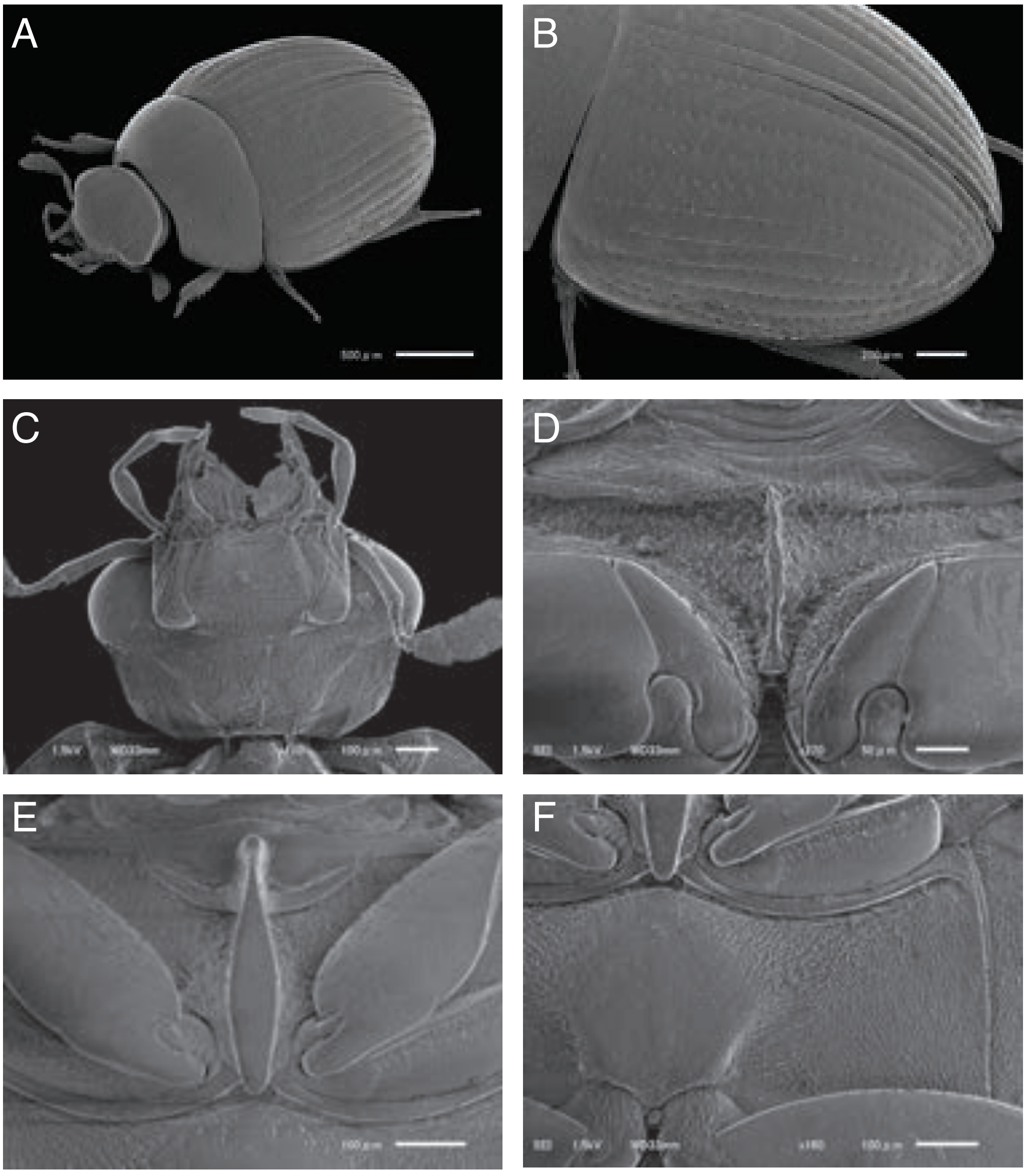

Figure 118. SEM images of *Cercyon* (*Clinocercyon*) sp.1. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

