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A new species of genus *Rhynchina* Guenée, 1854 from Mt Taibai, China (Lepidoptera, Erebidae, Hypeninae)

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Abstract

A new species, *Rhynchina taibaishana* Han, **sp. n.** is described from Mt Taibai, China. The new species is illustrated with images of adults and genitalia, and compared with *R. deqinensis* Han, 2008, *R. helga* Gaal, 1998 and *R. mandarinalis* Leech, 1900.

Keywords

China, Erebidae, Hypeninae, Lepidoptera, new species, *Rhynchina*

Introduction

The genus *Rhynchina* Guenée, 1854 is highly diverse and mostly distributed in the Eastern Palaearctic and Oriental regions. It contains more than 56 described species worldwide (Poole 1989; Lödl 1994, 1997, 1998a, b, c, 1999a, b, 2000; Mayerl and Lödl 1997, 1999; Gaal 1998; Lödl and Gaal 1998; Mayerl 1998; Chen 1999; Han 2008; Hacker et al. 2011; Hacker 2013; Pan and Han 2015; Pekarsky 2017). Among them, 20 species are recorded from China (Chen 1999; Han 2008; Pan and Han 2015; Pekarsky 2017).

In the present study, a new species is described from Mt Taibai, Shaanxi province, China. This new species is compared with its closest relatives, *R. deqinensis* Han, 2008 and *R. helga* Gaal, 1998; some specimens of *R. taibaishana* sp. n. and *R. mandarinalis* Leech, 1900 show also some resemblance in external appearance. All of these species are easily distinguished on the basis of their forewing patterns and configuration of genitalia.

Materials and methods

All material studied of the new taxon was collected by light trap. Abdomens were macerated in 10% NaOH solution to digest internal tissues; after careful cleaning and removal of scales and contents of coelom, genitalia were examined, compared, and described before being mounted onto microscope slides. Photographs of the adults were taken with a Nikon D300 digital camera and the genitalia were photographed via the Qcapture pro system. Figures were compiled in Adobe Photoshop v. 6.0. The type materials of the new species are deposited in the School of Forestry, Northeast Forestry University, Harbin, China (**NEFU**).

Taxonomic account

Genus *Rhynchina* Guenée, 1854

Rhynchina Guenée, 1854, in Boisduval & Guenée, Histoire Naturelle des Insectes, Species Général des Lépidoptères 8: 20. Type species: *Rhynchina pionealis* Guenée, 1854 [Central India].

Plumipalpia Hampson, 1898, Journal of the Bombay Natural History Society 11(4): 705. Type species: *Plumipalpia lignicolor* Hampson, 1898 [NW Himalayas, Kasauli].

Rhabinogana Draudt, 1950, Mitteilungen der münchner entomologischen Gesellschaft 40: 117. Type species: *Rhabinogana albistriga* Draudt, 1950 [China, Yangtse Valley, Batang; A-tun-tse].

Rhynchina taibaishana Han, sp. n.

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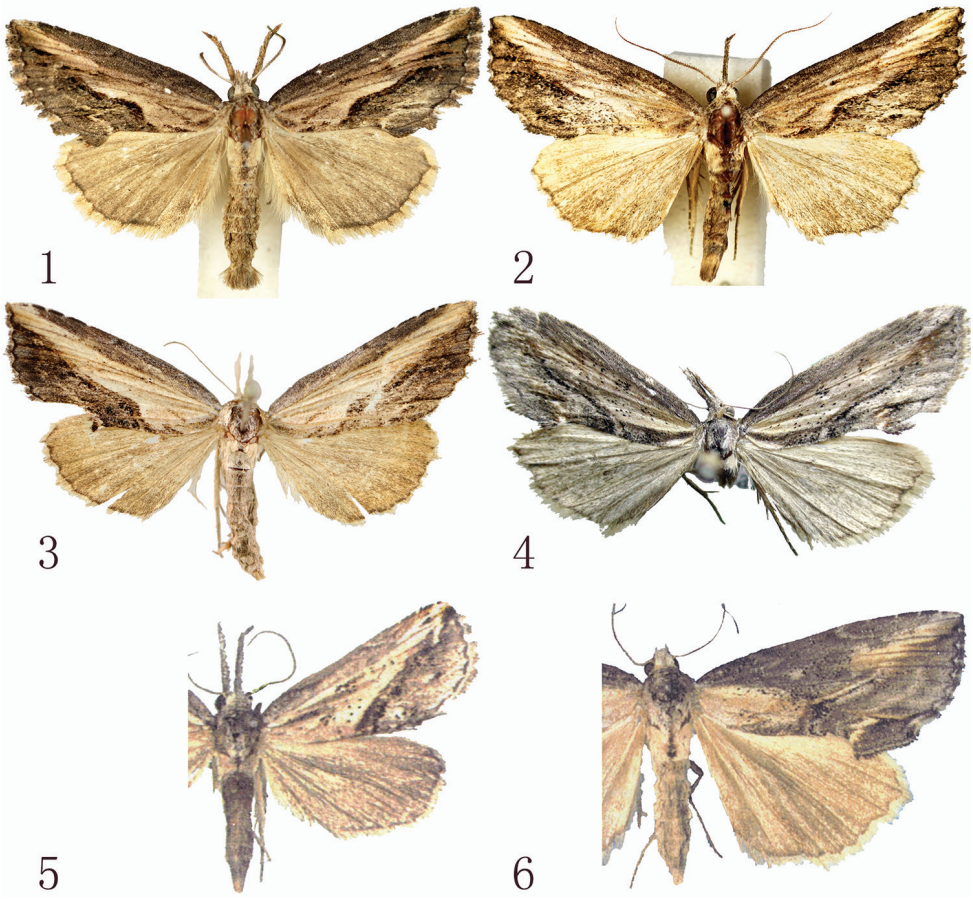
Figures 1–3, 7, 11, 14, 15

Holotype. ♂, China, Shaanxi Province, Mt Taibai, Haoping, 2–10.V.2010, leg. TY. Shao, XW. Liu [NEFU], genit. prep. hhl-2125-1.

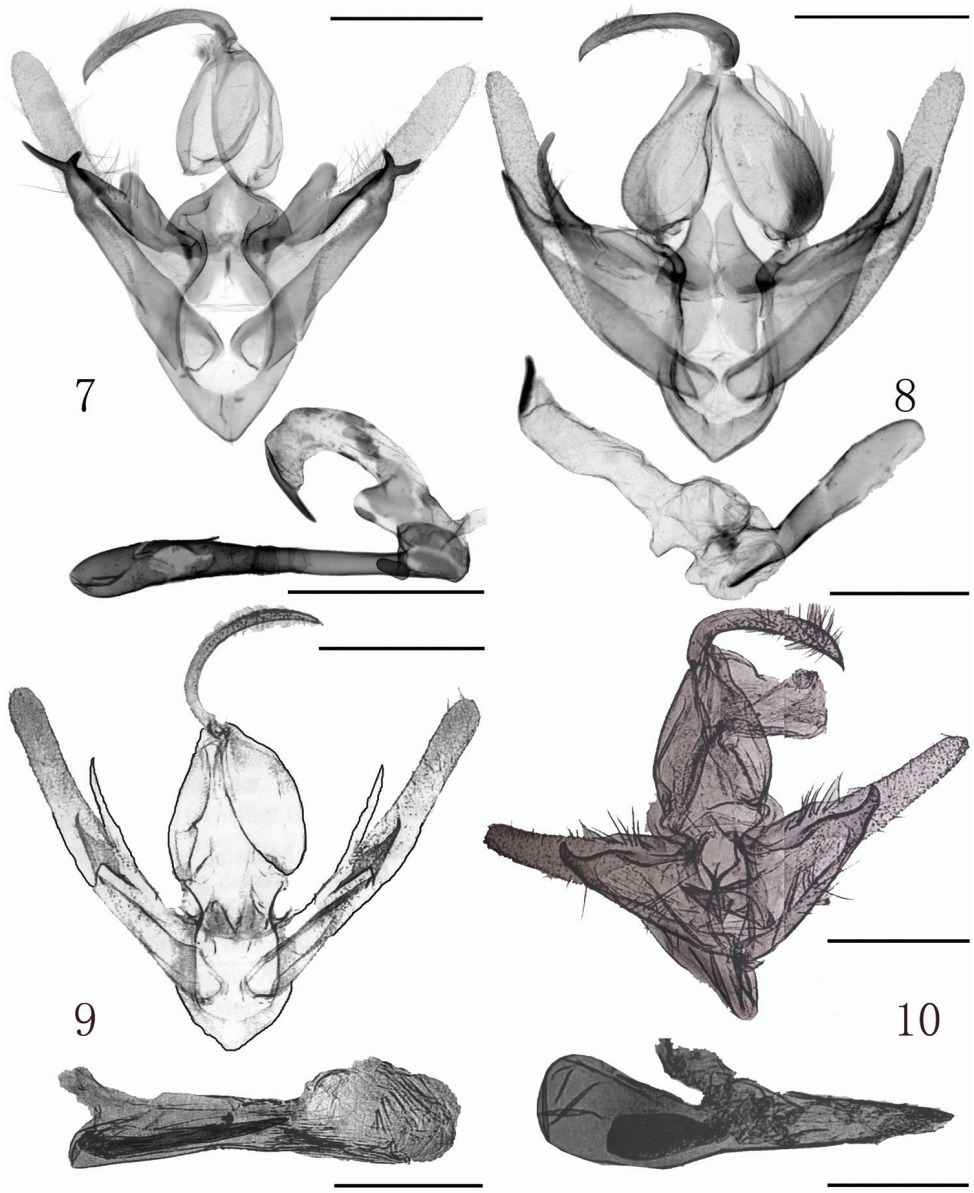
Paratypes. 1♂, 1♀, same data as holotype [NEFU], genit. prep. hhl-2124-1 (♂), hhl-3817-2 (♀).

Diagnosis. The adult of the new species is similar to *R. deqinensis* Han, 2008 (Fig. 4) and *R. helga* Gaal, 1998 (Fig. 5), but the forewing apex of *R. taibaishana* is sharper than that in *R. deqinensis* and *R. helga*. The postmedial line of *R. taibaishana* undulates more obviously, and bends strongly at CuA_2, but that of *R. deqinensis* and *R. helga* is smooth. The terminal line is strongly serrated in *R. taibaishana*, but in *R. deqinensis* and *R. helga* it is rather smooth. The orbicular spot of *R. taibaishana* is small, black and indistinct in some specimens, while in *R. deqinensis* and *R. helga* it consists of fine black speckles. In the male genitalia, the costal process of *R. taibaishana* (Fig. 7) is stout and extends over 1/3 the length of valva, but in *R. deqinensis* (Fig. 8) and *R. helga* (Fig. 9) the costal pro-



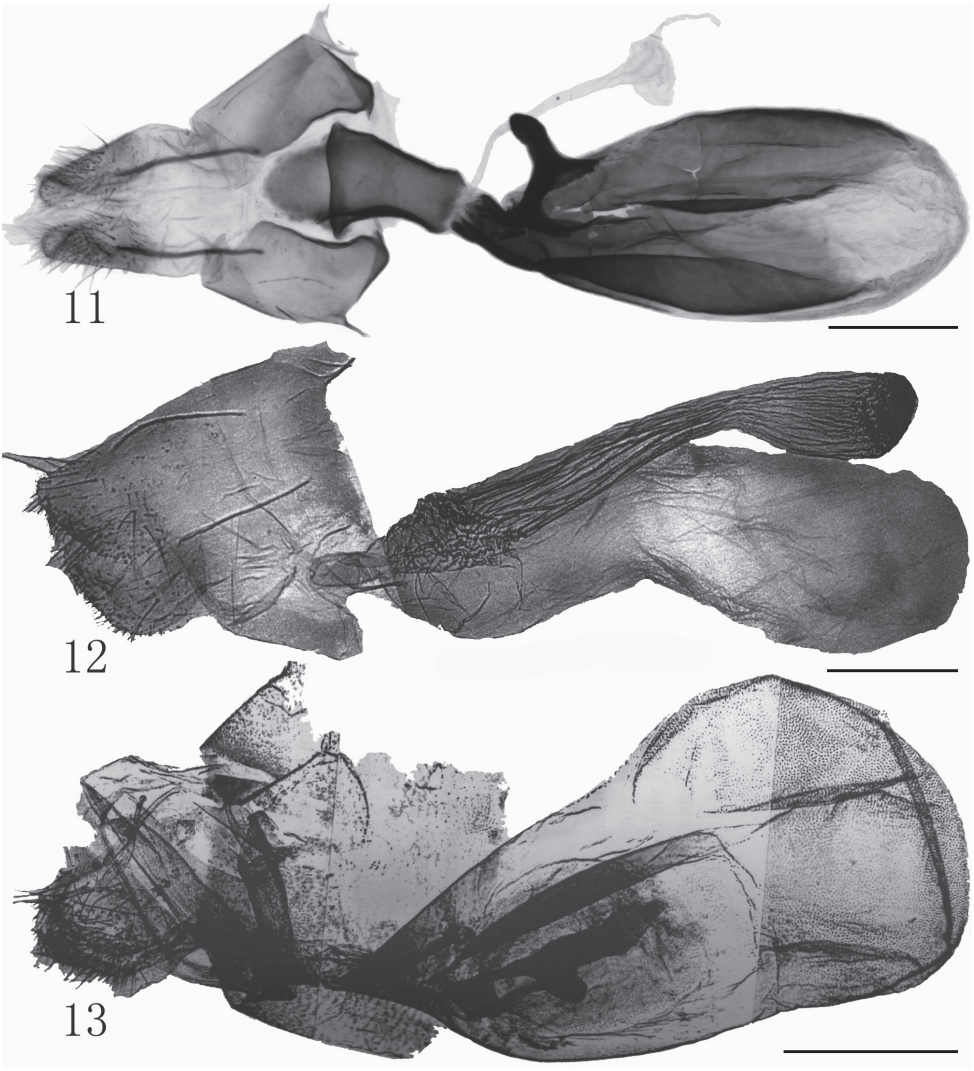
Figures 1–6. *Rhynchina* spp., adults **1** *R. taibaishana* sp. n., male, holotype **2** ditto, male, paratype **3** ditto, female, paratype **4** *R. deqinensis* Han, 2008, male, holotype **5** *R. helga* Gaal, 1998 (after Mayerl and Lödl 1999) **6** *R. mandarinalis* Leech, 1900 (after Mayerl and Lödl 1999).

cess is very short or small and indistinct. The claspers of *R. taibaishana* are asymmetrical and finger-like, the left one twice as long as the right one, but in *R. deqinensis* they are symmetrical, curved and finger-like, and in *R. helga*, also symmetrical but spine-like. The ampulla in *R. taibaishanna* is short and slightly curved, reaching to the costal margin in the right valva, while that of left valva is somewhat shorter; in *R. deqinensis* and *R. helga*, the ampulla extends along the main axis of valva, while that of *R. helga* is sharp apically and slightly curved. The cornutus of *R. taibaishana* is shorter than that of *R. helga*, and longer than in *R. deqinensis*. In the female genitalia, the corpus bursae of *R. taibaishana* (Fig. 11) is long, oval shaped, its posterior 3/4 sclerotized and bearing a strongly extended sclerotized signum, but the corpus bursae of *R. helga* (Fig. 12) is longer, slightly constricted and bent at the middle and membranous throughout and without a signum, but with large ridged appendix bursae, which is absent in *R. taibaishana*.



Figures 7–10. *Rhynchina* spp., male genitalia **7** *R. taibaishana* sp. n., holotype **8** *R. deqinensis* Han, 2008, holotype **9** *R. helga* Gaal, 1998 (after Mayerl and Lödl 1999) **10** *R. mandarinalis* Leech, 1900 (after Mayerl and Lödl 1999). Scale bar: 1 mm.

Externally *R. taibaishana* is also similar to *R. mandarinalis* Leech, 1900 (Fig. 6), but it differs by the continuous yellow-brown oblique band runing from the apex to the basal part of forewing. In *R. mandarinalis* the forewing shows apical and basal yellowish brown patches, which are connected by a thin, yellowish brown-bordered



Figures 11–13. *Rhynchina* spp., female genitalia **11** *R. taibaishana* sp. n., paratype **12** *R. helga* Gaal, 1998 (after Mayerl and Lödl 1999) **13** *R. mandarinalis* Leech, 1900 (after Mayerl and Lödl 1999). Scale bar: 1 mm.

blackish line. In the male genitalia, the valva of *R. taibaishan* shows parallel costal and ventral margin up to the cucullus, while the valva of *R. mandarinalis* (Fig. 10) is apically tapered. The costa of *R. taibaishan* is strongly developed, while in *R. mandarinalis* it is not expressed. These two species are especially different in the female genitalia (Figs 11, 13), particurlarly in the shape of corpus bursae, which is long-ovoid and sclerotized in the posterior 3/4 in *R. taibaishana*, but broader and pear-shaped, membranous, and bearing small surface granulation in *R. mandarinalis* (Fig. 13). Both species have a strongly sclerotized, outwardly extended finger-like signum on posterior part.

Description. Adult (Figs 1–3). Wingspan 26–29 mm. Head, thorax and abdomen pale yellowish brown with grey scales. Male antenna ciliate. Labial palpi long, upcurved. Forewing yellowish brown, with dark brown and some black suffusion; basal line dark brown, short, arched, feebly distinct; antemedial line black, strongly waved at veins 1A+2A, and distinct only at costal and inner margins; postmedial line double, black, its outer border indistinct at anterior 1/2 and distinct at posterior 1/2 inner border well distinct on costal area, then greatly outwardly produced beyond discal cell, albeit fading in correspondence to pale oblique band bisecting apical area, then slightly undulated and internally oblique to inner margin; subterminal line yellow, a jagged wave, distinct from M_1 to inner margin, with sharp angle between CuA_2 and 1A+2A; pale yellowish brown oblique band crosses wing from apex to base; orbicular spot small, dark brown, indistinct; reniform spot dark brown, obscure; tornus extended out with tuft of grayish brown scales; interspaces M_1-M_2, M_2-M_3 and M_3-CuA_1 crossed with a black streak each; costal, adterminal and tornal fields blackish grey; terminal line black; fringe chequered yellowish brown and smoky black, with paler basal dots between the veins. Hindwing light yellowish brown, irrorated with dark brown scales; terminal line thin, black; fringe yellow and black.

Male genitalia. (Fig. 7) Tegumen broad, oblong, 4/5 as long as vinculum. Vinculum V-shaped. Valva narrow, bar-like, elongated; costal process flat, stout, sclerotized and blunt, swollen medially, not reaching middle part of valva; sacculus rather swollen, sclerotized; clasper and ampulla fused, heavily sclerotized, asymmetrical; ampulla short and slightly curved, reaching costal margin on right valva, slightly shorter on left valva; left clasper twice as long as right one, narrow, finely pointed, right one stubby. Uncus long and narrow, bent subbasally, sickle shaped, apical part hooked. Juxta inverted funnel-shaped, sclerotized. Aedeagus long, cylindrical, straight, tapered apically, carina broad, sclerotized; vesica membranous, with broad irregular-shaped basal part, small sack-shaped basal diverticulum, and very long, cylindrical medial diverticulum, armed with long thin apical cornutus connected basally to the vesical membrane for half of its length.