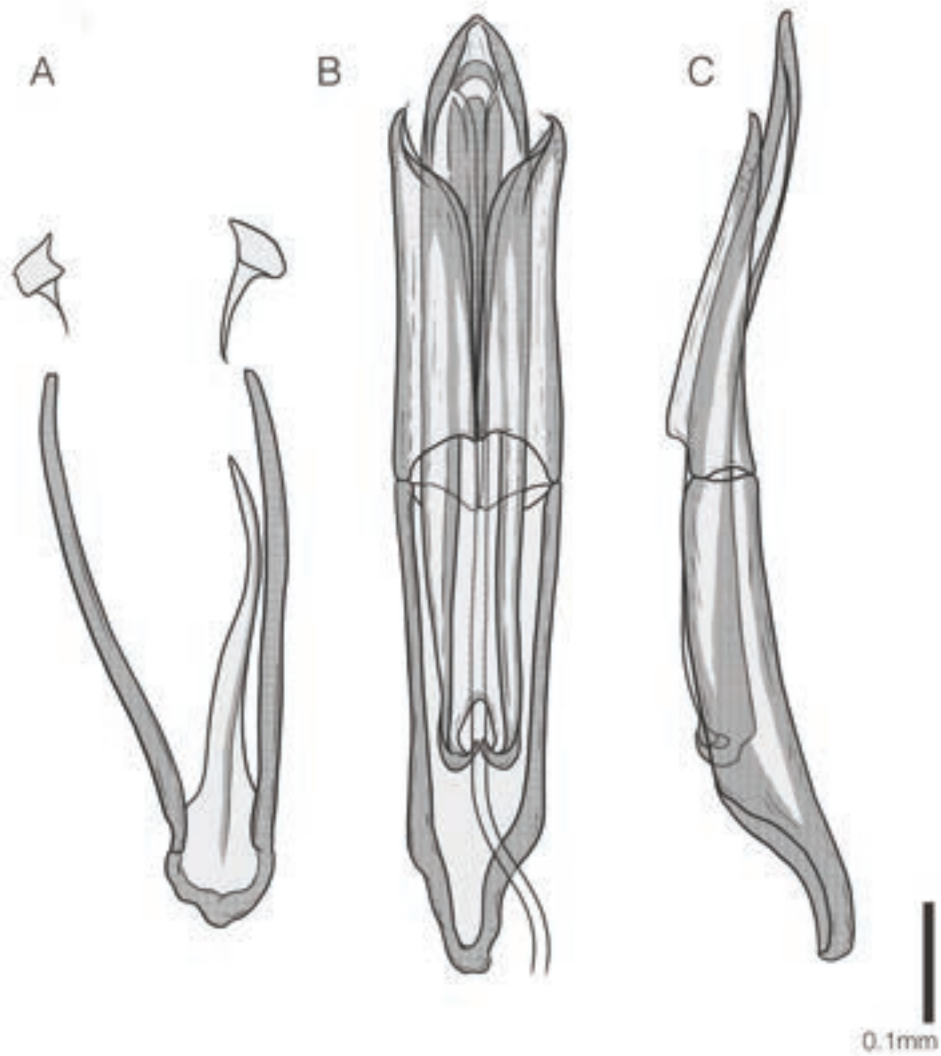

Figure 119. *Cercyon* (*Clinocercyon*) sp.1, male genitalia. A) 9th tergite; B) aedeagus, dorsal view; C) aedeagus, lateral view.

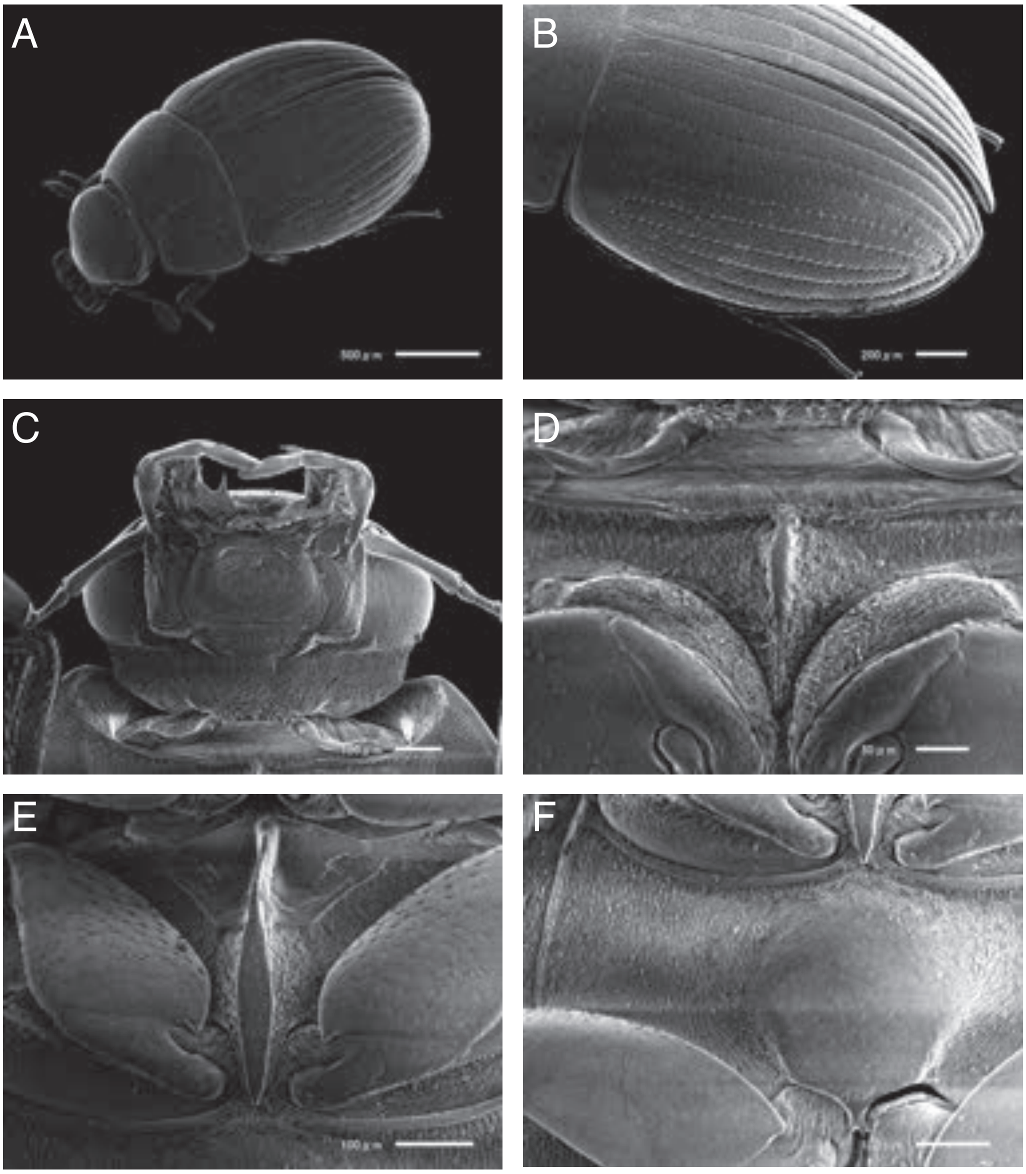

Figure 120. SEM images of *Cercyon* (*Cercyon*) sp.2. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

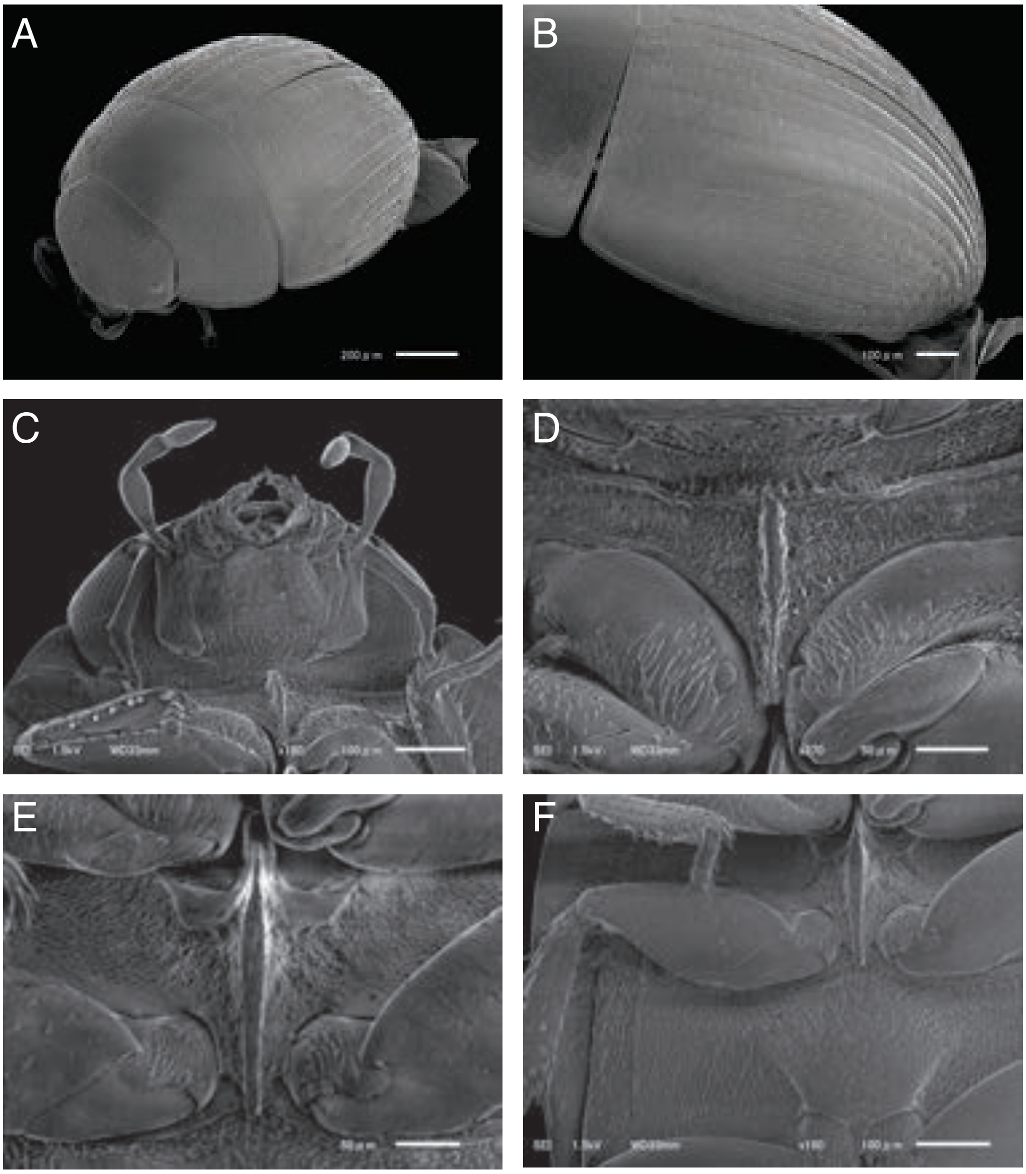

Figure 121. SEM images of *Cercyon* (*Cercyon*) sp.3. A) Full body, dorsal oblique; B) left elytra, lateral; C) head, ventral; D) proventrite; E) mesoventral process; F) metaventrite.