Female genitalia. (Fig. 11) Ostium bursae wider than ductus bursae; antrum cylindrical, sclerotized, slightly curved, and constricted proximally, its dorsal part with a liguliform process, about 1/2 as long as remainder of antrum; ductus bursae very short, about 1/2 length of antrum, sclerotized, joined to this by narrow membranous tract; corpus bursae elongated, ovoid, sclerotized posteriorly for 3/4 of its length, bearing in caudal part strong sclerotized, outwardly extended thumb-like signum, with broad horn-shaped base. Apophyses anteriores very short, broad basally; apophyses posteriors relatively long, about 5 times longer than anteriores; papillae anales elongate, broad.

Distribution. (Fig. 14) China (Shaanxi Province: Mt Taibai).

Etymology. The species name "*taibaishana*" refers to the type locality, Mt Taibai.

Bionomics. (Fig. 15) The species was collected in a broad-leaved forest with shrubs. All individuals have been attracted at ultra violet light in May 2010.

Figures 14, 15. 14 Collection site of *R. taibaishana* sp. n., Haoping protection station **15** Collection site composed of mainly broad-leaved forest and mixed shrubs.

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CHECKLIST

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An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea)

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Abstract

This paper presents an updated checklist of the butterflies of Europe, together with their original name combinations, and their occurrence status in each European country. According to this checklist, 496 species of the superfamily Papilionoidea occur in Europe. Changes in comparison with the last version (2.6.2) of Fauna Europaea are discussed. Compared to that version, 16 species are new additions, either due to cryptic species most of which have been discovered by molecular methods (13 cases) or due to discoveries of Asian species on the eastern border of the European territory in the Ural mountains (three cases). On

the other hand, nine species had to be removed from the list, because they either do not occur in Europe or lost their species status due to new evidence. In addition, three species names had to be changed and 30 species changed their combination due to new evidence on phylogenetic relationships. Furthermore, minor corrections were applied to some authors' names and years of publication. Finally, the name *Polyommatus ottomanus* Lefèbvre, 1831, which is threatened by its senior synonym *Lycaena legeri* Freyer, 1830, is declared a *nomen protectum*, thereby conserving its name in the current combination *Lycaena ottomana*.

Keywords
checklist, butterflies, Europe

Introduction

Butterflies constitute one of the best-known groups of insects and have become important models to study speciation, community ecology, biogeography, climate change, and insect-plant interactions. With close to 19,000 described species [18,768 presumably valid species recorded by 2011; that figure is higher today, i.e., ca. 19,000 species], they represent about 12% of currently known species of Lepidoptera (Van Nieukerken et al. 2011). According to current molecular systematics (Mutanen et al. 2010; Heikkilä et al. 2012; Espeland et al. 2018), the single butterfly superfamily Papilionoidea comprises 7 families (Table 1, Fig. 1) and includes the Hesperiidae (skippers) and Hedylidae (moth butterflies). The skippers have previously been thought to represent the sister group to the butterflies and were often placed in a separate superfamily Hesperioidea, but the molecular results indicate that the family Papilionidae is the sister to the remaining butterflies, which also include the small Neotropical family Hedylidae with only 36 species. Apart from the latter family, all butterfly families are represented on all continents except Antarctica, although most species of Riodinidae are confined to the Neotropical Region. Butterfly diversity is particularly high in the tropics, especially the Neotropics, and only 496 species are found in Europe according to the present checklist.

The taxonomy of butterflies started in 1758 with the Swedish naturalist Carl von Linné (Latinised to Carolus Linnaeus), who introduced binominal nomenclature and described the highest number of European butterfly species, all of them in a single genus *Papilio*. Seventy-one of them currently still hold the names given by Linné, albeit mostly in different genera. Other authors who described many new species during the 18th century were the German entomologists Eugen Johann Christoph Esper and Jacob Hübner, the Danish entomologist Johann Christian Fabricius, as well as the Austrian lepidopterist Johann Ignaz Schiffermüller (the latter in an anonymous publication usually referred to as [Denis & Schiffermüller], but see Kudrna and Belicek (2005), Sattler and Tremewan (2009) and Kudrna (2015) for a controversial debate on this topic). By 1820, half of the European butterfly fauna had been validly described, and species were placed in a growing number of genera (starting with *Hesperia* Fabricius, 1793 as the second-named genus for the skippers). During the 19th century, more than 60 European lepidopterists continued the inventory of Europe's butterfly fauna, and the first overview of Palearctic butterflies (and other Lepidoptera) was published by Seitz (1907–1909). At that time, already 90% of Europe's butterfly species had

Table 1. Family systematics of butterflies.

Superfamily Papilionoidea Latreille, [1802]	Genera*	Species*
Family Papilionidae Latreille, [1802]	32	570
Family Hedylidae Guenée, [1858]	1	36
Family Hesperiidae Latreille, 1809	570	4113
Family Pieridae Swainson, 1820	91	1164
Family Riodinidae Grote, 1895	146	1532
Family Lycaenidae [Leach], [1815]	416	5201
Family Nymphalidae Rafinesque, 1815	559	6152

* global number of genera and species according to van Nieukerken et al. (2011)

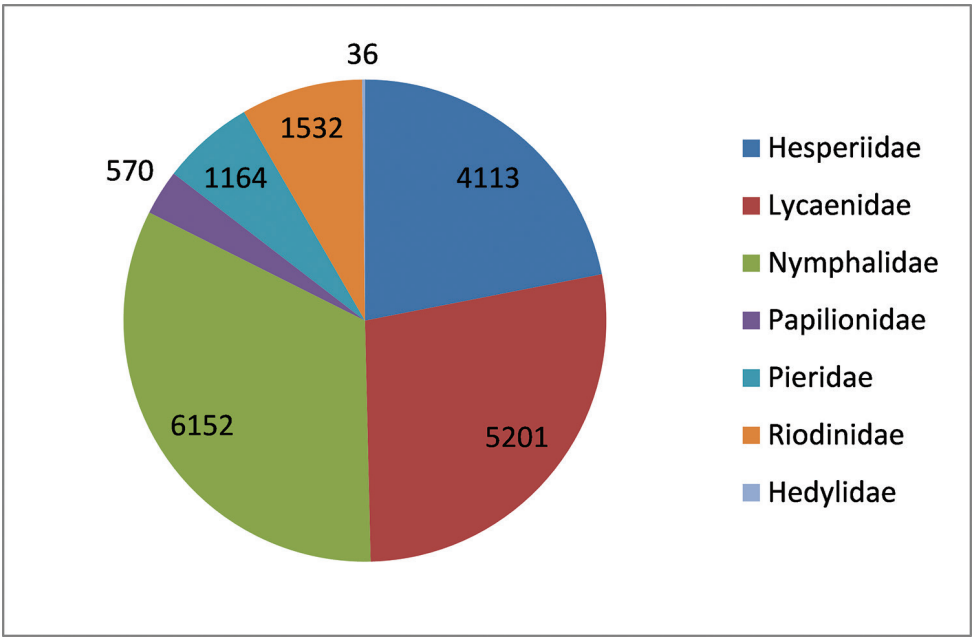

Figure 1. Global species richness of butterfly families.

been described and the rate of newly discovered species slowed down (Fig. 2). Another milestone for butterfly research in Europe was the field guide of Higgins and Riley (1970), which included distribution maps of Western Palearctic butterflies, and led to a growing interest in butterflies across Europe. This field guide was also translated into other languages (e.g., German, French, and Spanish) and updated several times (most recently by Tolman and Lewington 2008). However, despite their somehow misleading titles, these guides excluded large parts of eastern Europe (i.e., Belarus, Ukraine, Moldova and most of Russia (apart from Kaliningrad enclave) and therefore all the species from the Ural mountains). The proliferation of butterfly field guides by various authors across Europe also led to an increasing confusion of butterfly nomenclature due to different taxonomic concepts. The first step to standardize European butterfly

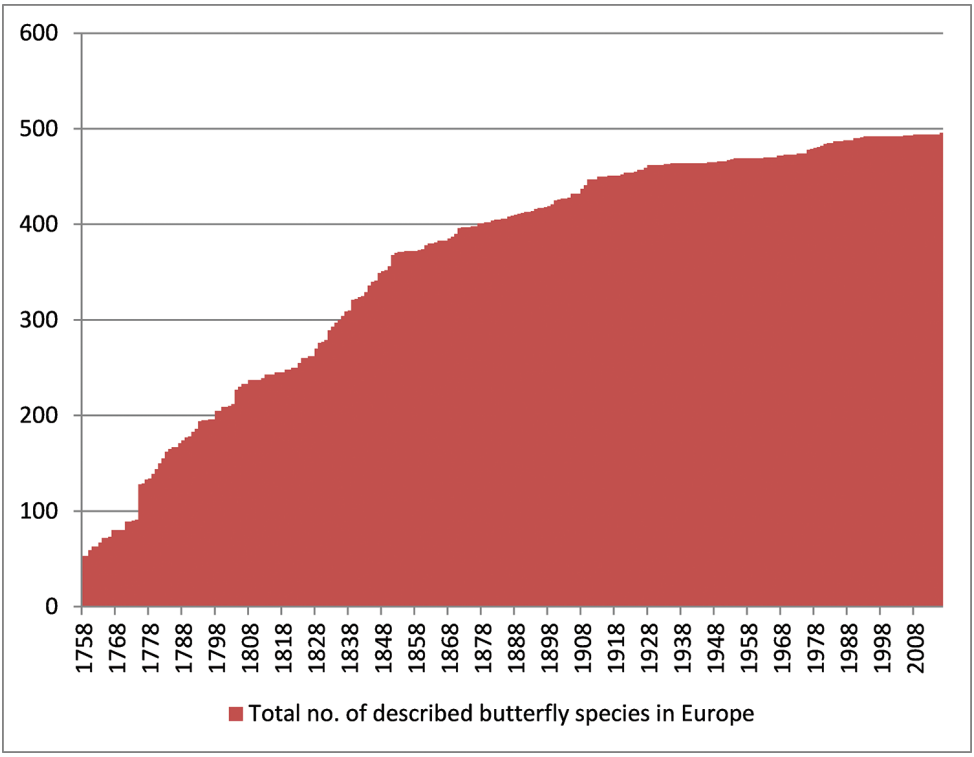

Figure 2. Cumulative number of described European butterfly species per year according to current taxonomy.

taxonomy and the precursor of our list was the book (and accompanying CD) by Karsholt and Razowski (1996). It constituted a country-level checklist of all European Lepidoptera, but excluding the Mid-Atlantic islands (i.e., Canary Islands, Madeira, and Azores) and contained 440 butterfly species. This book was also the basis for the list of Lepidoptera in the online database Fauna Europaea, a project under the auspices of the European Commission, which started in 2000 (De Jong et al. 2014) and aimed to provide checklists for all European animal species. This database, which went online on 16 December 2004, also included Cyprus and the Mid-Atlantic islands, which are hotspots of narrow endemics. At about the same time, the first distribution atlas of all European butterflies was published by Kudrna (2002), and finally a butterfly field guide appeared which covered most of the West Palearctic region including all of Europe (Tshikolovets 2011).

The last comprehensive update of the butterfly checklist in Fauna Europaea happened 7 years ago (Karsholt and Nieukerken 2011), and the checklist presented here was first developed as an update to the online database. Unfortunately, funding for Fauna Europaea was discontinued after the initial 4-years funding period and the outdated Fauna Europaea website was only saved due to the commitment of the Natural History Museum in Berlin that set up a new one. However, its functionality is still very

limited and the update process severely hampered due to shortage of funding. For this reason, we decided to publish this updated distributional checklist in order to address the need of the lepidopterological community and the public at large. It intends to cover the significant progress in butterfly systematics and faunistics, which was brought about in particular by the advancement of molecular methods.

Materials and methods

This updated checklist is based on the last version of Fauna Europaea (2.6.2). This version is almost identical to the most recent Lepidoptera update in version 2.4 (online on 28 January 2011) but includes some emendations by the staff of the Fauna Europaea office in Berlin that had not been approved by the Lepidoptera group coordinators (Erik van Nieukerken and Ole Karsholt). The geographic area covered remains the same: It includes the European mainland to the eastern slopes of the Ural mountains, plus the Macaronesian islands (excluding the Cape Verde Islands) and Cyprus, with the Caucasus and western Kazakhstan excluded (Fig. 3). Included are the British Isles and all Mediterranean islands under European administration, as well as the Greek offshore islands along the Turkish coastline. Iceland has no native butterfly species. Distributional information is based on political units at country level as in Fauna Europaea, following the ISO-3166 code. However, with the exception of the Macaronesian Islands, the additional regional splits of several countries in Fauna Europaea (mainly for Russia and some island territories) were not adopted.

The following categories are used to explain the distribution:

A Absent (never recorded in the respective country or island group or only doubtful records)

P Present (native or well-established populations, including alien species such as the South African *Cacyreus marshalli*)

P? Possibly present (recorded but continued presence doubtful; usually these are species with range limits near the border of the respective country)

M Regular migrant (species which has no permanent populations, e.g., because it cannot overwinter, but is observed almost every year; included are extinct species if they are still observed as regular migrants)

I Irregular vagrant (irregular vagrants or introductions which do not reproduce or only irregularly, including temporary or recently established populations)

Ex Regionally extinct (native species which have become extinct, even though vagrants might be seen occasionally)

It should be noted that the "Extinct" category is used in a rather strict sense, in line with the IUCN Guidelines which demand that exhaustive surveys have been undertaken to prove that 'there is no reasonable doubt that the last individual has died'. In some cases, this has led to species being recorded as "Present", even though they are most probably

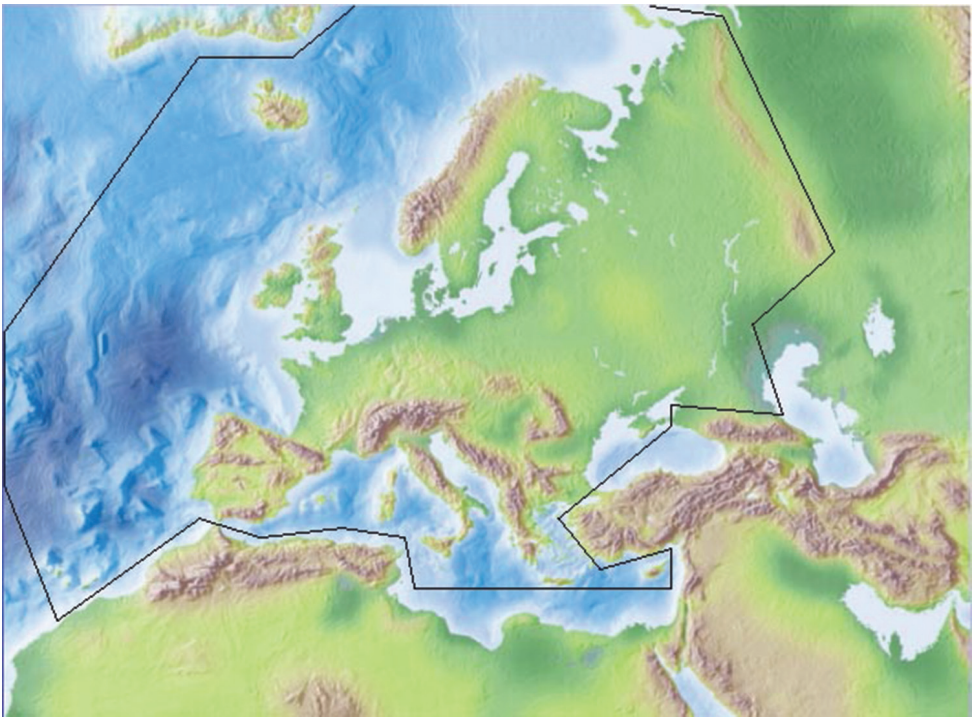

Figure 3. Boundaries of Europe according to Fauna Europaea (from de Jong et al. 2014).

extinct, e.g., *Colias myrmidone* in Austria (no proof for more than 25 years; H. Höttinger, pers. comm.). In addition, some of the national Red List Assessments are already outdated, even though attempts have been made to update those. An example for an update is the status of the Madeiran endemic *Pieris wollastoni*, whose last reliable record is from 1986. It was classified as "Critically Endangered (Possibly Extinct)" in its last Red List assessment (Van Swaay et al. 2010), but is now classified as "Extinct", because extensive surveys in recent years have failed to prove its continued presence. This is the only European butterfly species which is known to have become globally extinct in historical times.

According to the concept of Fauna Europaea, changes were only carried out if supported by newly published research. This restriction helps to stabilize nomenclature, but can also lead to inconsistent results, e.g., due to the retention of some weakly differentiated taxa, whose species status is questionable, but for which no new published evidence is available. Potential examples in our list are *Lysandra caelestissima* (Verity, 1921), *Polyommatus nephohiptamenos* (Brown & Coutsis, 1978), *Hipparchia neapolitana* (Stauder, 1921), *Hipparchia sbordonii* Kudrna, 1984, *Satyrus virbius* Herrich-Schäffer, 1844, and *Pieris balcana* Lorković, 1969.

The main criterion whether to include or exclude a species taxon based on new (and possibly contradictory) publications was evidence for species status from at least two character sets, e.g., mitochondrial as well as nuclear DNA, or differences in morphology and karyology.

Nomenclatural changes are annotated with reference to the sources and strictly follow the last (fourth) edition of the International Code of Zoological Nomenclature (ICZN 1999). This includes the controversial article 34.2, which mandates that »the ending of a Latin or Latinised adjectival or participial species-group name must agree in gender with the generic name with which it is at any time combined«. Due to its linguistic complexity, this rule has led to many wrong or ambiguous decisions and causes additional instability of nomenclature each time a species name is transferred to another genus. Therefore a majority of lepidopterists, including the group editors of Fauna Europaea, have decided to ignore this rule and use the original spelling instead (de Jong et al. 2014). Difficulties with the gender agreement rule in Lepidoptera are as old as binominal nomenclature, because there is not even an agreement about the gender of the genus *Papilio*. Therefore Carl von Linné used nouns as species names and avoided the use of adjectives (Welter-Schultes 2013). However, for easy reference to Fauna Europaea and other databases, we also list the original ending and compiled a comprehensive list of original combinations, using various sources such as the LepIndex (Beccaloni et al. 2003), PESI (2018), FUNET (Savela 2018) and Tshikolovets (2011). In case of doubts or discrepancies, the original publications were checked as well.

In a few cases, necessary changes due to new nomenclatural findings have not been carried out yet, because they would result in the replacement of a well-established name by an (almost) unknown synonym. Such cases should be referred to the International Commission on Zoological Nomenclature for ruling, and changes implemented only after a decision has been made by the Commission. One such case is the well-established name *Parnassius phoebus*, which has turned out to represent another Asian *Parnassius* species which is currently known as *Parnassius ariadne* (Lederer, 1853) (see Hanus and Thèye 2010) and would thus need to be replaced. After the first attempt to preserve this name (Balletto and Bonelli 2014) failed (ICZN 2017), a second proposal has recently been submitted to the Commission (Lukhtanov et al. in press). According to article 82.1 of the code, prevailing usage has to be maintained until the case has been decided by the Commission.