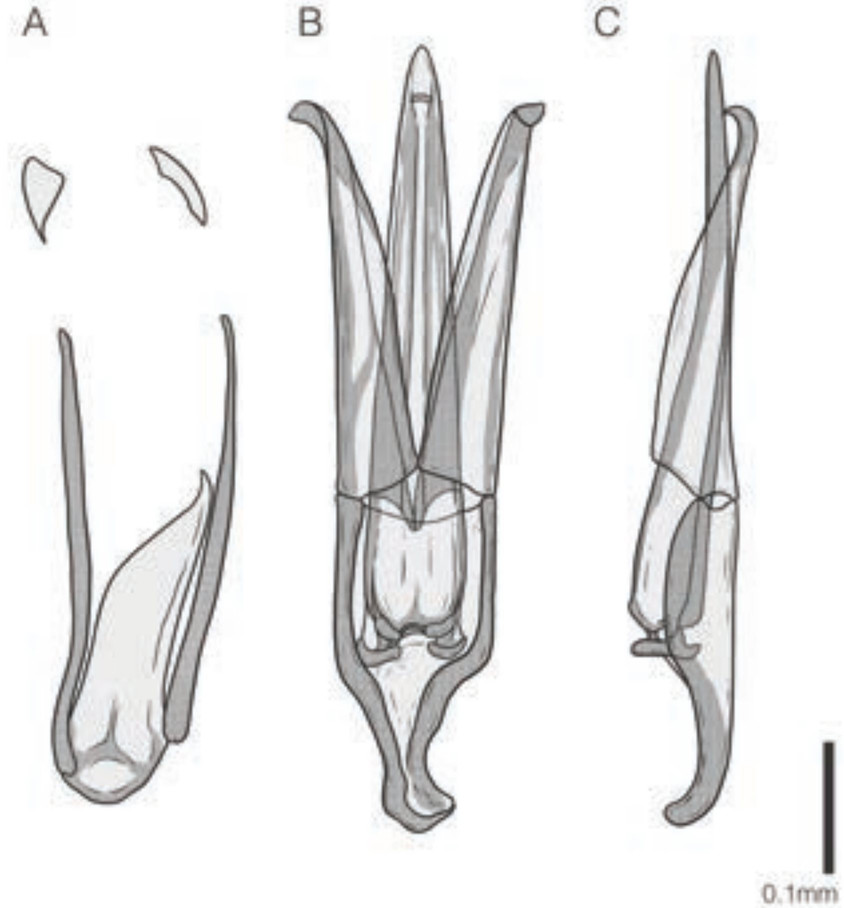

Figure 122. *Cercyon* (*Cercyon*) sp.3, male genitalia. A) 9th tergite; B) aedeagus, dorsal view; C) aedeagus, lateral view.

Figure 123. *Microchaetes* sp., habitus. A) Dorsal; B) ventral.

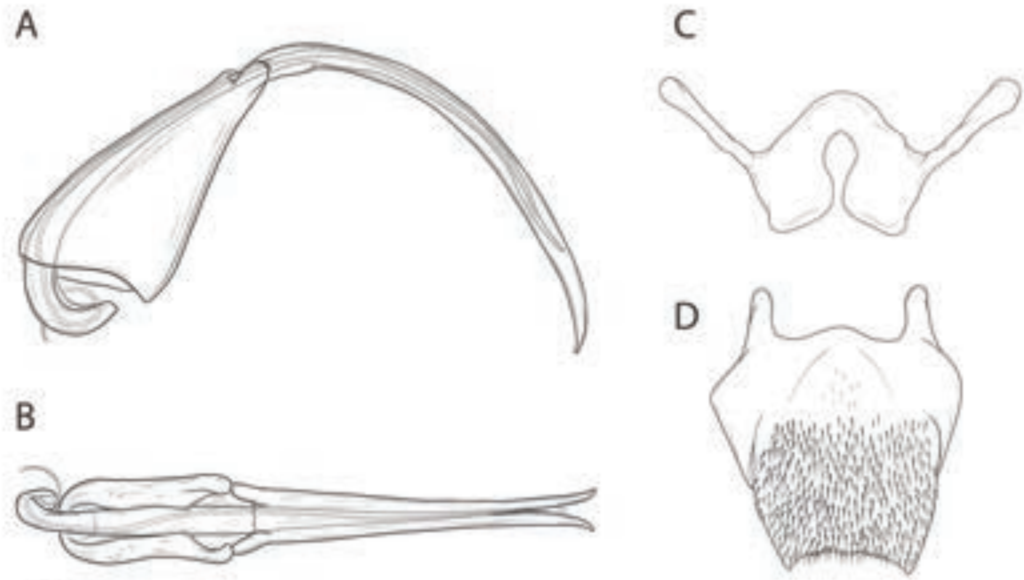

Figure 124. *Microchaetes* sp., male terminalia. A) Aedeagus, lateral; B) aedeagus, dorsal; C) abdominal tergite VIII; D) abdominal tergite IX (pygidium).

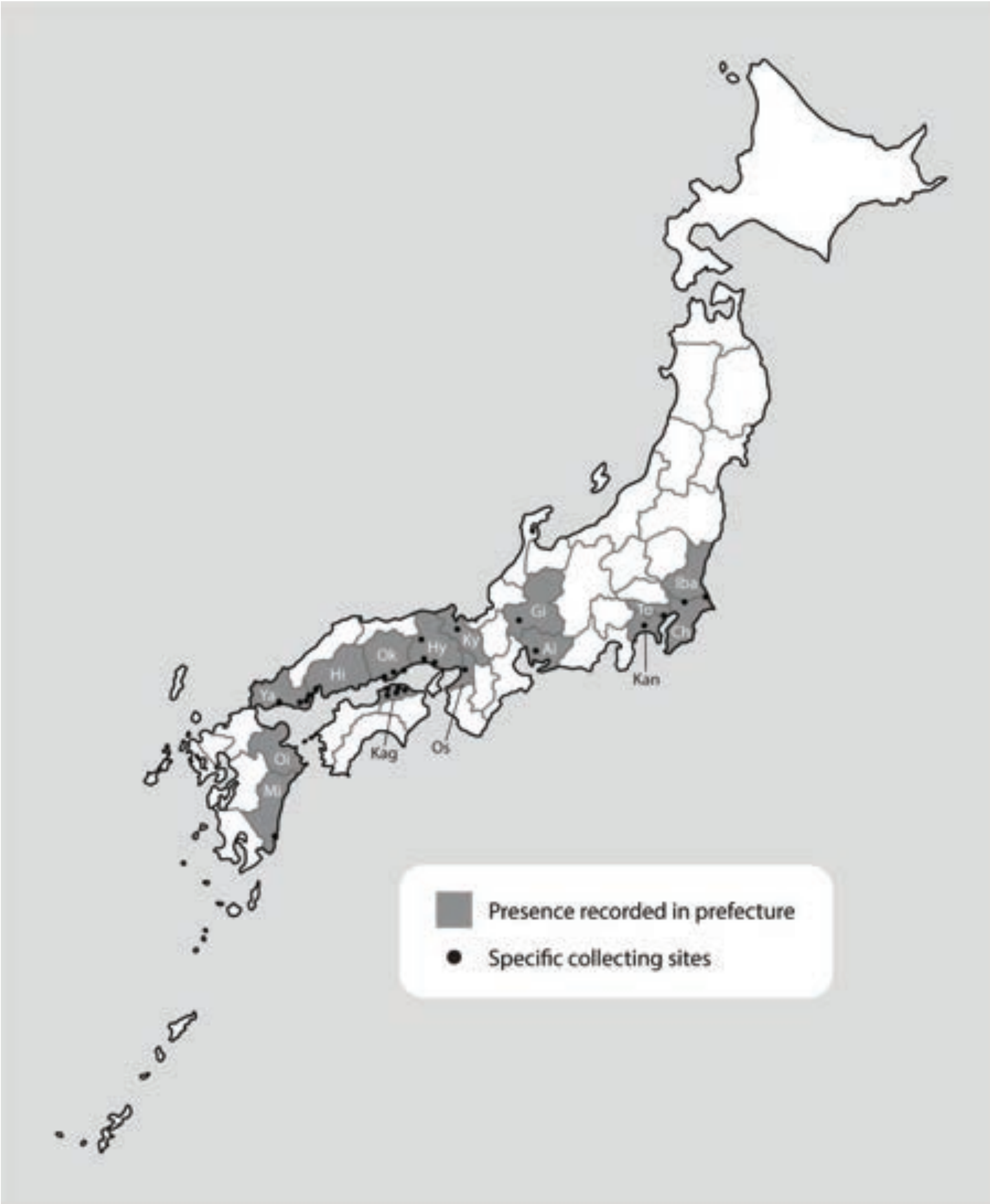

Figure 125. Distribution map of *Microchaetes* sp. recorded in Japan.
Abbreviations: **Ai**, Aichi; **Ch**, Chiba; **Gi**, Gifu; **Hi**, Hiroshima; **Hy**, Hyogo; **Iba**, Ibaraki; **Kag**, Kagawa; **Kan**, Kanagawa; **Ky**, Kyoto; **Oi**, Oita; **Ok**, Okayama; **Os**, Osaka; **To**, Tokyo; **Ya**, Yamaguchi.

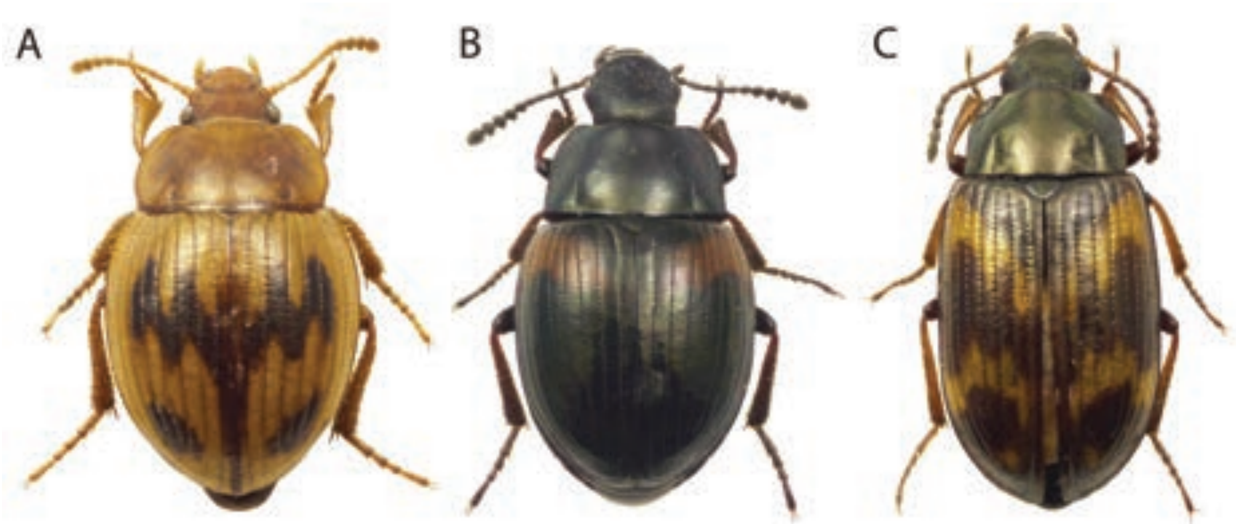

Figure 126. Habitus of A) P*haleromela picta*, B) *P. subhumeralis*, and C) *P. variegata*.