An exceptional case which would cause a large number of changes in the names of Lepidoptera are many of the names published by [Denis & Schiffermüller] (1775) which are lacking a sufficient description, but have already been used for a very long time. In accordance with the opinion of the Fauna Europaea editorial team, we have not replaced these names. The effect on butterfly taxonomy would be rather marginal, however, because only one butterfly species would have to change its name (*Nymphalis vaualbum* to *Nymphalis l-album* (Esper, 1781)) and five others only their authorship, see Kudrna and Belicek (2005). We are looking forward to a decision of the ICZN to solve this matter (see Kudrna 2015).

Another case concerns the genus name *Muschampia* Tutt, 1906 (type species: *Papilio proto* Ochsenheimer, 1808; currently known as *Muschampia proto* (Ochsenheimer, 1808)), which appears to be a subjective synonym of the genus name *Sloperia* Tutt, 1906 (type species: *Hesperia poggei* Lederer, 1858; currently known as *Muschampia poggei* (Lederer, 1858)). Both genus names were published in the same paper and

Hemming (1967) was the first to note that *Sloperia* should have precedence over *Muschampia*, because Warren (1926) as the first reviser chose *Sloperia*. However, the name *Muschampia* has remained in prevailing use during the last 90 years and, in addition, there is evidence from molecular data (Wiemers et al. unpublished) that the current classification of the species presently placed in the genera *Carcharodus* and *Muschampia* needs to be substantially revised. However, molecular data are still missing for most of the (mainly Asian) species currently placed in *Muschampia*, and therefore we suggest to postpone a rearrangement until better data become available.

Finally, one of us (GL) discovered that *Polyommatus ottomanus* Lefèbvre was published in 1831 (and not in 1830) and therefore has to be regarded as a subjective junior synonym of *Lycaena legeri* Freyer, 1830. This would mean that the well-established name of the species currently known as *Lycaena ottomana* (Lefèbvre, [1831]) would need to be changed to a name which has not been used for this species during the past century. However, according to article 23.9.1 of the Code, the prevailing usage must be maintained when the senior synonym (i.e., *legeri* Freyer) has not been used as a valid name after 1899 (article 23.9.1.1), and the junior synonym has been used, as its presumed valid name, in at least 25 works, published by at least ten authors during the last 50 years and encompassing a span of not less than ten years (article 23.9.1.2). In our opinion, the condition of article 23.9.1.1 applies in this case, and evidence that the conditions of article 23.9.1.2 are met, are given in Appendix 1 herein. Therefore, we regard the name *Lycaena legeri* Freyer as invalid and qualified as a *nomen oblitum* and declare the name *Lycaena ottomana* Lefèbvre as valid and qualified as a *nomen protectum*, which has precedence over the former as long as both names are thought to represent subjective synonyms.

Results and discussion

The updated species list of European butterflies includes 496 species, which belong to 110 genera in 21 subfamilies and six families (Tables 2 and 4; Fig. 4). A list of main authors with some additional data is given in Table 5. An electronic version of the checklist that includes a country-based distributional checklist is found in Suppl. material 1, Suppl. material 2.

Compared to the last version 2.6.2 of Fauna Europaea, nine species have been excluded from the list (Table 6). On the other hand, 15 species were added to the list. Another recently discovered species, *Spialia rosae* Hernández-Roldán, Dapporto, Dincă, Vicente & Vila, 2016, has already been added to the Fauna Europaea database.

Apart from the changes due to the gender agreement provision (Table 7), only three species names had to be changed due to new nomenclatural evidence: *Pyrgus bellieri* (Oberthür, 1910) to *Pyrgus foulquieri* (a name which had already been used in previous field guides), *Proterebia afra* (Fabricius, 1787) to *Proterebia phegea* (hopefully solving a longstanding controversy, see e.g., Jutzeler and Lafranchis 2011), and the mandatory change of *Pseudochazara hippolyte* (Esper, 1783) to *Pseudochazara mercurius* due to primary homonomy.

Table 2. Updated checklist of the butterflies of Europe.

Taxon	Original combination	Notes
Papilionidae		
Papilioninae		
Iphiclides podalirius (Linnaeus, 1758)	*Papilio podalirius*	
Iphiclides feisthamelii (Duponchel, 1832)	*Papilio feisthamelii*	1
Papilio alexanor Esper, 1800	*Papilio alexanor*	
Papilio machaon Linnaeus, 1758	*Papilio machaon*	
Papilio hospiton Gené, 1839	*Papilio hospiton*	2
Parnassiinae		
Parnassius mnemosyne (Linnaeus, 1758)	*Papilio mnemosyne*	
Parnassius phoebus (Fabricius, 1793)	*Papilio phoebus*	
Parnassius apollo (Linnaeus, 1758)	*Papilio apollo*	
Archon apollinus (Herbst, 1798)	*Papilio apollinus*	
Zerynthia cerisy (Godart, [1824])	*Thais cerisy*	
Zerynthia cretica (Rebel, 1904)	*Thais cerisyi cretica*	
Zerynthia caucasica (Lederer, 1864)	*Thais cerisyi caucasica*	
Zerynthia rumina (Linnaeus, 1758)	*Papilio rumina*	
Zerynthia polyxena ([Denis & Schiffermüller], 1775)	*Papilio polyxena*	
Zerynthia cassandra (Geyer, [1828])	*Papilio cassandra*	3
Hesperiidae		
Heteropterinae		
Heteropterus morpheus (Pallas, 1771)	*Papilio morpheus*	
Carterocephalus silvicola (Meigen, 1829)	*Hesperia silvicola*	
Carterocephalus palaemon (Pallas, 1771)	*Papilio palaemon*	
Hesperiinae		
Pelopidas thrax (Hübner, [1821])	*Gegenes thrax*	
Borbo borbonica (Boisduval, 1833)	*Hesperia borbonica*	
Gegenes pumilio (Hoffmansegg, 1804)	*Papilio pumilio*	
Gegenes nostrodamus (Fabricius, 1793)	*Hesperia nostrodamus*	
Ochlodes sylvanus (Esper, 1777)	*Papilio sylvanus*	
Hesperia comma (Linnaeus, 1758)	*Papilio comma*	
Thymelicus christi Rebel, 1894	*Thymelicus christi*	
Thymelicus acteon (Rottemburg, 1775)	*Papilio acteon*	
Thymelicus hyrax (Lederer, 1861)	*Hesperia hyrax*	
Thymelicus sylvestris (Poda, 1761)	*Papilio sylvestris*	
Thymelicus lineola (Ochsenheimer, 1808)	*Papilio lineola*	
Pyrginae		
Spialia phlomidis (Herrich-Schäffer, 1845)	*Hesperia phlomidis*	
Spialia sertorius (Hoffmansegg, 1804)	*Hesperia sertorius*	
Spialia therapne (Rambur, 1832)	*Hesperia therapne*	
Spialia rosae Hernández-Roldán, Dapporto, Dincă, Vicente & Vila, 2016	*Spialia rosae*	4
Spialia orbifer (Hübner, [1823])	*Papilio orbifer*	
Carcharodus tripolinus (Verity, 1925)	*Erynnis alceae tripolina*	5
Carcharodus alceae (Esper, 1780)	*Papilio alceae*	
Muschampia cribrellum (Eversmann, 1841)	*Hesperia cribrellum*	
Muschampia tessellum (Hübner, [1803])	*Papilio tessellum*	
Muschampia proto (Ochsenheimer, 1808)	*Papilio proto*	

Taxon	Original combination	Notes
Carcharodus lavatherae (Esper, 1783)	*Papilio lavatherae*	
Carcharodus orientalis Reverdin, 1913	*Carcharodus orientalis*	
Carcharodus floccifera (Zeller, 1847)	*Hesperia floccifera*	
Carcharodus stauderi Reverdin, 1913	*Carcharodus stauderi*	
Carcharodus baeticus (Rambur, 1839)	*Spilothyrus baeticus*	
Erynnis tages (Linnaeus, 1758)	*Papilio tages*	
Erynnis marloyi (Boisduval, 1834)	*Thanaos marloyi*	
Pyrgus malvoides (Elwes & Edwards, 1897)	*Hesperia malvoides*	
Pyrgus malvae (Linnaeus, 1758)	*Papilio malvae*	
Pyrgus carthami (Hübner, [1813])	*Papilio carthami*	
Pyrgus sidae (Esper, 1784)	*Papilio sidae*	
Pyrgus centaureae (Rambur, 1839)	*Hesperia centaureae*	
Pyrgus cacaliae (Rambur, 1839)	*Hesperia cacaliae*	
Pyrgus andromedae (Wallengren, 1853)	*Syrichtus andromedae*	
Pyrgus serratulae (Rambur, 1839)	*Hesperia serratulae*	
Pyrgus armoricanus (Oberthür, 1910)	*Syrichthus armoricanus*	
Pyrgus alveus (Hübner, [1803])	*Papilio alveus*	
Pyrgus warrenensis (Verity, 1928)	*Hesperia warrenensis*	
Pyrgus foulquieri (Oberthür, 1910)	*Syrichthus alveus foulquieri*	6
Pyrgus onopordi (Rambur, 1839)	*Hesperia onopordi*	
Pyrgus carlinae (Rambur, 1839)	*Hesperia carlinae*	
Pyrgus cirsii (Rambur, 1839)	*Hesperia cirsii*	
Pyrgus cinarae (Rambur, 1839)	*Hesperia cinarae*	
Pieridae		
Dismorphiinae		
Leptidea duponcheli (Staudinger, 1871)	*Leucophasia duponcheli*	
Leptidea morsei (Fenton, 1882)	*Leptosia morsei*	
Leptidea juvernica Williams, 1946	*Leptidea sinapis juvernica*	7
Leptidea sinapis (Linnaeus, 1758)	*Papilio sinapis*	
Leptidea reali Reissinger, 1990	*Leptidea sinapis reali*	
Coliadinae		
Gonepteryx rhamni (Linnaeus, 1758)	*Papilio rhamni*	
Gonepteryx cleobule (Hübner, [1831])	*Anteos cleobule*	8
Gonepteryx cleopatra (Linnaeus, 1767)	*Papilio cleopatra*	
Gonepteryx maderensis C. Felder, 1862	*Gonopteryx cleopatra maderensis*	
Gonepteryx farinosa (Zeller, 1847)	*Rhodocera farinosa*	
Catopsilia florella (Fabricius, 1775)	*Papilio florella*	
Colias hyale (Linnaeus, 1758)	*Papilio hyale*	
Colias alfacariensis Ribbe, 1905	*Colias hyale alfacariensis*	
Colias phicomone (Esper, [1780])	*Papilio phicomone*	
Colias aurorina Herrich-Schäffer, 1850	*Colias aurorina*	
Colias chrysotheme (Esper, [1781])	*Papilio chrysotheme*	
Colias erate (Esper, [1805])	*Papilio erate*	
Colias crocea (Geoffroy, 1785)	*Papilio croceus*	5, 9
Colias myrmidone (Esper, [1781])	*Papilio myrmidone*	
Colias caucasica Staudinger, 1871	*Colias myrmidone caucasica*	
Colias palaeno (Linnaeus, [1760])	*Papilio palaeno*	10
Colias tyche (Böber, 1812)	*Papilio tyche*	

Taxon	Original combination	Notes
Colias hecla Lefèbvre, 1836	*Colias hecla*	
Pierinae		
Colotis evagore (Klug, 1829)	*Pontia evagore*	
Aporia crataegi (Linnaeus, 1758)	*Papilio crataegi*	
Pontia chloridice (Hübner, [1813])	*Papilio chloridice*	
Pontia callidice (Hübner, [1800])	*Papilio callidice*	
Pontia edusa (Fabricius, 1777)	*Papilio edusa*	
Pontia daplidice (Linnaeus, 1758)	*Papilio daplidice*	
Pieris krueperi Staudinger, 1860	*Pieris krueperi*	
Pieris brassicae (Linnaeus, 1758)	*Papilio brassicae*	
Pieris wollastoni (Butler, 1886)	*Ganoris wollastoni*	
Pieris cheiranthi (Hübner, [1808])	*Papilio cheiranthi*	
Pieris rapae (Linnaeus, 1758)	*Papilio rapae*	
Pieris mannii (Mayer, 1851)	*Pontia mannii*	
Pieris ergane (Geyer, [1828])	*Papilio ergane*	
Pieris bryoniae (Hübner, [1806])	*Papilio bryoniae*	
Pieris napi (Linnaeus, 1758)	*Papilio napi*	
Pieris balcana Lorković, [1969]	*Pieris balcana*	11
Euchloe tagis (Hübner, [1804])	*Papilio tagis*	
Euchloe eversi Stamm, 1963	*Euchloe belemia eversi*	
Euchloe grancanariensis Acosta, 2008	*Euchloe belemia grancanariensis*	
Euchloe hesperidum Rothschild, 1913	*Euchloe belemia hesperidum*	
Euchloe belemia (Esper, 1800)	*Papilio belemia*	
Euchloe insularis (Staudinger, 1861)	*Anthocharis tagis insularis*	
Euchloe crameri Butler, 1869	*Euchloe crameri*	
Euchloe simplonia (Freyer, 1829)	*Pontia simplonia*	
Euchloe ausonia (Hübner, [1804])	*Papilio ausonia*	
Euchloe charlonia (Donzel, 1842)	*Anthocharis charlonia*	
Euchloe penia (Freyer, 1851)	*Pontia penia*	
Euchloe bazae Fabiano, 1993	*Euchloe charlonia bazae*	
Zegris pyrothoe (Eversmann, 1832)	*Pontia pyrothoe*	
Zegris eupheme (Esper, [1804])	*Papilio eupheme*	
Anthocharis euphenoides Staudinger, 1869	*Anthocharis euphenoides*	
Anthocharis cardamines (Linnaeus, 1758)	*Papilio cardamines*	
Anthocharis gruneri Herrich-Schäffer, 1851	*Anthocharis gruneri*	
Anthocharis damone Boisduval, 1836	*Anthocharis damone*	
Riodinidae		
Nemeobiinae		
Hamearis lucina (Linnaeus, 1758)	*Papilio lucina*	
Lycaenidae		
Lycaeninae		
Lycaena dimorpha (Staudinger, 1881)	*Polyommatus dimorphus*	5, 12
Lycaena helle ([Denis & Schiffermüller], 1775)	*Papilio helle*	
Lycaena alciphron (Rottemburg, 1775)	*Papilio alciphron*	
Lycaena thetis Klug, 1834	*Lycaena thetis*	
Lycaena thersamon (Esper, 1784)	*Papilio thersamon*	
Lycaena dispar ([Haworth], 1802)	*Papilio dispar*	
Lycaena hippothoe (Linnaeus, [1760])	*Papilio hippothoe*	10

Taxon	Original combination	Notes
Lycaena candens (Herrich-Schäffer, 1844)	*Polyommatus candens*	
Lycaena ottomana (Lefèbvre, [1831])	*Polyommatus ottomanus*	5, 13
Lycaena bleusei (Oberthür, 1884)	*Polyommatus xanthe* f. *bleusei*	
Lycaena phlaeas (Linnaeus, [1760])	*Papilio phlaeas*	10
Lycaena virgaureae (Linnaeus, 1758)	*Papilio virgaureae*	
Lycaena tityrus (Poda, 1761)	*Papilio tityrus*	
Aphnaeinae		
Cigaritis acamas (Klug, 1834)	*Lycaena acamas*	14
Theclinae		
Thecla betulae (Linnaeus, 1758)	*Papilio betulae*	
Favonius quercus (Linnaeus, 1758)	*Papilio quercus*	
Laeosopis roboris (Esper, [1793])	*Papilio roboris*	15
Tomares ballus (Fabricius, 1787)	*Papilio ballus*	
Tomares nogelii (Herrich-Schäffer, 1851)	*Thecla nogelii*	
Tomares callimachus (Eversmann, 1848)	*Lycaena callimachus*	
Callophrys avis Chapman, 1909	*Callophrys avis*	
Callophrys suaveola (Staudinger, 1881)	*Thecla suaveola*	
Callophrys rubi (Linnaeus, 1758)	*Papilio rubi*	
Callophrys chalybeitincta Sovinsky, 1905	*Callophrys rubi chalybeitincta*	
Neolycaena rhymnus (Eversmann, 1832)	*Lycaena rhymnus*	
Satyrium pruni (Linnaeus, 1758)	*Papilio pruni*	
Satyrium ilicis (Esper, 1779)	*Papilio ilicis*	
Satyrium esculi (Hübner, [1804])	*Papilio esculi*	
Satyrium ledereri (Boisduval, 1848)	*Lycaena ledereri*	
Satyrium w-album (Knoch, 1782)	*Papilio w-album*	
Satyrium spini ([Denis & Schiffermüller], 1775)	*Papilio spini*	
Satyrium acaciae (Fabricius, 1787)	*Papilio acaciae*	
Polyommatinae		
Leptotes pirithous (Linnaeus, 1767)	*Papilio pirithous*	
Cyclyrius webbianus (Brullé, 1839)	*Polyommatus webbianus*	
Azanus ubaldus (Stoll, 1782)	*Papilio ubaldus*	
Azanus jesous (Guérin-Méneville, 1849)	*Polyommatus jesous*	
Lampides boeticus (Linnaeus, 1767)	*Papilio boeticus*	
Cacyreus marshalli Butler, 1898	*Cacyreus marshalli*	
Celastrina argiolus (Linnaeus, 1758)	*Papilio argiolus*	
Tarucus theophrastus (Fabricius, 1793)	*Hesperia theophrastus*	
Tarucus balkanicus (Freyer, 1844)	*Lycaena balkanica*	5
Phengaris alcon ([Denis & Schiffermüller], 1775)	*Papilio alcon*	
Phengaris arion (Linnaeus, 1758)	*Papilio arion*	
Phengaris teleius (Bergsträsser, 1779)	*Papilio teleius*	
Phengaris nausithous (Bergsträsser, 1779)	*Papilio nausithous*	
Turanana taygetica (Rebel, 1902)	*Lycaena panagaea taygetica*	
Pseudophilotes bavius (Eversmann, 1832)	*Lycaena bavius*	
Pseudophilotes barbagiae De Prins & van der Poorten, 1982	*Pseudophilotes barbagiae*	
Pseudophilotes abencerragus (Pierret, 1837)	*Argus abencerragus*	
Pseudophilotes panoptes (Hübner, [1813])	*Papilio panoptes*	
Pseudophilotes vicrama (Moore, 1865)	*Polyommatus vicrama*	
Pseudophilotes baton (Bergsträsser, 1779)	*Papilio baton*	