Figure 127. Habitat of A, C) *Phaleromela. subhumeralis* (Japan, Hokkaido, near the mouth of Ishikari River) and B, D, E) *P. picta* (USA, Washington, Golden Gardens Park, Seattle).

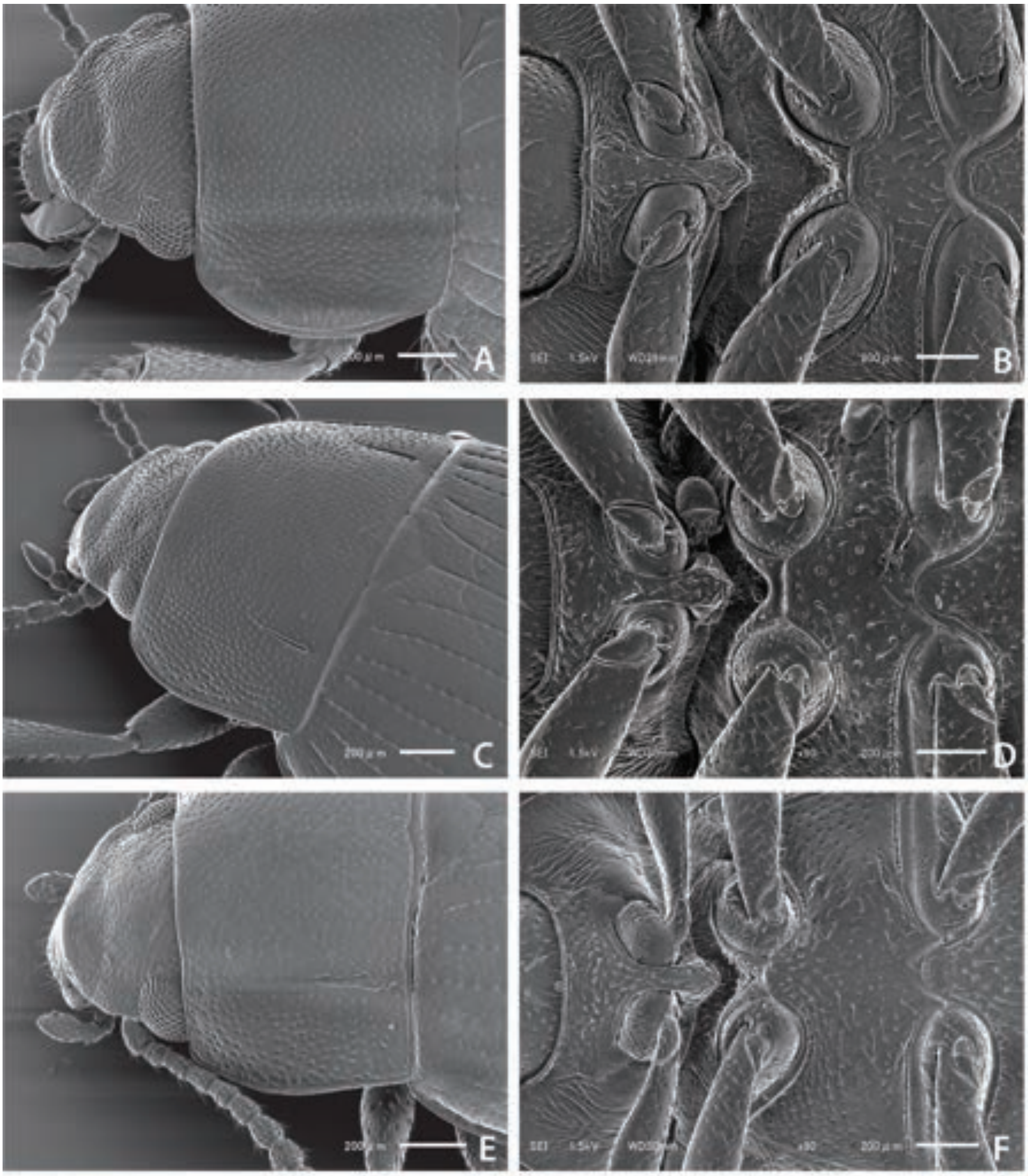

Figure 128. Scanning electron microscope images; A) *Phaleromela. picta* pronotum, oblique; B) *P. picta* ventral thoracic details; C) *P. subhumeralis* pronotum; D) *P. subhumeralis* ventral thoracic details; E) *P. variegata* pronotum; F) *P. variegata* ventral thoracic details.