Taxon	Original combination	Notes
Scolitantides orion (Pallas, 1771)	*Papilio orion*	
Praephilotes anthracias (Christoph, 1877)	*Lycaena anthracias*	
Iolana iolas (Ochsenheimer, 1816)	*Lycaena iolas*	
Iolana debilitata (Schultz, 1905)	*Lycaena jolas* var. *debilitata*	16
Glaucopsyche melanops (Boisduval, 1828)	*Polyommatus melanops*	
Glaucopsyche paphos Chapman, 1920	*Glaucopsyche paphos*	
Glaucopsyche alexis (Poda, 1761)	*Papilio alexis*	
Zizeeria knysna (Trimen, 1862)	*Lycaena knysna*	
Zizeeria karsandra (Moore, 1865)	*Polyommatus karsandra*	
Tongeia fischeri (Eversmann, 1843)	*Lycaena fischeri*	
Cupido argiades (Pallas, 1771)	*Papilio argiades*	
Cupido decoloratus (Staudinger, 1886)	*Lycaena argiades decolorata*	5
Cupido alcetas (Hoffmansegg, 1804)	*Papilio alcetas*	
Cupido osiris (Meigen, 1829)	*Polyommatus osiris*	
Cupido minimus (Fuessly, 1775)	*Papilio minimus*	
Cupido lorquinii (Herrich-Schäffer, 1850)	*Lycaena lorquinii*	17
Luthrodes galba (Lederer, 1855)	*Lycaena galba*	18
Freyeria trochylus (Freyer, 1844)	*Lycaena trochylus*	18,19
Plebejus argus (Linnaeus, 1758)	*Papilio argus*	
Plebejus idas (Linnaeus, [1760])	*Papilio idas*	10
Plebejus bellieri (Oberthür, 1910)	*Lycaena bellieri*	
Plebejus argyrognomon (Bergsträsser, 1779)	*Papilio argyrognomon*	
Agriades orbitulus (Prunner, 1798)	*Papilio orbitulus*	18
Agriades optilete (Knoch, 1781)	*Papilio optilete*	18
Agriades pyrenaicus (Boisduval, 1840)	*Lycaena orbitulus* var. *pyrenaica*	5, 18
Agriades dardanus (Freyer, 1843)	*Lycaena dardanus*	18
Agriades zullichi Hemming, 1933	*Agriades zullichi*	18
Agriades glandon (Prunner, 1798)	*Papilio glandon*	18
Agriades aquilo (Boisduval, 1832)	*Argus aquilo*	18
Plebejidea loewii (Zeller, 1847)	*Lycaena loewii*	18
Eumedonia eumedon (Esper, 1780)	*Papilio eumedon*	18
Kretania psylorita (Freyer, 1845)	*Lycaena psylorita*	18
Kretania hesperica (Rambur, 1839)	*Polyommatus hespericus*	5, 18
Kretania eurypilus (Freyer, 1851)	*Lycaena eurypilus*	18
Kretania trappi (Verity, 1927)	*Lycaena trappi*	18
Kretania sephirus (Frivaldszky, 1835)	*Lycaena sephirus*	18
Kretania pylaon (Fischer, 1832)	*Lycaena pylaon*	18
Cyaniris semiargus (Rottemburg, 1775)	*Papilio semiargus*	
Glabroculus cyane (Eversmann, 1837)	*Lycaena cyane*	18
Aricia morronensis (Ribbe, 1910)	*Lycaena idas morronensis*	
Aricia anteros (Freyer, 1838)	*Lycaena anteros*	
Aricia cramera (Eschscholtz, 1821)	*Lycaena cramera*	
Aricia nicias (Meigen, 1829)	*Polyommatus nicias*	20
Aricia artaxerxes (Fabricius, 1793)	*Hesperia artaxerxes*	
Aricia montensis Verity, 1928	*Aricia medon montensis*	
Aricia agestis ([Denis & Schiffermüller], 1775)	*Papilio agestis*	
Neolysandra coelestina (Eversmann, 1843)	*Lycaena coelestina*	18
Lysandra hispana (Herrich-Schäffer, 1851)	*Lycaena coridon* var. *hispana*	18

Taxon	Original combination	Notes
Lysandra corydonius (Herrich-Schäffer, 1852)	*Lycaena coridon corydonius*	18
Lysandra bellargus (Rottemburg, 1775)	*Papilio bellargus*	18
Lysandra coridon (Poda, 1761)	*Papilio coridon*	18
Lysandra caelestissima (Verity, 1921)	*Agriades coridon caelestissima*	18
Lysandra albicans (Gerhard, 1851)	*Lycaena coridon* var. *albicans*	18
Polyommatus escheri (Hübner, [1823])	*Papilio escheri*	
Polyommatus thersites (Cantener, 1835)	*Argus thersites*	
Polyommatus daphnis ([Denis & Schiffermüller], 1775)	*Papilio daphnis*	
Polyommatus amandus (Schneider, 1792)	*Papilio amandus*	
Polyommatus golgus (Hübner, [1813])	*Papilio golgus*	
Polyommatus nivescens (Keferstein, 1851)	*Lycaena dorylas* var. *nivescens*	
Polyommatus dorylas ([Denis & Schiffermüller], 1775)	*Papilio dorylas*	
Polyommatus celina (Austaut, 1879)	*Lycaena celina*	21
Polyommatus icarus (Rottemburg, 1775)	*Papilio icarus*	
Polyommatus eros (Ochsenheimer, 1808)	*Papilio eros*	
Polyommatus damon ([Denis & Schiffermüller], 1775)	*Papilio damon*	
Polyommatus damone (Eversmann, 1841)	*Lycaena damone*	
Polyommatus damocles (Herrich-Schäffer, 1844)	*Lycaena damocles*	
Polyommatus admetus (Esper, 1783)	*Papilio admetus*	
Polyommatus ripartii (Freyer, 1830)	*Lycaena ripartii*	
Polyommatus nephohiptamenos (Brown & Coutsis, 1978)	*Agrodiaetus nephohiptamenos*	
Polyommatus iphigenia (Herrich-Schäffer, 1847)	*Lycaena iphigenia*	
Polyommatus violetae (Gómez-Bustillo, Expósito & Martínez, 1979)	*Agrodiaetus violetae*	
Polyommatus fulgens (Sagarra, 1925)	*Hirsutina dolus* r. *fulgens*	22
Polyommatus fabressei (Oberthür, 1910)	*Lycaena rippertii* r. *fabressei*	
Polyommatus dolus (Hübner, [1823])	*Papilio dolus*	
Polyommatus humedasae (Toso & Balletto, 1976)	*Agrodiaetus humedasae*	
Polyommatus timfristos Lukhtanov, Vishnevskaya & Shapoval, 2016	*Polyommatus timfristos*	23
Polyommatus orphicus Kolev, 2005	*Polyommatus orphicus*	
Polyommatus aroaniensis (Brown, 1976)	*Agrodiaetus alcestis aroaniensis*	
Nymphalidae		
Limenitidinae		
Neptis sappho (Pallas, 1771)	*Papilio sappho*	
Neptis rivularis (Scopoli, 1763)	*Papilio rivularis*	
Limenitis reducta Staudinger, 1901	*Limenitis camilla reducta*	
Limenitis populi (Linnaeus, 1758)	*Papilio populi*	
Limenitis camilla (Linnaeus, 1764)	*Papilio camilla*	
Heliconiinae		
Issoria lathonia (Linnaeus, 1758)	*Papilio lathonia*	
Issoria eugenia (Eversmann, 1847)	*Argynnis eugenia*	
Brenthis hecate ([Denis & Schiffermüller], 1775)	*Papilio hecate*	
Brenthis ino (Rottemburg, 1775)	*Papilio ino*	
Brenthis daphne ([Denis & Schiffermüller], 1775)	*Papilio daphne*	
Argynnis paphia (Linnaeus, 1758)	*Papilio paphia*	
Argynnis pandora ([Denis & Schiffermüller], 1775)	*Papilio pandora*	
Argynnis laodice (Pallas, 1771)	*Papilio laodice*	
Speyeria aglaja (Linnaeus, 1758)	*Papilio aglaja*	24

Taxon	Original combination	Notes
Fabriciana elisa (Godart, 1823)	*Argynnis elisa*	24
Fabriciana niobe (Linnaeus, 1758)	*Papilio niobe*	24
Fabriciana adippe ([Denis & Schiffermüller], 1775)	*Papilio adippe*	24
Boloria eunomia (Esper, 1800)	*Papilio eunomia*	25
Boloria graeca (Staudinger, 1870)	*Argynnis pales graeca*	
Boloria pales ([Denis & Schiffermüller], 1775)	*Papilio pales*	
Boloria alaskensis (Holland, 1900)	*Argynnis alaskensis*	
Boloria napaea (Hoffmansegg, 1804)	*Papilio napaea*	
Boloria aquilonaris (Stichel, 1908)	*Argynnis aquilonaris*	
Boloria tritonia (Böber, 1812)	*Papilio tritonia*	
Boloria polaris (Boisduval, 1828)	*Argynnis polaris*	
Boloria thore (Hübner, [1804])	*Papilio thore*	26
Boloria selene ([Denis & Schiffermüller], 1775)	*Papilio selene*	
Boloria euphrosyne (Linnaeus, 1758)	*Papilio euphrosyne*	
Boloria dia (Linnaeus, 1767)	*Papilio dia*	
Boloria improba (Butler, 1877)	*Argynnis improba*	
Boloria frigga (Thunberg, 1791)	*Papilio frigga*	27
Boloria freija (Thunberg, 1791)	*Papilio freija*	27
Boloria selenis (Eversmann, 1837)	*Argynnis selenis*	
Boloria oscarus (Eversmann, 1844)	*Argynnis oscarus*	
Boloria titania (Esper, [1793])	*Papilio titania*	
Boloria chariclea (Schneider, 1794)	*Papilio chariclea*	
Boloria angarensis (Erschoff, 1870)	*Argynnis angarensis*	
Apaturinae		
Apatura iris (Linnaeus, 1758)	*Papilio iris*	
Apatura metis Freyer, 1829	*Apatura metis*	
Apatura ilia ([Denis & Schiffermüller], 1775)	*Papilio ilia*	
Nymphalinae		
Araschnia levana (Linnaeus, 1758)	*Papilio levana*	
Vanessa virginiensis (Drury, 1773)	*Papilio cardui virginiensis*	
Vanessa cardui (Linnaeus, 1758)	*Papilio cardui*	
Vanessa vulcania Godart, 1819	*Vanessa vulcania*	
Vanessa atalanta (Linnaeus, 1758)	*Papilio atalanta*	
Aglais io (Linnaeus, 1758)	*Papilio io*	
Aglais urticae (Linnaeus, 1758)	*Papilio urticae*	
Aglais ichnusa (Hübner, [1824])	*Papilio ichnusa*	28
Polygonia egea (Cramer, 1775)	*Papilio egea*	
Polygonia c-album (Linnaeus, 1758)	*Papilio c-album*	
Nymphalis vaualbum ([Denis & Schiffermüller], 1775)	*Papilio vau album*	
Nymphalis polychloros (Linnaeus, 1758)	*Papilio polychloros*	
Nymphalis xanthomelas ([Denis & Schiffermüller], 1775)	*Papilio xanthomelas*	
Nymphalis antiopa (Linnaeus, 1758)	*Papilio antiopa*	
Hypolimnas misippus (Linnaeus, 1764)	*Papilio misippus*	
Euphydryas desfontainii (Godart, 1819)	*Papilio desfontainii*	
Euphydryas aurinia (Rottemburg, 1775)	*Papilio aurinia*	
Euphydryas cynthia ([Denis & Schiffermüller], 1775)	*Papilio cynthia*	
Euphydryas iduna (Dalman, 1816)	*Melitaea iduna*	
Euphydryas maturna (Linnaeus, 1758)	*Papilio maturna*	

Taxon	Original combination	Notes
Euphydryas intermedia (Ménétriés, 1859)	*Melitaea maturna intermedia*	
Melitaea trivia ([Denis & Schiffermüller], 1775)	*Papilio trivia*	
Melitaea didyma (Esper, 1778)	*Papilio didyma*	
Melitaea arduinna (Esper, 1783)	*Papilio arduinna*	
Melitaea aetherie (Hübner, [1826])	*Papilio aetherie*	
Melitaea phoebe ([Denis & Schiffermüller], 1775)	*Papilio phoebe*	
Melitaea ornata Christoph, 1893	*Melitaea phoebe ornata*	29
Melitaea cinxia (Linnaeus, 1758)	*Papilio cinxia*	
Melitaea diamina (Lang, 1789)	*Papilio diamina*	
Melitaea celadussa Fruhstorfer, 1910	*Melitaea athalia celadussa*	30
Melitaea deione (Geyer, [1832])	*Papilio deione*	
Melitaea britomartis Assmann, 1847	*Melitaea britomartis*	
Melitaea athalia (Rottemburg, 1775)	*Papilio athalia*	
Melitaea varia Herrich-Schäffer, 1851	*Melitaea varia*	31
Melitaea parthenoides Keferstein, 1851	*Melitaea athalia parthenoides*	
Melitaea aurelia Nickerl, 1850	*Melitaea aurelia*	
Melitaea asteria Freyer, 1828	*Melitaea asteria*	
Libytheinae		
Libythea celtis (Laicharting, 1782)	*Papilio celtis*	
Danainae		
Danaus plexippus (Linnaeus, 1758)	*Papilio plexippus*	
Danaus chrysippus (Linnaeus, 1758)	*Papilio chrysippus*	
Charaxinae		
Charaxes jasius (Linnaeus, 1767)	*Papilio jasius*	
Satyrinae		
Coenonympha phryne (Pallas, 1771)	*Papilio phryne*	
Coenonympha oedippus (Fabricius, 1787)	*Papilio oedippus*	
Coenonympha dorus (Esper, 1782)	*Papilio dorus*	
Coenonympha thyrsis (Freyer, 1845)	*Hipparchia thyrsis*	
Coenonympha pamphilus (Linnaeus, 1758)	*Papilio pamphilus*	
Coenonympha tullia (Müller, 1764)	*Papilio tullia*	
Coenonympha rhodopensis Elwes, 1900	*Coenonympha tiphon rhodopensis*	
Coenonympha amaryllis (Stoll, 1782)	*Papilio amaryllis*	
Coenonympha glycerion (Borkhausen, 1788)	*Papilio glycerion*	
Coenonympha corinna (Hübner, [1804])	*Papilio corinna*	
Coenonympha leander (Esper, 1784)	*Papilio leander*	
Coenonympha hero (Linnaeus, [1760])	*Papilio hero*	10
Coenonympha gardetta (Prunner, 1798)	*Papilio gardetta*	
Coenonympha orientalis Rebel, 1909	*Coenonympha arcania* var. *orientalis*	32
Coenonympha arcania (Linnaeus, [1760])	*Papilio arcania*	10
Kirinia roxelana (Cramer, 1777)	*Papilio roxelana*	
Kirinia climene (Esper, 1783)	*Papilio climene*	
Lopinga achine (Scopoli, 1763)	*Papilio achine*	
Pararge xiphia (Fabricius, 1775)	*Papilio xiphia*	
Pararge xiphioides Staudinger, 1871	*Pararge xiphia xiphioides*	
Pararge aegeria (Linnaeus, 1758)	*Papilio aegeria*	
Lasiommata maera (Linnaeus, 1758)	*Papilio maera*	
Lasiommata deidamia (Eversmann, 1851)	*Hipparchia deidamia*	

Taxon	Original combination	Notes
Lasiommata petropolitana (Fabricius, 1787)	*Papilio maera petropolitana*	
Lasiommata paramegaera (Hübner, [1824])	*Papilio paramegaera*	
Lasiommata megera (Linnaeus, 1767)	*Papilio megera*	
Melanargia russiae (Esper, 1783)	*Papilio russiae*	
Melanargia larissa (Geyer, [1828])	*Papilio larissa*	
Melanargia lachesis (Hübner, 1790)	*Papilio lachesis*	
Melanargia galathea (Linnaeus, 1758)	*Papilio galathea*	
Melanargia ines (Hoffmansegg, 1804)	*Papilio ines*	
Melanargia arge (Sulzer, 1776)	*Papilio arge*	
Melanargia pherusa (Boisduval, 1833)	*Arge pherusa*	
Melanargia occitanica (Esper, [1793])	*Papilio arge occitanica*	
Hipparchia fatua Freyer, 1843	*Hipparchia fatua*	33
Hipparchia statilinus (Hufnagel, 1766)	*Papilio statilinus*	
Hipparchia tilosi Manil, 1984	*Hipparchia wyssii tilosi*	
Hipparchia bacchus (Higgins, 1967)	*Pseudotergumia wyssii bacchus*	
Hipparchia wyssii (Christ, 1889)	*Satyrus fidia wyssii*	
Hipparchia tamadabae Owen & Smith, 1992	*Hipparchia wyssi tamadabae*	
Hipparchia gomera (Higgins, 1967)	*Pseudotergumia wyssii gomera*	
Hipparchia fidia (Linnaeus, 1767)	*Papilio fidia*	
Hipparchia neomiris (Godart, 1823)	*Satyrus neomiris*	34
Hipparchia autonoe (Esper, 1783)	*Papilio autonoe*	
Hipparchia hermione (Linnaeus, 1764)	*Papilio hermione*	
Hipparchia syriaca (Staudinger, 1871)	*Satyrus hermione syriaca*	
Hipparchia fagi (Scopoli, 1763)	*Papilio fagi*	
Hipparchia mersina (Staudinger, 1871)	*Satyrus semele mersina*	
Hipparchia miguelensis (Le Cerf, 1935)	*Satyrus azorinus miguelensis*	
Hipparchia azorina (Strecker, 1899)	*Satyrus azorinus*	5, 35
Hipparchia senthes (Fruhstorfer, 1908)	*Eumenis semele senthes*	
Hipparchia maderensis (Bethune-Baker, 1891)	*Satyrus semele maderensis*	
Hipparchia semele (Linnaeus, 1758)	*Papilio semele*	
Hipparchia blachieri (Fruhstorfer, 1908)	*Eumenis semele blachieri*	
Hipparchia aristaeus (Bonelli, 1826)	*Papilio aristaeus*	
Hipparchia volgensis (Mazokhin-Porshnyakov, 1952)	*Satyrus semele volgensis*	
Hipparchia neapolitana (Stauder, 1921)	*Satyrus neapolitana*	
Hipparchia leighebi Kudrna, 1976	*Hipparchia semele leighebi*	
Hipparchia pellucida (Stauder, 1924)	*Satyrus semele pellucida*	36
Hipparchia sbordonii Kudrna, 1984	*Hipparchia sbordonii*	
Hipparchia cypriensis (Holik, 1949)	*Satyrus semele cypriensis*	
Hipparchia cretica (Rebel, 1916)	*Satyrus semele cretica*	
Hipparchia christenseni Kudrna, 1977	*Hipparchia christenseni*	
Minois dryas (Scopoli, 1763)	*Papilio dryas*	
Brintesia circe (Fabricius, 1775)	*Papilio circe*	
Arethusana arethusa ([Denis & Schiffermüller], 1775)	*Papilio arethusa*	
Oeneis tarpeia (Pallas, 1771)	*Papilio tarpeia*	
Oeneis bore (Schneider, 1792)	*Papilio bore*	
Oeneis ammon Elwes, 1899	*Oeneis bore* var. *ammon*	37
Oeneis melissa (Fabricius, 1775)	*Papilio melissa*	
Oeneis magna Graeser, 1888	*Oeneis jutta magna*	

Taxon	Original combination	Notes
Oeneis jutta (Hübner, [1806])	*Papilio jutta*	
Oeneis norna (Thunberg, 1791)	*Papilio norna*	
Oeneis polixenes (Fabricius, 1775)	*Papilio polixenes*	
Oeneis glacialis (Moll, 1785)	*Papilio glacialis*	38
Satyrus ferula (Fabricius, 1793)	*Papilio ferula*	
Satyrus virbius Herrich-Schäffer, 1844	*Satyrus virbius*	
Satyrus actaea (Esper, 1781)	*Papilio actaea*	
Chazara briseis (Linnaeus, 1764)	*Papilio briseis*	
Chazara prieuri (Pierret, 1837)	*Satyrus prieuri*	
Chazara persephone (Hübner, [1805])	*Papilio persephone*	
Pseudochazara geyeri (Herrich-Schäffer, 1846)	*Satyrus geyeri*	
Pseudochazara graeca (Staudinger, 1870)	*Satyrus pelopea graeca*	
Pseudochazara amymone Brown, 1976	*Pseudochazara amymone*	
Pseudochazara anthelea (Hübner, [1824])	*Papilio anthelea*	
Pseudochazara amalthea (Frivaldszky, 1845)	*Hipparchia amalthea*	39
Pseudochazara williamsi (Romei, 1927)	*Satyrus hippolyte williamsi*	
Pseudochazara euxina (Kuznetsov, 1909)	*Hipparchia euxina*	
Pseudochazara mercurius (Staudinger, 1887)	*Satyrus mercurius*	40
Pseudochazara cingovskii (Gross, 1973)	*Satyrus sintenisi cingovskii*	
Pseudochazara tisiphone Brown, [1981]	*Pseudochazara cingovskii tisiphone*	39
Pseudochazara orestes De Prins & van der Poorten, 1981	*Pseudochazara orestes*	
Ypthima asterope (Klug, 1832)	*Hipparchia asterope*	
Proterebia phegea (Borkhausen, 1788)	*Papilio phegea*	41
Hyponephele huebneri Koçak, 1980	*Hyponephele huebneri*	
Hyponephele lycaon (Kühn, 1774)	*Papilio lycaon*	
Hyponephele lupina (Costa, 1836)	*Satyrus lupinus*	5
Aphantopus hyperantus (Linnaeus, 1758)	*Papilio hyperantus*	
Pyronia cecilia (Vallantin, 1894)	*Epinephele ida cecilia*	
Pyronia tithonus (Linnaeus, 1771)	*Papilio tithonus*	42
Pyronia bathseba (Fabricius, 1793)	*Papilio bathseba*	
Maniola jurtina (Linnaeus, 1758)	*Papilio jurtina*	
Maniola nurag (Ghiliani, 1852)	*Satyrus nurag*	
Maniola chia Thomson, 1987	*Maniola chia*	
Maniola megala (Oberthür, 1909)	*Epinephele janira megala*	
Maniola cypricola (Graves, 1928)	*Epinephele cypricola*	
Maniola telmessia (Zeller, 1847)	*Hipparchia telmessia*	
Maniola halicarnassus Thomson, 1990	*Maniola halicarnassus*	
Erebia edda Ménétriés, 1851	*Erebia edda*	
Erebia fasciata Butler, 1868	*Erebia fasciata*	
Erebia discoidalis (Kirby, 1837)	*Hipparchia discoidalis*	
Erebia rossii (Curtis, 1835)	*Hipparchia rossii*	43
Erebia cyclopius (Eversmann, 1844)	*Hipparchia cyclopius*	
Erebia embla (Thunberg, 1791)	*Papilio embla*	
Erebia disa (Thunberg, 1791)	*Papilio disa*	
Erebia meolans (Prunner, 1798)	*Papilio meolans*	
Erebia dabanensis Erschoff, 1872	*Erebia dabanensis*	44
Erebia jeniseiensis Trybom, 1877	*Erebia ligea jeniseiensis*	
Erebia claudina (Borkhausen, 1789)	*Papilio claudina*	

Taxon	Original combination	Notes
Erebia manto ([Denis & Schiffermüller], 1775)	*Papilio manto*	
Erebia ottomana Herrich-Schäffer, 1847	*Erebia dromus ottomana*	
Erebia hispania Butler, 1868	*Erebia hispania*	
Erebia rondoui Oberthür, 1908	*Erebia rondoui*	
Erebia callias Edwards, 1871	*Erebia callias*	45
Erebia tyndarus (Esper, 1781)	*Papilio tyndarus*	
Erebia cassioides (Hohenwarth, 1792)	*Papilio cassioides*	46
Erebia nivalis Lorković & Lesse, 1954	*Erebia nivalis*	
Erebia neleus (Freyer, 1832)	*Hipparchia neleus*	47
Erebia calcarius Lorković, 1953	*Erebia tyndarus calcarius*	
Erebia arvernensis Oberthür, 1908	*Erebia tyndarus arvernensis*	47
Erebia oeme (Hübner, [1804])	*Papilio oeme*	
Erebia gorge (Hübner, [1804])	*Papilio gorge*	
Erebia sthennyo Graslin, 1850	*Erebia sthennyo*	
Erebia pandrose (Borkhausen, 1788)	*Papilio pandrose*	
Erebia eriphyle (Freyer, 1836)	*Hipparchia eriphyle*	
Erebia epistygne (Hübner, [1819])	*Papilio epistygne*	
Erebia euryale (Esper, 1805)	*Papilio euryale*	
Erebia palarica Chapman, 1905	*Erebia palarica*	
Erebia ligea (Linnaeus, 1758)	*Papilio ligea*	
Erebia pluto (Prunner, 1798)	*Papilio pluto*	
Erebia aethiopellus (Hoffmansegg, 1806)	*Papilio aethiopellus*	
Erebia gorgone Boisduval, 1833	*Erebia gorgone*	
Erebia rhodopensis Nicholl, 1900	*Erebia gorgone rhodopensis*	
Erebia mnestra (Hübner, [1804])	*Papilio mnestra*	
Erebia albergana (Prunner, 1798)	*Papilio alberganus*	5
Erebia sudetica Staudinger, 1861	*Erebia melampus sudetica*	
Erebia melampus (Fuessly, 1775)	*Papilio melampus*	
Erebia triarius (Prunner, 1798)	*Papilio triarius*	
Erebia polaris Staudinger, 1861	*Erebia medusa* var. *polaris*	48
Erebia medusa ([Denis & Schiffermüller], 1775)	*Papilio medusa*	
Erebia aethiops (Esper, 1777)	*Papilio aethiops*	
Erebia pharte (Hübner, [1804])	*Papilio pharte*	
Erebia christi Rätzer, 1890	*Erebia christi*	
Erebia orientalis Elwes, 1900	*Erebia epiphron orientalis*	
Erebia epiphron (Knoch, 1783)	*Papilio epiphron*	
Erebia flavofasciata Heyne, 1895	*Erebia flavofasciata*	
Erebia montana (Prunner, 1798)	*Papilio montanus*	5
Erebia styx (Freyer, 1834)	*Hipparchia styx*	
Erebia stiria (Godart, [1824])	*Satyrus stirius*	5
Erebia scipio Boisduval, 1833	*Erebia scipio*	49
Erebia pronoe (Esper, 1780)	*Papilio pronoe*	
Erebia melas (Herbst, 1796)	*Papilio melas*	
Erebia lefebvrei (Boisduval, 1828)	*Satyrus lefebvrei*	
Erebia zapateri Oberthür, 1875	*Erebia zapateri*	
Erebia neoridas (Boisduval, 1828)	*Satyrus neoridas*	

Table 3. Annotations to the updated checklist of the butterflies of Europe.

1	*Iphiclides feisthamelii* is considered a separate species based on differences in adult morphology (Coutsis and van Oorschot 2011, Lafranchis et al. 2015) and nuclear genetic markers (Wiemers and Gottsberger 2010; Dincă et al. 2015), despite very local hybridisation along the contact zone in southern France (Lafranchis et al. 2015) and extensive mitochondrial introgression in the Iberian Peninsula (Wiemers and Gottsberger 2010; Dincă et al. 2015). Its distribution includes the SW part of France, the Iberian Peninsula, and northern Africa.
2	Author of the name is Giuseppe Gené (1800–1847), not Achille Guenée.
3	Dapporto (2009) has shown that *Zerynthia cassandra* from peninsular Italy is a separate species based on differences in genital morphology. This was further confirmed by molecular studies (Zinetti et al. 2013).
4	*Spialia rosae* has been recognised as a separate species endemic to mountains of Spain based on differences in ecology and evidence from molecular studies (mitochondrial DNA, chemical profiles) (Hernández-Roldán et al. 2016, 2018). The species has already been included in Fauna Europaea (2018).
5	Gender agreement changes were applied consistently in accordance with Art. 31.2 and Art. 34.2 (ICZN 1999).
6	As descriptions of both *Syrichtus alveus f. foulquieri* and *Syrichtus alveus f. bellieri* were published simultaneously (Oberthür, 1910), the name used by the first reviser (i. e. Rebel 1914), *Pyrgus foulquieri*, should be used in accordance with Art. 24.2.1 and Art. 24.2.2 (ICZN 1999).
7	Recent studies have shown that *Leptidea reali* actually comprises two species, *L. reali* and *L. juvernica*. *L. reali* is known from south-western Europe (Spain, S France and Italy) and is replaced by *L. juvernica* in the rest of the continent (Dincă et al. 2011b). *L. sinapis*, *L. reali,* and *L. juvernica* are reproductively isolated due to female mate choice (Dincă et al. 2013).
8	The year of the publication of the name *Anteos cleobule* is 1831, not 1830 (the original plate [79], published in 1824, carried no names).
9	The name *Papilio croceus* should be credited to Geoffroy in Fourcroy, 1785, not to Fourcroy (Ganglbauer and Heyden 1906, D'Aguilar and Raimbault 1990, Grieshuber et al. 2012).
10	The date of the publication of the names by Linnaeus in Fauna Svecica (ed. 2) is 14 November 1760, not 1761 (see Evenhuis 1997, Bousquet 2016).
11	The year of the publication of the name *Pieris balcana* is 1969, not 1970. The publication year of volume 21 (1–4) (1968) of *Biološki glasnik* [= volume 70 of *Periodicum Biologorum*] is printed on the cover page as "1969" and, moreover, Lorković´s personal copy held in the Croatian Natural History museum has a hand written addition of the publication year "1969" in the header of his article (Šašić, pers. comm.). Additionally, the author´s name is misspelled and should be Lorković (see also Lorković 1969).
12	According to Lvovsky and Morgun (2007) the species is present in Russia south of the Urals in the Orenburg region. The subspecies *Lycaena dimorpha irghiza* was originally described as a subspecies of *L. japhetica* (Nekrutenko 1985), but we follow the decision in the taxonomic review by Lukhtanov (2000).
13	The year of the publication of the name *Polyommatus ottomanus* is 1831, not 1830. Lefèbvre cited the date 1830, which corresponds to the date of submission of his article, but the issue of the journal was published in January 1831. See Lefèbvre (1831)
14	The generic names *Apharitis* and *Spindasis* were synonymised with *Cigaritis* due to morphological similarities (see Heath and Pringle 2011).
15	The name *Papilio roboris* was first published in 1793, not 1789 (Lamas 2013).
16	*Iolana debilitata* has been recognised as a separate species based on constant differences in adult morphology (Dumont 2004) and mitochondrial DNA – barcoding gene (Dincă et al. 2015).
17	The year of the publication of the name and plates for *Cupido lorquinii* is 1850, not 1847 (Hemming 1937, Heppner 1982).
18	Genus level classification in the subfamily Polyommatinae follows Talavera et al. (2013) based on molecular phylogeny. This arrangement partially concurs with differences in genital morphology (see Balletto et al. 2014, Coutsis 2017).
19	The year of the publication of the name *Lycaena trochylus* is 1844, not 1845 (Tremewan 1988, Olivier 2000).
20	The year of the publication of the name *Polyommatus nicias* is ante September 1829, not 1830 (Griffin 1931).
21	*Polyommatus celina* has been recognised as a separate species distributed in the Iberian Peninsula, northern Africa, Sardinia and Sicily based on molecular markers and adult morphology (Wiemers et al. 2010; Dincă et al. 2011a).
22	The author´s surname Sagarra should be without the particle "de". It is listed as such in the members list of the Institució Catalana d'Història Natural in 1925 bulletin Vol. 5 – Num. 1. Generally, when the particle is written in lowercase, it should be treated as a suffix that goes after the first name (Welter-Schultes 2013).
23	*Polyommatus timfristos* is considered a separate species due to differences in haploid chromosome number compared to *P. aroaniensis* and mitochondrial DNA – barcoding gene (Vishnevskaya et al. 2016).

24	Genus level classification in the tribe Argynnini follows De Moya et al. (2017) based on molecular phylogenetics. It is corroborated by extensive differences in genital morphology (Simonsen 2006a, 2006b).
25	The name *Papilio eunomia* was first published in 1800, not 1799 (Poche, 1938).
26	The name *Papilio thore* was first published in 1804, not 1803 (Hemming 1937).
27	Description of *Boloria freija* and *Boloria frigga* must be credited to Thunberg, not to Becklin (Thunberg wrote Becklin's dissertation), see Karsholt and Nielsen (1986).
28	*Papilio ichnusa* was first described by Hübner (ante 23 December) 1824. *Vanessa ichnusa* Bonelli was published in February 1825 and is a junior secondary homonym and junior subjective synonym, see Hemming (1937).
29	Among the species with red headed larvae within the *Melitaea phoebe* species group only *M. ornata* is present in Europe in southeastern Russia, the Balkan Peninsula, Spain, southeastern France, and southern Italy. *M. telona* is limited to the Levant and *M. punica* to northern Africa (Toth et al. 2014).
30	*Melitaea celadussa* Fruhstorfer, 1910 is considered a separate species distributed in western Europe that differs in genital morphology (Higgins 1932) and molecular markers (Leneveu et al. 2009, Dincă et al. 2015) from *M. athalia*, with hybrids known from the contact zone (Achtelik 2006; Oorschot and Coutsis 2014). The species was referred to also as *M. nevadensis* Oberthür, 1904, which is a junior primary homonym of *Melitaea parthenie* var. *nevadensis* Spuler, 1901, currently regarded as a junior subjective synonym of *Melitaea parthenoides* Keferstein, 1851.
31	*Melitaea varia* was first described by Herrich-Schäffer (1851) in *Systematische Bearbeitung der Schmetterlinge von Europa* Vol. 6(48): 2 (Hemming 1937). *Melitaea parthenie* var. *varia* Meyer-Dür, 1852 (not 1851) is a junior primary homonym.
32	The name *Coenonympha arcánia* var. *orientális* [sic] appeared in part 4 of the ninth edition of Berge's *Schmetterlingsbuch*, which was published on 22 May 1909 (Lempke 1949), not in 1910.
33	The name *Hipparchia fatua* was first published in 1843, not 1844 (Olivier 2000).
34	The name *Satyrus neomiris* was first published in 1823, not 1822. *Satyrus neomiris* first appeared on page 19 in Godart's *Tableau méthodique des lépidoptères*..., published in 1823. The vernacular name Godart used in vol. 2 of *Hist. nat. Lépid. Pap. France*, pp. 88–89, pl. 11, figs. 1–2 (1822), »Satyre néomiris«, is unavailable, as it is not a scientific name.
35	The name *Satyrus azorinus* was first published in 1899, not 1898.
36	The name *Satyrus semele pellucida* was first published on 15 May 1924, not in 1923.
37	*Oeneis ammon* is present in Europe in the Polar Urals (Tsvetkov 2006).
38	The name *Papilio glacialis* was first published in 1785, not 1783.
39	Based on differentiation in mtDNA (barcodes) and differences in morphology, *Pseudochazara amalthea* and *P. tisiphone* are considered separate species from allopatric *P. anthelea* and *P. mniszechii* respectively (Verovnik and Wiemers 2016).
40	*Pseudochazara hippolyte* (Esper, 1783) is a junior primary homonym of *Papilio hyppolite* Drury, 1782. The oldest available name for this taxon is *Satyrus mercurius* Staudinger, 1887.
41	*Papilio afer* Esper, 1783 is a junior primary homonym of *Papilio afer* Drury, 1782 (see Koçak 1981), as is *Papilio afra* Fabricius, 1787, because it differs only in gender. Therefore the oldest available name is *Papilio phegea* Borkhausen, 1788.
42	The name *Papilio tithonus* was first published in 1771 in *Mantissa Plantarum Altera*, not in 1767.
43	The name *Hipparchia rossii* was first published in November 1835, not in 1834.
44	The name *Erebia dabanensis* was published on 13 November 1872, not in 1871.
45	Recently, a population of *Erebia* was discovered in the Polar Urals and described as a new species, *E. churkini* Bogdanov, 2008, but is now considered a subspecies of *Erebia callias* (Tatarinov & Gorbunov, 2015). However, no further material is available, therefore it is tentatively considered as part of the European fauna. *Erebia callias* is a member of the *tyndarus* group (Albre et al. 2008) and ranges from the mountains of the Asian part of Russia and Mongolia to Colorado (USA).
46	The author of the name *Papilio cassioides* is Hohenwarth alone as indicated on page III of Reiner and Hohenwarth (1792), not Reiner and Hohenwarth.
47	Based on molecular data and differences in wing patterns *Erebia cassioides* has been split into three allopatric species (Schmitt et al. 2016). *E. cassioides* is limited to the eastern Alps, *E. arvernensis* is distributed in the western Alps, Cantabrian mountains and Pyrénées, while *E. neleus* is present in the mountains of the Balkan Peninsula and the southern Carpathians.
48	The name *Erebia medusa polaris* was first published in September 1861, not in 1871.
49	The year of publication of the name *Erebia scipio* by Boisduval is 1833, not 1832 (Cowan 1970).

Table 4. Species richness of European butterfly families and subfamilies.

Family	Subfamily	Genera	Species
Hesperiidae		**13**	**47**
	Hesperiinae	6	11
	Heteropterinae	2	3
	Pyrginae	5	33
Lycaenidae		**39**	**130**
	Aphnaeinae	1	1
	Lycaeninae	1	13
	Polyommatinae	30	98
	Theclinae	7	18
Nymphalidae		**41**	**246**
	Apaturinae	1	3
	Charaxinae	1	1
	Danainae	1	2
	Heliconiinae	6	32
	Libytheinae	1	1
	Limenitidinae	2	5
	Nymphalinae	8	37
	Satyrinae	21	165
Papilionidae		**5**	**15**
	Papilioninae	2	5
	Parnassiinae	3	10
Pieridae		**11**	**57**
	Coliadinae	3	18
	Dismorphiinae	1	5
	Pierinae	7	34
Riodinidae		**1**	**1**
	Nemeobiinae	1	1
Total	**21**	**110**	**496**

A larger number of changes concern the genus names. Most of them are in the family Lycaenidae, where 26 species changed their genus name, mainly based on the molecular study by Talavera et al. (2013), which substantially improved our knowledge of phylogenetic relationships of the subtribe Polyommatina. However, none of the genus names is new and many of them have already been used with the same species. In addition, four species formerly placed in the genus *Argynnis* were transferred into the genera *Fabriciana* and *Speyeria*, based on the study by De Moya et al. (2017). The former genus name had already been used previously for the same species, whereas the latter seems new to European lepidopterists, but is commonly used in North America. Although it could be argued that the change was avoidable by keeping a larger genus *Argynnis*, a solution originally also favoured by Simonsen et al. (2006), this would have meant to rename a large number of North American butterflies currently placed in the genus *Speyeria*, and was rejected by North American lepidopterists. Therefore, the recommended changes appear to cause the least changes on a global level and will hopefully contribute to a more consistent taxonomy of Holarctic Argynnini.