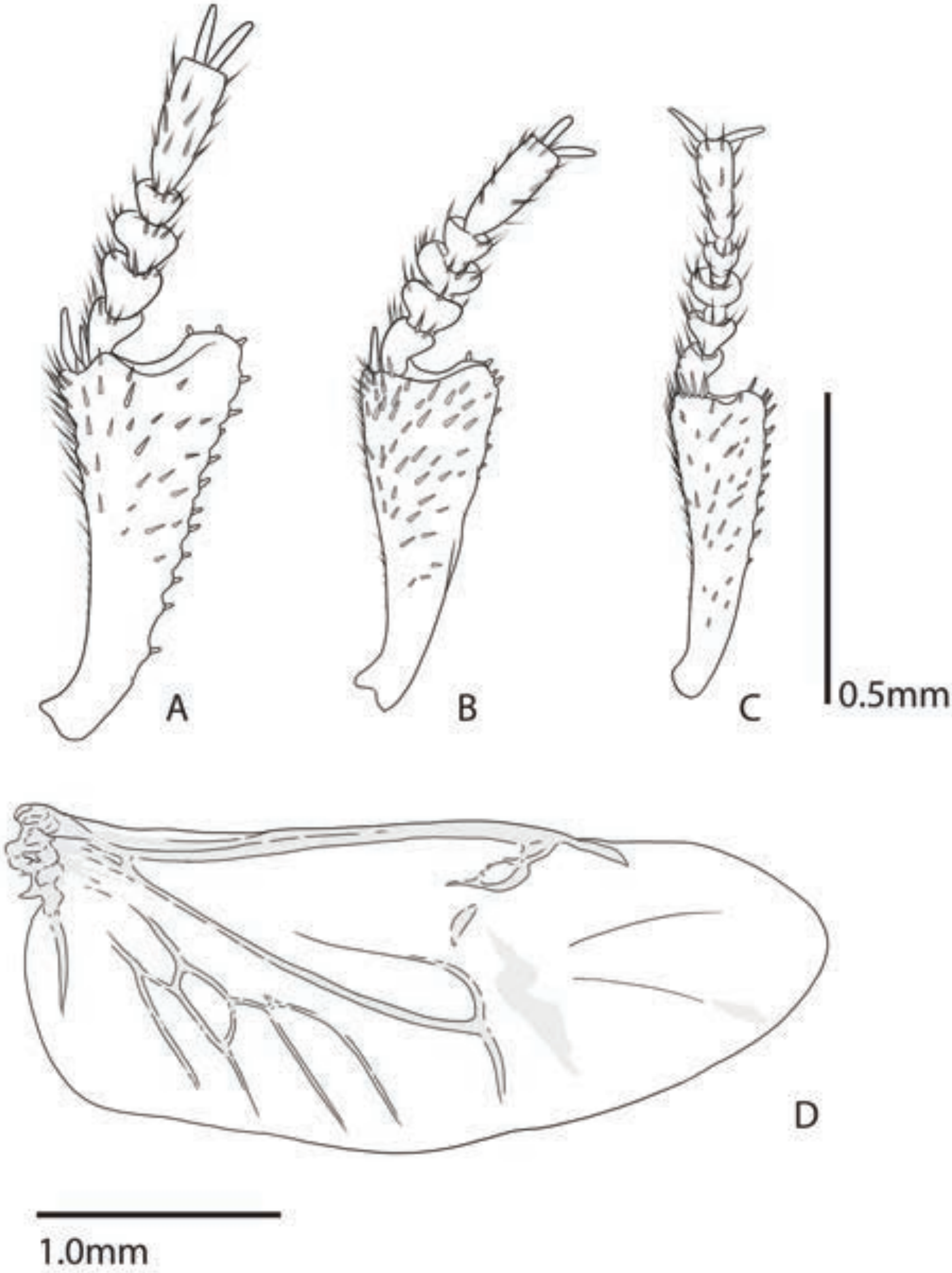

Figure 129. Illustrations of male right protarsi, dorsal view, of A) *Phaleromela picta*; B) *P. subhumeralis*, and C) *P. variegata* and D) right wing of *P. variegata*.