Table 5. Authors of currently valid European butterfly species (with a minimum of three described taxa).

Author	Life data	Nationality	Species	Period
Linnaeus, Carolus	1707–1778	Swedish	71	1758–1771
Poda von Neuhaus, Nicolaus (Nikolaus)	1723–1798	Austrian	4	1761
Scopoli, Giovanni Antonio	1723–1788	Italian	4	1763
Pallas, Peter Simon	1741–1811	German	8	1771
Schiffermüller, Johann Ignaz	1727–1806	Austrian	21	1775
Fabricius, Johan Christian	1745–1808	Danish	16	1775–1793
Rothenburg [alias Rottemburg], Siegmund Adrian von	1745–1797	German	8	1775
Esper, Eugen Johann Christoph	1742–1810	German	32	1777–1805
Bergsträsser, Johann Andreas Benignus	1732–1812	German	5	1779–1780
Knoch, August Wilhelm	1742–1818	German	3	1781–1783
Borkhausen, Moritz Balthasar	1760–1806	German	4	1788–1789
Hübner, Jacob	1761–1826	German	31	1790–1831
Thunberg, Carl Peter	1743–1828	Swedish	5	1791
Schneider, David Hinrich	1755–1826	German	3	1792–1794
Prunner, Leonhard von	17??–1830	German	8	1798
Hoffmansegg, Johann Centurius Graf von	1766–1849	German	6	1804–1806
Ochsenheimer, Ferdinand	1767–1822	German	4	1808–1816
Godart, Jean Baptiste	1775–1825	French	6	1819–1824
Freyer, Christian Friedrich	1794–1885	German	16	1828–1851
Boisduval, Jean Baptiste Alphonse Dechauffour de	1799–1879	French	13	1828–1848
Geyer, Carl	1802–1889	German	4	1828–1832
Klug, Johann Christoph Friedrich	1775–1856	German	4	1829–1834
Meigen, Johann Wilhelm	1764–1845	German	3	1829
Eversmann, Eduard Friedrich von	1794–1860	Russian	14	1832–1851
Rambur, Jules Pierre	1801–1870	French	10	1832–1839
Herrich-Schäffer, Gottlieb August Wilhelm	1799–1874	German	14	1844–1852
Zeller, Philipp Christoph	1808–1883	German	4	1847
Lederer, Julius	1821–1870	Austrian	3	1855–1864
Staudinger, Otto	1830–1900	German	17	1860–1901
Butler, Arthur Gardiner	1844–1925	British	6	1868–1898
Oberthür, Charles	1845–1924	French	9	1875–1910
Rebel, Hans	1861–1940	Austrian	5	1894–1916
Elwes, Henry John	1846–1922	British	3	1899–1900
Chapman, Thomas Algernon	1842–1921	British	3	1905–1920
Fruhstorfer, Hans	1866–1922	German	3	1908–1910
Verity, Ruggero	1883–1959	Italian	5	1921–1928
Kudrna, Otakar	1939–	Czech	3	1976–1984
Brown, John	19??–	British	3	1976–1981

Finally, quite a number of minor changes have been implemented, which correct mistakes in names of authors, year of publication, or the incorrect use of parentheses for species that have changed generic combinations. An example is the change of year for 6 butterfly names due to a correction of the publication date of Linnaeus' Fauna Svecica. Evenhuis (1997: 480) has shown convincingly that this edition was actually published on [14 November 1760], not "1761" as stated in the title page of the work and Bousquet (2016) also agrees with that year of publication.

Table 6. Butterfly species excluded from the European list with explanations.

Turanana panagaea (Herrich-Schäffer, 1851)	Distributed outside Europe in the Asian part of Turkey and replaced by *Turanana taygetica* in Europe (Hesselbarth et al. 1995; Coutsis 2005). [Junior subjective synonym of *Lycaena endymion* Gerhard, 1851; misspelled as *Turanana panagea* in Fauna Europaea]
Polyommatus eleniae Coutsis & De Prins, 2005	Considered conspecific with *Polyommatus orphicus* based on the equal haploid chromosome number and no differences in mitochondrial DNA – barcoding gene (Vishnevskaya et al. 2016).
Polyommatus galloi (Balletto & Toso, 1979)	According to the molecular study of Vila et al. (2010) *P. galloi* represents an isolated population of *Polyommatus ripartii* and is not considered as a separate species.
Polyommatus menalcas (Freyer, 1837)	Distributed outside Europe in Asian part of Turkey (Hesselbarth et al. 1995).
Polyommatus pljushtchi Lukhtanov & Budashkin, 1993	Species status is based on erroneous sequences (opinion in Kudrna et al. (2011); Shapoval and Lukhtanov (2015).) Considered here as ssp. of *Polyommatus damone* (Eversmann, 1841).
Melitaea punica Oberthür, 1876	Distributed outside Europe in northern Africa (Toth et al. 2014).
Melitaea telona Fruhstorfer, 1908	Distributed outside Europe in Levant (Toth et al. 2014).
Pseudochazara mniszechii (Herrich-Schäffer, 1851)	Distributed outside Europe in Asian part of Turkey (Hesselbarth et al. 1995). *P. tisiphone*, often considered as a subspecies of *P. mniszechii*, was shown not to be closely related to it (Verovnik and Wiemers 2016).
Pseudochazara beroe (Freyer, 1843)	Distributed outside Europe in Asian part of Turkey (Hesselbarth et al. 1995).

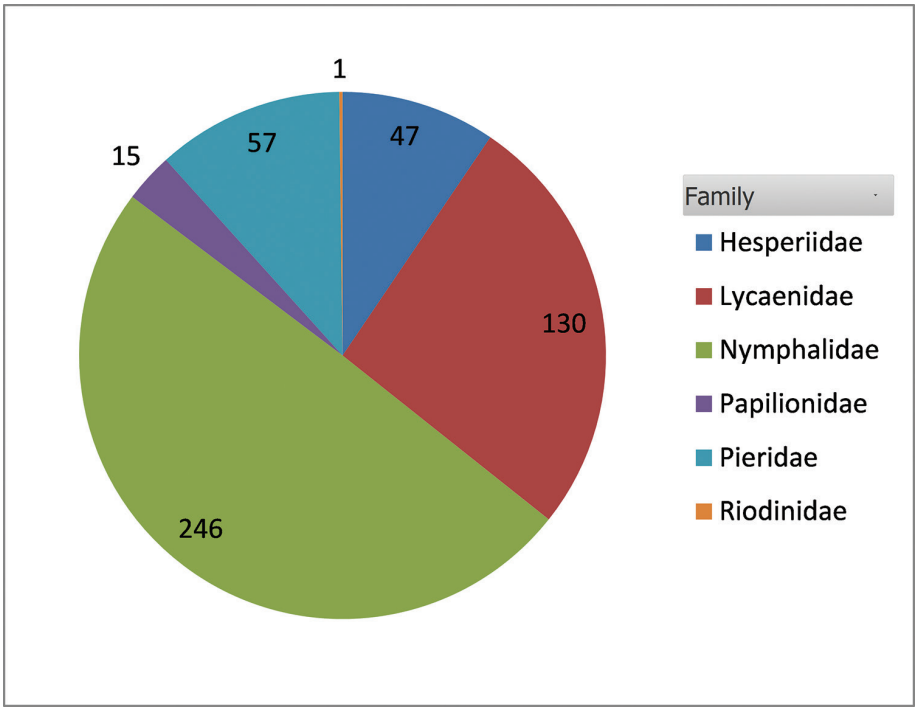

Figure 4. Species richness of butterfly families in Europe.

Table 7. List of the 14 European butterfly species that are affected by the gender agreement provision.

Name	Original species epithet
Agriades pyrenaicus	*pyrenaica*
Carcharodus tripolinus	*tripolina*
Colias crocea	*croceus*
Cupido decoloratus	*decolorata*
Erebia aethiopella	*aethiopellus*
Erebia albergana	*alberganus*
Erebia montana	*montanus*
Erebia stiria	*stirius*
Hipparchia azorina	*azorinus*
Hyponephele lupina	*lupinus*
Kretania hesperica	*hespericus*
Lycaena dimorpha	*dimorphus*
Lycaena ottomana	*ottomanus*
Tarucus balkanicus	*balkanica*

Conclusions

Taking into account the many recent research findings, especially those with molecular methods, we think that the new taxonomy represents a step forward in stabilizing European butterfly taxonomy and nomenclature. Nevertheless, we have to note that some groups, e.g., the genera *Euchloe*, *Callophrys*, *Pseudophilotes*, *Melitaea*, and *Hipparchia*, as well as the subgenus *Agrodiaetus* of the genus *Polyommatus* are still in need of revision, which will certainly lead to additional changes in the future. Furthermore, we still have large knowledge gaps for species in other regions of the Palearctic region (especially in Central Asia), which might require changes in order to achieve a consistent taxonomy of Palearctic and Holarctic butterflies.

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Appendix 1

Evidence that the junior synonym *Polyommatus ottomanus* Lefèbvre, 1831 has been used to denote the taxon currently known as *Lycaena ottomana* (Lefèbvre, [1831]), in at least 25 works, published by at least 10 authors during the last 50 years and encompassing a span of not less than 10 years, and thus fulfilling the conditions of article 23.9.1.2 of the code in order to reverse the precedence of *Lycaena legeri* Freyer, 1830.

Already during the decades immediately following the publication of *legeri* Freyer, this name does not seem to have been used but as a subjective junior synonym of *ot-*

tomanus Lefèbvre. The latter name was thought to represent the valid name and was first used in its original combination (*Polyommatus ottomanus*) and starting from the 20th century mostly in the combination of *Chrysophanus ottomanus*:

- Brullé (1832): *Polyommatus ottomanus* Lef.
- Herrich-Schäffer (1843): *Polyomm. Ottomanus* Lef.; synonym: *Legeri*
- Mann (1862): *Polyommatus ottomanus* Lef.
- Lang (1884): *Polyommatus Ottomanus,* Lefebrve [sic]; synonym: *Legeri,* Frr.
- Rebel (1903): *Chrysophanus Ottomanus* Lef.
- Spuler (1908): *Chrysóphanus ottománus* Lef.
- Courvoisier (1921): *Chrysophanus ottomanus* Lefebvre 1830; synonym: *legeri* Freyer, 1832
- Galvagni (1924): *Chrysophanus ottomanus* Lef.
- Rebel and Zerny (1934): *Chrysophanus ottomanus* Lef.
- Kanus (1963): *Heodes* (*Chrysophanus*) *ottomanus* Lef.

During the last 50 years we are not aware of any use of *legeri* Freyer, except as a subjective junior synonym of *ottomanus* Lefèbvre. The latter name was mostly used in the combination of *Heodes ottomanus* and later as *Lycaena ottomanus* or, due to the gender agreement rule of the code, as *Lycaena ottomana*:

1. Higgins and Riley (1970): *Heodes ottomanus* Lefèbvre, 1830
2. Higgins (1975): *Heodes ottomanus* Lefèbvre 1830
3. Higgins and Riley (1978): *Heodes ottomanus* Lefèbvre 1830
4. Schmidt-Koehl (1980): *Heodes ottomanus* Lefebvre, 1830
5. Krzywicki (1981): *Heodes ottomanus* Lefevre [sic]
6. Wiemers (1983): *Heodes ottomanus ottomanus* Lef.
7. Higgins and Riley (1983): *Heodes ottomanus* Lefèbvre, 1830
8. Kudrna (1986): *Lycaena ottomanus* Lefebvre, 1830
9. Jakšić (1988): *Lycaena ottomanus* Lefèbvre, 1830
10. Schaider and Jakšić (1989): *Lycaena ottomanus* Lef.
11. Hesselbarth et al. (1995): *Lycaena ottomana* (Lefebvre, [1830]); synonym: "Gen. IX. *Lycaena*. 182. Pap. *Legeri*" Freyer, C.F., [Dezember] 1830
12. Karsholt and Razowki (1996): *Lycaena ottomanus* (Lefèbvre, 1830)
13. Pamperis (1997): *Heodes ottomanus*
14. Jakšić (1998): *Lycaena ottomanus* Lefèbvre, 1830
15. Tolman and Lewington (1998): *Lycaena ottomana* (Lefèbvre, 1830)
16. Abadjiev (2001): *Lycaena ottomana* (Lefebvre, [1830])
17. Bozano and Weidenhoffer (2001): *Lycaena ottomanus* (Lefebvre, 1830); synonym: *legeri* Freyer, 1839
18. Mihoci et al. (2005): *Lycaena ottomanus* (Lefèbvre, 1830)
19. Coutsis and Ghavalas (2006): *Lycaena ottomanus* (Lefebvre, 1830)
20. Wagener (2006): *Lycaena ottomanus* (Lefebvre, 1830)
21. Settele et al. (2008): *Lycaena ottomana* (Lefebvre, 1830)

22. Tolman and Lewington (2008): *Lycaena ottomana* Lefèbvre, 1830
23. Pamperis (2009): *Lycaena ottomanus*
24. Van Swaay et al. (2010): *Lycaena ottomana* (Lefèbvre, 1830)
25. Tshikolovets (2011): *Lycaena ottomana* (Lefebvre, [1830]); synonym: *legeri* Freyer, 1839
26. Kemal and Koçak (2011): *Lycaena* (*Heodes*) *ottomanus* (Lefèbvre, [1830]); synonym: *legeri* Freyer, 1830
27. Kudrna et al. (2011): *Lycaena ottomana* (Lefebvre, 1831)
28. Koren et al. (2012): *Lycaena ottomana* (Lefèbvre, 1830)
29. Verovnik & Popović (2012): *Lycaena ottomanus* (Lefèbvre, 1830)
30. Kudrna et al. (2015): *Lycaena ottomana* (Lefebvre, 1831)
31. Çalişkan (2016): *Lycaena ottomanus* (Lefèbvre, [1830])

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Supplementary material 1

Distributional checklist of European butterflies (country checklist)

Authors: Martin Wiemers, Emilio Balletto, Vlad Dincă, Zdenek Faltynek Fric, Gerardo Lamas, Vladimir Lukhtanov, Miguel L. Munguira, Chris A. M. van Swaay, Roger Vila, Albert Vliegenthart, Niklas Wahlberg, Rudi Verovnik

Data type: occurrence

Link: https://doi.org/10.3897/zookeys.811.28712.suppl1

Supplementary material 2

Distributional checklist of European butterflies (CoL)

Authors: Martin Wiemers, Emilio Balletto, Vlad Dincă, Zdenek Faltynek Fric, Gerardo Lamas, Vladimir Lukhtanov, Miguel L. Munguira, Chris A. M. van Swaay, Roger Vila, Albert Vliegenthart, Niklas Wahlberg, Rudi Verovnik

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On a new species of freshwater crab, *Indochinamon khinpyae*, from northern Myanmar (Crustacea, Brachyura, Potamidae)

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Abstract

A new species of freshwater crab of the genus *Indochinamon* Yeo & Ng, 2007 (family Potamidae), is described from highlands north of Myitkyina in Kachin State, Myanmar. *Indochinamon khinpyae* **sp. n.** is distinguished from congeners by its very rugose carapace, broad male pleon and distinctively structured male first gonopod; and is the first potamid species recorded from northern Myanmar.

Keywords

Taxonomy, freshwater crab, Burma, Potaminae, *Indochinamon*, new species, description

Introduction

The freshwater crabs (Brachyura, Potamidae, Gecarcinucidae) of Indochina are very diverse, with the fauna still in a survey and discovery stage. The fauna of Myanmar (= Burma) in particular, is poorly known, with most of the recognised species described in the early 1900s (see Yeo and Ng 1999; Cumberlidge et al. 2012). Recent efforts in recording the crab fauna have only just started (e.g., Ng 1996, 2018; Ng and Kosuge 1997; Ng and Whitten 2017), with many parts of the country still barely explored. The second author recently obtained several lots of freshwater crabs from northern Myanmar, one of which proved to belong to a new species of Potamidae.

Material and methods

The terminology used follows Ng (1988) with recent changes by Davie et al. (2015). The abbreviations G1 and G2 are used for the male first and second gonopods, respectively. Measurements provided, in millimetres, are of the maximum carapace width and length, respectively. The material examined is deposited in the Museo Civico di Storia Naturale "Giacoma Doria" (MGE), Genova, Italy; Naturhistorisches Museum Basel (MBA), Basel, Switzerland; Muséum national d'Histoire naturelle (MNHN), Paris, France; Naturalis [formerly Rijksmuseum van Natuurlijke Histoire, RMNH], Leiden, The Netherlands; Senckenbergischen Naturforschenden Gesellschaft (SMF), Frankfurt am Main, Germany; Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum, National University of Singapore; and the Zoological Survey of India (ZSI), Calcutta, India.

Systematics

Family Potamidae Ortmann, 1896 sensu Yeo and Ng (2004)

Genus *Indochinamon* Yeo & Ng, 2007

Type species. *Potamon villosum* Yeo & Ng, 1998, by original designation.

Remarks. The genus currently contains 38 species from Thailand, Vietnam, Laos, Myanmar, India and China (Table 1, updated from Ng et al. 2008; Naruse et al. 2018). Established by Yeo and Ng (2007) for Indochinese species previously placed in *Potamon* Savigny, 1816, s. lato, *Indochinamon* is defined by a suite of characters: carapace low with a relatively flat dorsal surface; the epigastric cristae are separated from the postorbital cristae by a distinct groove; the postorbital cristae is not confluent with the epibranchial tooth; the exopod of the third maxilliped has a long flagellum; the ambulatory legs are relatively short and stout; the male pleon is narrowly triangular; the sternopleonal cavity reaches an imaginary line joining the median parts of the coxae of the chelipeds; and the G1 terminal segment is relatively short, with the groove for the G2 marginal in position, and the dorsal flap is either absent or only low and broad.

Indochinamon khinpyae sp. n.

http://zoobank.org/878C53F6-38DA-42C3-B282-A1F6A56C0E92
Figs 1–4

Material examined. Holotype: male (57.1×43.2 mm) (ZRC 2018.0713), Malikha River, about 3.2 km from confluence point of Ayeyarwady River, north of Myitkyina, Kachin State, Myanmar, coll. Khin Pyae Pyae Thaw Thar, May 2018. Paratypes: 5 males (47.2×36.4 mm, 48.9×37.7 mm, 46.4×35.8 mm, 34.3×26.6 mm, 26.7×21.1 mm), 1 female (39.3×31.1 mm) (ZRC 2018.0714), same data as holotype.

Table 1. List of recognised *Indochinamon* species.

Indochinamon ahkense Naruse, Chia & Zhou, 2018 [type locality: Guangnan County, Yunnan Province, China]
Indochinamon andersonianum (Wood-Mason, 1871) [type locality: Momein, west Yunnan Province, China]
Indochinamon asperatum (Alcock, 1909) [type locality: Cachar Hills, India]
Indochinamon bavi Naruse, Nguyen & Yeo, 2011 [type locality: Ha Tay Province, northern Vietnam]
Indochinamon beieri (Pretzmann, 1966) [type locality: Dawane Hills, India]
Indochinamon bhumibol (Naiyanetr, 2001) [type locality: Loei Province, northern Thailand]
Indochinamon boshanense (Dai & Chen, 1985) [type locality: Boshan, Yunnan Province, China]
Indochinamon changpoense (Dai, 1995) [type locality: Jingping, Yunnan Province, China]
Indochinamon chinghungense (Dai, Song, He, Cao, Xu & Zhong, 1975) [type locality: Ching Hung, Yunnan Province, China]
Indochinamon chuahuong Do, Nguyen & Le, 2016 [type locality: Ha Noi province, northern Vietnam]
Indochinamon cua (Yeo & Ng, 1998) [type locality: Vinh Phu Province, northern Vietnam]
Indochinamon dangi Naruse, Nguyen & Yeo, 2011 [type locality: Dien Bien Province, northern Vietnam]
Indochinamon daweishanense (Dai, 1995) [type locality: Daweishan, Yunnan Province, China]
Indochinamon edwardsii (Wood-Mason, 1871) [type locality: Ponsee, Kahkyen Hills, Yunnan Province, China]
Indochinamon flexum (Dai, Song, Li & Liang, 1980) [type locality: Napo, Guangxi Province, China]
Indochinamon gengmaense (Dai, 1995) [type locality: Gengma, Yunnan Province, China]
Indochinamon guttum (Yeo & Ng, 1998) [type locality: Muang Saisombun, northern Laos]
Indochinamon hirtum (Alcock, 1909) [type locality: Sheetee Hills, Kakhyen Hills, Yunnan Province, China]
Indochinamon hispidum (Wood-Mason, 1871) [type locality: Ponsee, Kakhyen Hills, Yunnan Province, China]
Indochinamon jianchuanense (Dai & Chen, 1985) [type locality: Hengduan, Yunnan Province, China]
Indochinamon jinpingense (Dai, 1995) [type locality: Yunnan Province, China]
Indochinamon khinpyae sp. n. [type locality: Kachin State, Myanmar]
Indochinamon kimboiense (Dang, 1975) [type locality: Kim Boi Province, northern Vietnam]
Indochinamon lipkei (Ng & Naiyanetr, 1993) [type locality: Chiang Rai Province, northern Thailand]
Indochinamon lui Naruse, Chia & Zhou, 2018 [type locality: Yun County, Yunnan Province, China]
Indochinamon manipurense (Alcock, 1909) [type locality: Manipur Hills, India]
Indochinamon menglaense (Dai & Cai, 1998) [type locality: Xishuangbana, Yunnan Province, China]
Indochinamon mieni (Dang, 1967) [type locality: Son La Province, northern Vietnam]
Indochinamon orleansi (Rathbun, 1904) [type locality: northern Vietnam]
Indochinamon ou (Yeo & Ng, 1998) [type locality: Phongsali Province, northern Laos]
Indochinamon parpidum Naruse, Chia & Zhou, 2018 [type locality: Shiping County, Yunnan Province, China]
Indochinamon phongnha Naruse, Nguyen & Yeo, 2011 [type locality: Quang Binh Province, central Vietnam]
Indochinamon prolatum (Brandis, 2000) [type locality: Uthai Thani Province, central Thailand]
Indochinamon tannanti (Rathbun, 1904) [type locality: Lao Koi, Yunnan Province, China]
= *Potamon hokuoense* Dai, Song, He, Cao, Xu & Zhong, 1975 [type locality: Hekou, Yunnan Province, China]
Indochinamon tritum (Alcock, 1909) [type locality: Sheetee Hills, Kakhyen Hills, Yunnan Province, China]
Indochinamon tujiense Naruse, Chia & Zhou, 2018 [type localiy: Nanhua County, Yunnan Province, China]
Indochinamon villosum (Yeo & Ng, 1998) [type locality: Luang Nam Tha Province, northern Laos]
Indochinamon xinpingense (Dai & Bo, 1994) [type locality: Yuxi, Yunnan Province, China]
= *Potamon hispidum xingpingense* Bo, He, Huang, Fan, Dai & Chen, 1997 [type locality: Yuxi, Yunnan Province, China]
Indochinamon yunlongense (Dai, 1995) [type locality: Yunlong, Yunnan Province, China]

Comparative material. *Indochinamon ahkense* Naruse, Chia & Zhou, 2018 – paratypes: 4 males (largest 38.4×29.7 mm), 2 females (larger 43.1×33.2 mm) (ZRC 2013.0551), Shaping Village, Ahke Town, Guangnan County, Yunnan Province, China, coll. Z.L. Chen, 1 February 2004. *Indochinamon andersonianum* (Wood-Mason, 1871) – syntypes: 2 males (larger 36.4×28.3 mm), 1 female (42.9×33.5 mm) (ZSI 4045/4), Momein, West Yunnan, China, coll. J. Wood-Mason, no date; 1 male (49.5×37.0 mm) (SMF 2805), Mt. Carien, Myanmar, coll. L. Fea, 1885–1889; 1 female (47.9×36.9 mm) (ZSI 6916/3), Yunnan, coll. J. Anderson, no date; 11 juveniles (ZS1 6932/3), West Yunnan and Kahkhyen Hills, coll. J. Anderson, no date; 1 juvenile male, 3 females (largest 33.8×26.8 mm) (ZSI 6906/3), Kahkhyen Hills, Ponsee, Upper Burma, coll. J. Anderson, no date. *Indochinamon asperatum* (Alcock, 1909) – syntypes: 4 juvenile males (largest 18.1×15.3 mm), 1 juvenile female (19.2×15.7 mm) (ZSI 5543/10), Ganjam, Cachar Hills, coll. W. Partridge, no date. *Indochinamon bavi* Naruse, Nguyen & Yeo, 2011 – paratypes: 2 males (46.9×35.8 mm, 47.5×36.3 mm) (ZRC 2010.0167), Ba Vi National Park, Ha Tay Province, Vietnam, coll. V.Q. Nguyen, 19 June 2001. *Indochinamon bhumibol* (Naiyanetr, 2001) – 3 males (ZRC), Ban Nam Tob, Khao Luang, Amphoe Wang Saphung, Loei Province, Thailand, coll. W. Senama, 26 October 1982; 1 male (ZRC), Huai Phai Waterfall, Phu Rua, Amphoe Phu Rua, Loei Province, coll. Wiroon, 24 July 1982; 2 males (ZRC), Ban Na Wa, Amphoe Dan Sai, Loei Province, Thailand, coll. P. Naiyanetr, 11 April 1987. *Indochinamon boshanense* (Dai & Chen, 1985) – 1 male (50.4×37.1 mm) (ZRC 1998.811), Boshan, Yunnan Province, China, coll. A. Dai, 20 October 1981. *Indochinamon chinghungense* (Dai, Song, He, Cao, Xu & Zhong, 1975) – 1 male (50.5×38.2 mm) (ZRC 1997.749), Menghai County, 100 m asl, Yunnan County, China, coll. Y. Cai, 11 May 1994. *Indochinamon cua* (Yeo & Ng, 1998) – holotype: male (46.9×36.6 mm) (ZRC 1998.267), Tam Dao, Vinh Phu Province, northern Vietnam, coll. X.Q. Nguyen, 8 June 1997; paratypes: 2 females (larger 42.6×33.0 mm), 2 juvenile males (ZRC 1998.268–271), same locality and collector as holotype, March 1997. *Indochinamon dangi* Naruse, Nguyen & Yeo, 2011 – 4 males (29.6×23.0 – 48.4×37.6 mm), 2 females (45.2×33.9, 36.7×28.1 mm) (ZRC 2010.0175), upstream and waterfall of Muong Phang stream, Muong Phang, Dien Bien Province, 21°27.000'N, 103°10.548'E, 1070 m asl, coll. D.C.J. Yeo and A.D. Tran, 28 July 2004; 4 males (26.7×20.7 – 41.8×32.2 mm), 1 female (46.7×35.5 mm) (ZRC 2010.0176), Muong Phang stream, Muong Phang, Dien Bien Province, 21°27.159'N, 103°09.921'E, 976m asl, coll. D.C.J. Yeo and A.D. Tran, 26 July 2004. *Indochinamon edwardsii* (Wood-Mason, 1871) – 1 male (40.9×30.3 mm), 1 female (37.5×27.5 mm) (MGE III 228 bis), Mt. Catcin, Birmania (= Myanmar), coll. L. Fea, June–October 1886; 1 male (38.5×28.9 mm), 2 females (larger 33.9×25.5 mm) (MBA 51a), Katein Berge, northern Burma; 1 male (about 34.4 mm carapace width) (ZRC 1984.7036), Mount Katun, Burma (= Myanmar), coll. L. Fea, 1893. *Indochinamon flexum* (Dai, Song, Li & Liang, 1980) – 1 male (47.5×35.0 mm) (ZRC 1997.0750), Guangxi Autononmous Region, China, coll. Y. Song, 16 September 1997. *Indochinamon guttum* (Yeo & Ng, 1998) – holotype: male (62.2×45.7 mm) (ZRC 1998.272), Ban Long Cheng, Muang Saisombun, Saisombun

Special Zone, northern Laos, coll. V. Kittikoon, May 1995; paratypes: 1 male (43.8×34.7 mm) (ZRC 1998.273), same data as holotype; 1 female (33.1×25.3 mm) (ZRC 1998.0274), side of dam, Muang Saisombun, Saisombun Special Zone, northern Laos, coll. V. Kittikoon, May 1995; 8 specimens (largest male 51.3×38.8 mm) (MNHN-B 5316) "Haut Laos, Ban Nong", coll. Mission Permanente, 10 January 1906. *Indochinamon hirtum* (Alcock, 1909) – holotype: female (32.9×24.9 mm) (ZSI 6961/3), Sheetee Hill (= Shitee Doung), Kakhyen Hills, Yunnan, China, coll. J. Anderson, no date; 5 males (largest 37.8×28.0 mm), 2 females (ZSI 6961/3), same data as holotype. *Indochinamon hispidum* (Wood-Mason, 1871) – 1 juvenile female (ZSI 4007/4), Kakhyen Hills, Ponsee, Upper Burma, coll. J. Anderson, no date; 1 female (34.6×26.9 mm), 1 juvenile male (ZSI 7089-90/9), Moung Sal, Mehkok River, coll. Dr. Grey, no date. *Indochinamon jinpingense* (Dai, 1995) – 2 males (larger 64.0×47.0 mm) (ZRC 1998.266), Sin Ho District, Lai Chau Province, northern Vietnam, coll. V.D. Nguyen, November 1997. *Indochinamon kimboiense* (Dang, 1975) – 2 males (71.8×56.6 mm, 71.5×56.8 mm), 2 females (63.0×49.5 mm, 52.8×41.1 mm) (ZRC 2010.0165), Kim Boi area, Hoa Binh Province, Vietnam, purchased from villagers, 14 and 15 April 2007; 1 male (58.8×45.3 mm), 2 females (69.4×53.6 mm, 49.9×37.4 mm) (ZRC 2010.0166), stream in Cuc Phuong National Park, about 6 km from main gate, Ninh Binh Province, northern Vietnam, 20°18'N, 105°38'E, coll. D.C.J. Yeo, H.H. Ng and X.Q. Nguyen, 16 September 1997. *Indochinamon lipkei* (Ng & Naiyanetr, 1993) – holotype: male (56.8×42.8 mm) (RMNH D 42353), Chiang Khong District, Chiang Rai Province, northwestern Thailand, coll. P. Naiyanetr, June 1987. *Indochinamon manipurense* (Alcock, 1909) – syntypes: 1 male (39.9×31.5 mm), 1 female (40.1×30.4 mm) (ZSI 6923/3), Manipur Hills, India, coll H. H. Godwin-Austen, no date. *Indochinamon menglaense* (Dai & Cai, 1998) – 1 male (42.9×31.9 mm), 1 female (ZRC), Shangyong, Xishuangbana, Yunnan, China, coll. Y. Cai, 23 April 1994. *Indochinamon mieni* (Dang, 1967) – neotype: male (57.1×43.5 mm) (ZRC 1998.265), Thuan Chau District, Son La Province, northern Vietnam, coll. V.D. Nguyen, 1997; 1 juvenile female (ZRC), same data as neotype. *Indochinamon orleansi* (Rathbun, 1904) – holotype: male (42.4×32.3 mm) (MNHN-B 5262), "Tonkin, rivière Noire" (river Song Da), coll. Prince Henri d'Orleans, no date. *Indochinamon ou* (Yeo & Ng, 1998) – holotype: male (35.6×27.1 mm) (ZRC 1998.275), Nam Ou at confluence with Huay Nam, 21°4'10"N, 102°31'44"E, 3 km ESE of Muang Khoa, Phongsali Province, northern Laos, coll. M. Kottelat, 17 May 1997; 1 male (47.6×36.8 mm) (ZRC), dry evergreen forest mixed with bamboo, Nam Sa River, tributary of Nam Ou, 600 m asl, 22°5'31"N, 102°6'19"E, Phou Dendin, Phonsgali, northern Laos, coll. and date not known. *Indochinamon parpidum* Naruse, Chia & Zhou, 2018 – paratypes: 2 males (larger 43.4×32.3 mm), 2 females (larger 35.0×26.2 mm) (ZRC 2013.0558), Niujie Town, Shiping County, Yunnan Province, China, coll. H.C. Li, 23 February 2004. *Indochinamon phongnha* Naruse, Nguyen & Yeo, 2011 – paratypes: 5 males (25.4×20.2 – 44.2×33.2 mm), 6 females (17.9×14.1 – 43.0×32.6 mm), 1 juvenile (15.4×12.5 mm) (ZRC 2010.0168), Khe Con Khai stream, Cha Noi, Phong Nha, Quang Binh Province, Vietnam,17°38.196'N, 106°05.928'E, 263 m asl, coll. D.C.J. Yeo and A.D.

Tran, 13 July 2004; 2 males (34.3×26.6 mm, 31.9×24.9 mm), 3 females (38.3×29.9 – 54.8×41.4 mm), 1 juvenile (17.0×13.1 mm) (ZRC 2010.0169), Cha Noi, Phong Nha, Quang Binh Province, Vietnam, Stream under bridge, 17°38.397'N, 106°06.975'E, 261 m asl, coll. D.C.J. Yeo and A.D. Tran, 13 July 2004; 11 males (16.4×13.3 – 64.2×48.0 mm), 3 females (32.6×25.9 – 38.9×30.1 mm) (ZRC 2010.0170), Vuc Tro stream, Phong Nha, Quang Binh Province, 17°38.188'N, 106°12.810'E, coll. D.C.J. Yeo and A.D. Tran, 14 July 2004; 3 females (36.1×28.1 – 42.8×33.0 mm), 2 juveniles (19.6×15.3 mm, 17.3×13.6 mm) (ZRC 2010.0171), stream near Forest Ranger station 37, Phong Nha, Quang Binh Province Vietnam, 17°31.395'N, 106°17.716'E, 86 m asl, coll. D. C. J. Yeo and A. D. Tran, 15 July 2004; 3 males (49.8×37.8 – 53.0×41.5 mm) (ZRC 2010.0172), Chay stream, Quang Binh Province, Vietnam, 17°33.146'N, 106°14.425'E, 94 m asl, coll. D.C.J. Yeo and A.D. Tran, 17 July 2004; 1 male (61.9×47.3 mm) (ZRC 2010.0173), Km 23 + 800 HCM Way, near Hang So Dua, Pong Nha National Park, Quang Binh Province, Vietnam, coll. A.D. Tran, 11 August 2001; 1 male (56.9×44.0 mm), 1 female (54.2×40.8 mm) (ZRC 2010.0174), Thac Xoi waterfall, Phong Nha National Park, Quang Binh Province, Vietnam, coll. Q.K. Hoang and V.K. Dinl, 10 August 2002. *Indochinamon tannanti* (Rathbun, 1904) – holotype: female (35.5×27.7 mm) (MNHN-B 5313), "Tonkin, montagnes du Yunnan (via Lao Koi)", coll. Tannant, no date; 1 male (56.1×42.6 mm) (ZRC 1998.264), Hekou, Yunnan Province, southern China, coll. A.-Y. Dai, 29 November 1995. *Indochinamon tritum* (Alcock, 1909) – holotype: female (35.8×27.4 mm) (ZSI 4075/4), Sheetee Hill (= Shitee Doung), Kakhyen Hills, Yunnan, China, coll. J. Anderson, no date. *Indochinamon tujiense* Naruse, Chia & Zhou, 2018 – paratypes: 2 males (larger 33.1×25.0 mm), 1 female (31.4×23.6 mm) (ZRC 2013.0555), Mang Huai Town, Yun County, Yunnan Province, China, coll. Y.F. Lu, 24 February 2004; 2 males (larger 37.5×28.8 mm), 2 females (larger 38.6×28.6 mm) (ZRC 2013.0557), Mongku Town, Shuangjiang County, Yunnan Province, China, coll. O.C. Li, 26 February 2004. *Indochinamon villosum* (Yeo & Ng, 1998) – holotype: male (44.8×34.3 mm) (ZRC 1998.276), tributary of Nam Tha River about 800 m asl, Luang Nam Tha Province, northern Laos, coll. H. Morioka, 13 November 1997; paratypes: 7 males (largest 55.9×41.4 mm), 4 females, 1 juvenile (ZRC 1998.277–285, 807–809), same data as holotype; 2 females (larger 32.9×24.5 mm) (ZRC 1998.286–287), Nam Luang about 1 km upstream of Ban Nam Luang, Nam Tha watershed, Mekong basin, Luang Nam Tha Province, northern Laos, 21°9'5"N, 101°20'34"E, coll. M. Kottelat, 22 May 1997; 1 female (39.9×30.8 mm) (ZRC 1998.288), tributary of Nam Talan about 3 km S of Ban Nateuy, Nam Tha watershed, Mekong basin, Luang Nam Tha Province, northern Laos, coll. M. Kottelat, 20 May 1997.