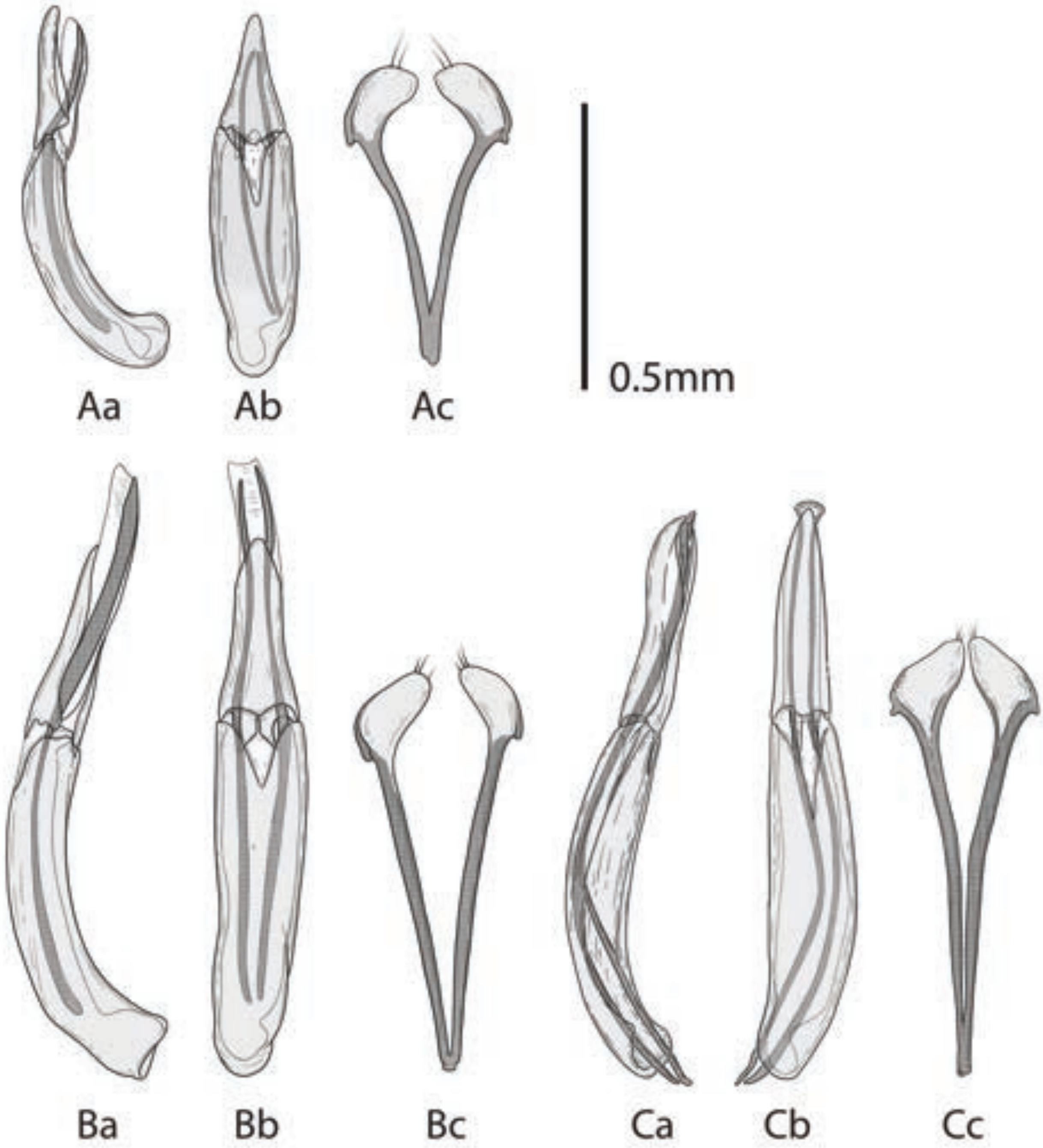

Figure 130. Illustrations of genitalia. A) *Phaleromela picta*: Aa) aedeagus lateral, Ab) aedeagus dorsal, Ac) gastral spicula; B) *P. subhumeralis*: Aa) aedeagus lateral, Ab) aedeagus dorsal, Ac) gastral spicula; and C) *P. variegata*: Ca) aedeagus lateral, Cb) aedeagus dorsal, Cc) gastral spicula.

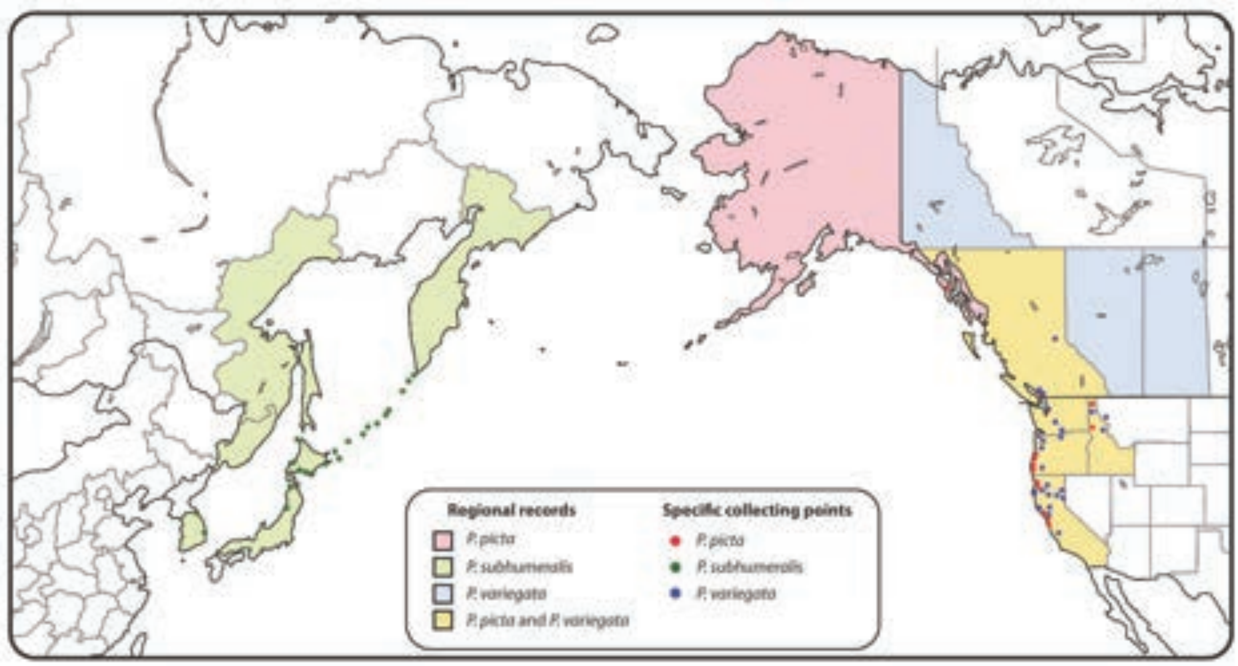

Figure 131. Distribution map. World distribution of *Phaleromela picta*, *P. subhumeralis*, and *P. variegata;* shaded areas represent regions (provinces, states, etc.) with species records, circles are specific recorded collecting points.