Diagnosis. Carapace with dorsal surface prominently rugose in large specimens (ca. 45 mm carapace width), frontal and orbital regions prominently rugose, lateral parts of anterolateral and branchial regions with strong oblique striae; mesogastric, urogastric, cardiac and intestinal regions with distinct rugosities and distinct granules (Fig. 2A, D, F); postorbital cristae distinct, margin uneven, outer edge relatively low,

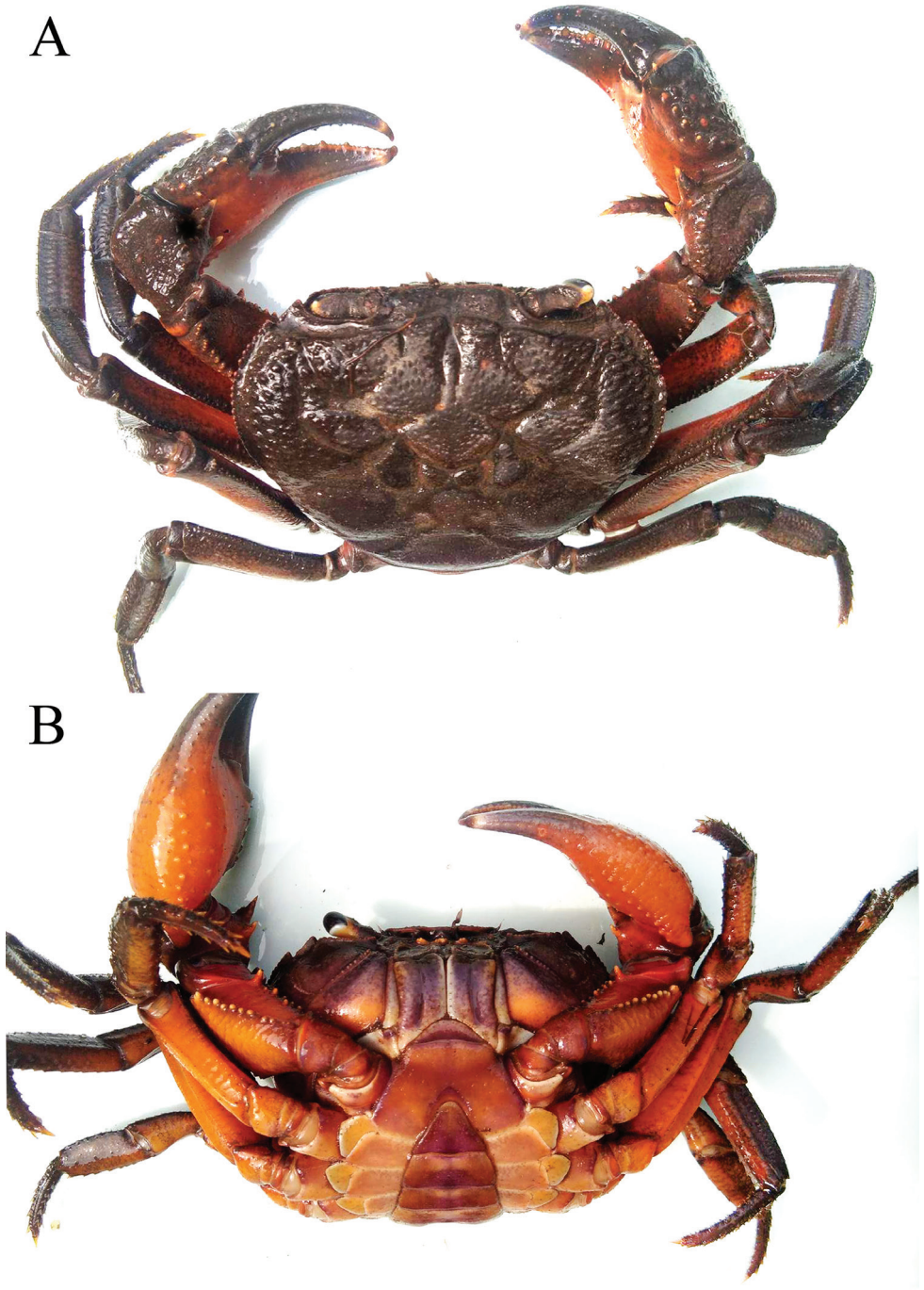

Figure 1. *Indochinamon khinpyae* sp. n., colour in life, holotype male (57.1×43.2 mm) (ZRC 2018.0713). **A** dorsal view **B** ventral view of cephalothorax.

not well marked (Fig. 2A, D, F); external orbital tooth distinct, separated from anterolateral margin by deep V-shaped cleft; epibranchial tooth prominent (Fig. 2A, F); anterolateral margin lined with sharp granules, appears serrated (Fig. 2A, F); posterior margin of epistome with distinct median triangle (Fig. 2D); outer surface of chela strongly rugose, upper part rugose with granules (Fig. 3H, I); male thoracic sternum, notably sternites 3 and 4, relatively broad, surface with pits and scattered short, stiff setae (Fig. 3A); male pleon triangular; telson triangular, lateral margins gently sinuous; somite 6 transversely rectangular, much wider than long, lateral margin gently convex (Fig. 3A, B); G1 relatively stout; outer margin of subterminal segment with distinct broad cleft on distal part, terminal segment subcylindrical, gently curving outwards, no visible dorsal flap, distal part tapering to rounded tip (Fig. 4A–D).

Description of male holotype. Carapace transversely ovate, distinctly wider than long (width to length ratio 1.32); dorsal surface gently convex from frontal view, regions not prominently inflated; with scattered very short setae, appears glabrous (Fig. 2A, D, F). Frontal and orbital regions prominently rugose; lateral parts of anterolateral and branchial regions covered with strong oblique striae; mesogastric, urogastric, cardiac and intestinal regions covered with rugosities and distinct granules; suborbital region with small granules on lateral parts; pterygostomial, subhepatic and sub-branchial regions rugose to granulose (Fig. 2A, D, F). Epigastric cristae distinct, rugose, not cristate, separated by broad, median Y-shaped furrow; epigastric cristae just anterior of postorbital cristae, separated by short furrow; postorbital cristae distinct, margin uneven, prominently raised, subparallel to frontal margin, outer edge relatively low, not prominent (Fig. 2A, D, F). Cervical grooves deep, not reaching lateral margins, connected to deep H-shaped median gastric groove (Fig. 2A, F). Frontal margin almost straight, appears entire in dorsal view, gently sinuous in frontal view (Fig. 2A, D, F). External orbital tooth distinct, triangular, outer margin more than twice length of inner margin, demarcated from rest of anterolateral margin by deep V-shaped cleft; epibranchial tooth prominent, sharp (Fig. 2A, F). Anterolateral margins convex, cristate, lined with sharp granules, appears serrated (Fig. 2A, F). Posterolateral margin gently sinuous, converging towards convex posterior carapace margin (Fig. 2A, F). Orbits subovate; eye filling orbital space; eye peduncle relatively short, stout; cornea large, round, pigmented (Fig. 2D). Supraorbital margin almost straight (Fig. 2F). Suborbital margin concave, complete, lined with low granules (Fig. 2D). Antennae short, stretching across base of eyes; antennules short, folding transversely in rectangular fossa (Fig. 2D). Posterior margin of epistome with distinct median triangle, lateral margin sinuous (Fig. 2D).

Third maxillipeds covering most of buccal cavity when closed; ischium subrectangular, with distinct median groove, surface with scattered pits and short setae; merus subquadrate, slightly wider than long, surface rugose, margins cristate, anteroexternal angle angular but not produced; exopod slender, reaching to about one-third length of merus, with elongate flagellum that reaches across width of merus (Fig. 3F).

Chelipeds asymmetrical, right larger (Fig. 2A). Anterior margin of basis-ischium lined with small sharp granules; margins of merus lined with low sharp granules, appears weakly serrated. Outer surface of carpus rugose, inner distal angle with large sharp

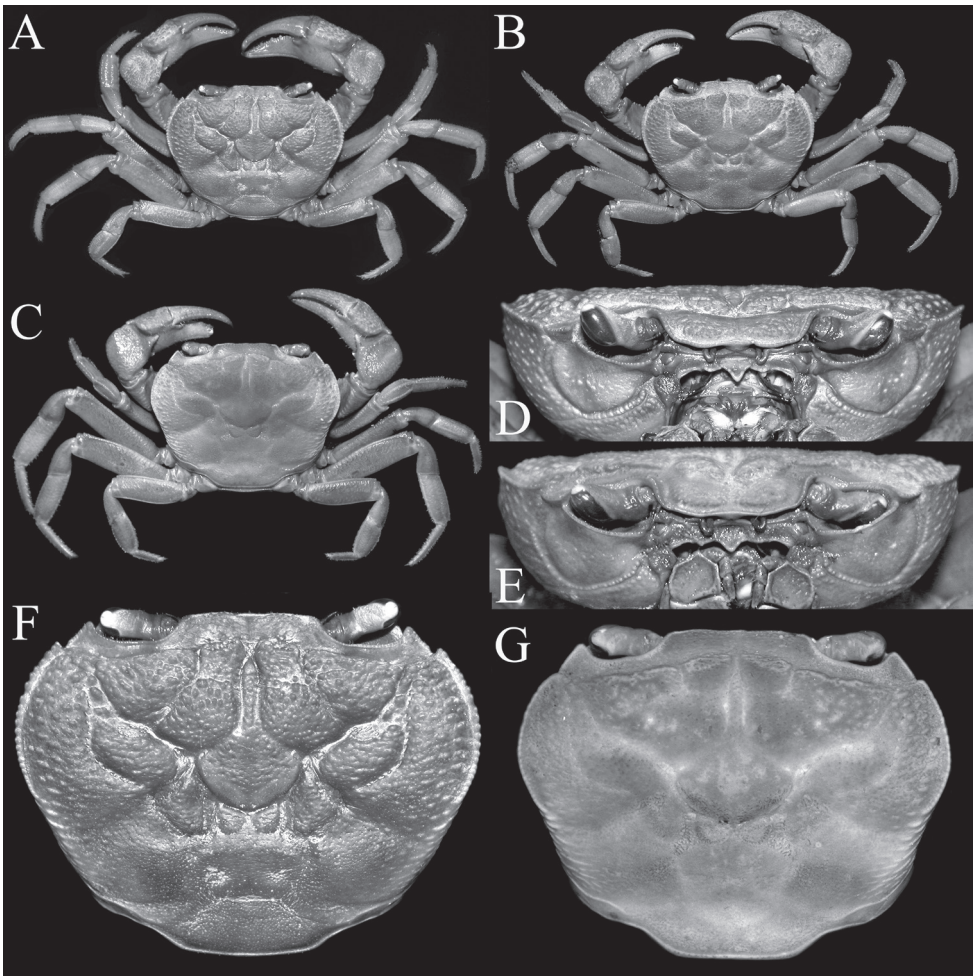

Figure 2. *Indochinamon khinpyae* sp. n. **A, D, F** holotype male (57.1×43.2 mm) (ZRC 2018.0713) **B, E** paratype male (47.2×36.4 mm) (ZRC 2018.0714) **C, G** paratype male (34.3×26.6 mm) (ZRC 2018.0714). **A–C** overall habitus **D, E** frontal view of cephalothorax **F, G** dorsal view of carapace.

tooth and basal tooth (Fig. 2A). Outer surfaces of chelae strongly rugose, upper part rugose with granules; major chela stouter, shorter than minor chela (Fig. 3H, I). Fingers of major chela short, stout, gently curved, subequal to palm, outer surface lined with 3 rows of pits; cutting edges of both fingers with variously sized sharp teeth and denticles; dorsal margin of dactylus with low tubercles and granules (Figs 2A, 3H). Fingers of minor chela similar to major chela in form but relatively more slender (Figs 2A, 3I).

Ambulatory legs short, segments relatively stout; second pair longest, last pair shortest (Fig. 2A). Merus short, stout, outer surface rugose, dorsal margin uneven, subcristate, without subdistal spine or tooth; carpus rugose, dorsal margin with crista, outer surface with low submedian crista on first to third legs, that on fourth leg

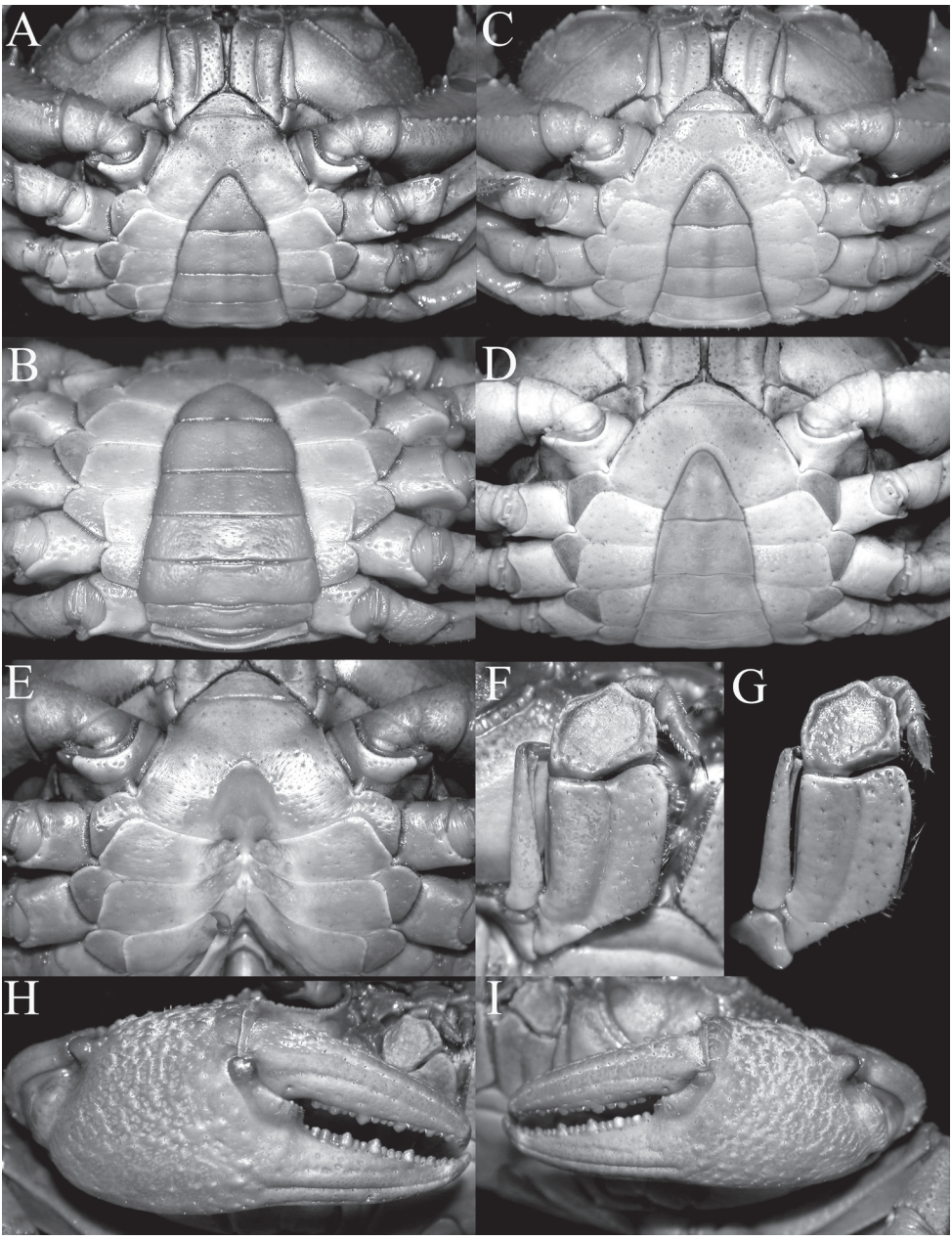

Figure 3. *Indochinamon khinpyae* sp. n. **A, B, E, F, H, I** holotype male (57.1×43.2 mm) (ZRC 2018.0713) **C, G** paratype male (47.2×36.4 mm) (ZRC 2018.0714) **D** paratype male (34.3×26.6 mm) (ZRC 2018.0714). **A, C, D** anterior thoracic sternum and pleon **B** posterior thoracic sternum and pleon **E** sternopleonal cavity **F, G** right third maxilliped **H** outer view of right chela **I** outer view of left chela.

smooth; dorsal margin of propodus with crista, outer surface with low, submedian crista; dactylus relatively short, gently curved, quadrate in cross section, margins with short, sharp pectinate spines (Fig. 2A).

Thoracic sternum, notably sternites 3 and 4, relatively broad, surface with pits and scattered short, stiff setae (Fig. 3A). Sternites 1, 2 completely fused to form broadly triangular plate; separated from sternite 3 by distinct, gently concave suture (towards buccal cavity); sternites 3, 4 completely fused, with shallow incomplete groove demarcating suture (Fig. 3A, B, E). Penis coxal, on condyle of coxa of fourth ambulatory leg. Sternopleonal cavity deep, reaching imaginary line connecting posterior edges of cheliped coxae (Fig. 3A, E). Male pleonal locking tubercle low, round, on posterior third of sternite 5 (Fig. 3E).

Pleon triangular, all somites and telson free; telson triangular, lateral margins gently sinuous; somite 6 transversely rectangular, much wider than long, lateral margin gently convex; somites 3–5 trapezoidal, gradually decreasing in width, increasing in length; somites 1 and 2 subrectangular, very wide, reaching to bases of coxae of fourth ambulatory legs, thoracic sternite 8 not visible when pleon closed (Fig. 3A, B).

G1 relatively stout; subterminal segment gently sinuous, proximal part broad, gradually tapering to median part, outer margin with distinct broad cleft on distal part; clearly separated from terminal segment by prominent dilation; terminal segment subcylindrical, no dorsal flap visible, gently curving outwards, distal part tapering to rounded tip (Fig. 4A–D). G2 elongate, much longer than G1; basal segment longer than distal segment (Fig. 4E).

Variation. The carapace tends to get less broad in smaller specimens and females (width to length ratio 1.26–1.30). The regions in smaller specimens is less sculptured (Fig. 2B, E) with the rugosities restricted mostly to lateral margins (Fig. 2C, G). The third maxilliped ischium is slightly longer in smaller individuals (Fig. 3G). The male pleon is proportionately less broad in smaller individuals with somite 6 more quadrate as they are smaller (Fig. 3C, D). In adult males, the G1 does not vary substantially although the cleft on the outer part of the distal section of the G1 subterminal segment is relatively less distinct (Fig. 4F). Smaller males (ca. 30 mm carapace width), however, not only have the G1 terminal segment relatively shorter and less curved, the cleft on the subterminal segment is also not discernible (Fig. 4H). The adult female has the pleon completely covering the thoracic sternum (Fig. 5A), the vulva is large, raised, ovate and positioned on the anterior half of sternite 6, pushing into the margin with sternite 5 (Fig. 5B).

Etymology. The species is named after Ms Khin Pyae Pyae Thaw Thar who collected the specimens used for this study. Her name is used here as a noun in apposition.

Colour. In life, the dorsal surfaces of the carapace and outer surfaces of the chelipeds are dark brown; with the ventral surfaces orangish-red; and the ambulatory legs are dark brown to orangish red (Fig. 1).

Habitat. The type locality, Malikha, is a fast-flowing river, the substrate consisting of rocks of various sizes, with the bank sandy. The banks are densely lined with tall trees. This river is a branch of the Ayeyarwady River (= Ayrwarwady River or Myitsone) and is about 43 km north of Myitkyina, the capital city of Kachin State.

Remarks. Five species of *Indochinamon* have been reported from and near Myanmar: *I. andersonianum*, *I. edwardsii*, *I. hirtum*, *I. hispidum* and *I. tritum* (cf. Alcock 1909, 1910; Bott 1970; Yeo and Ng 2007). All these species were collected by John Anderson from the area east of Bhamo, mostly in the Kakhyen Hills (= Kachin Moun-

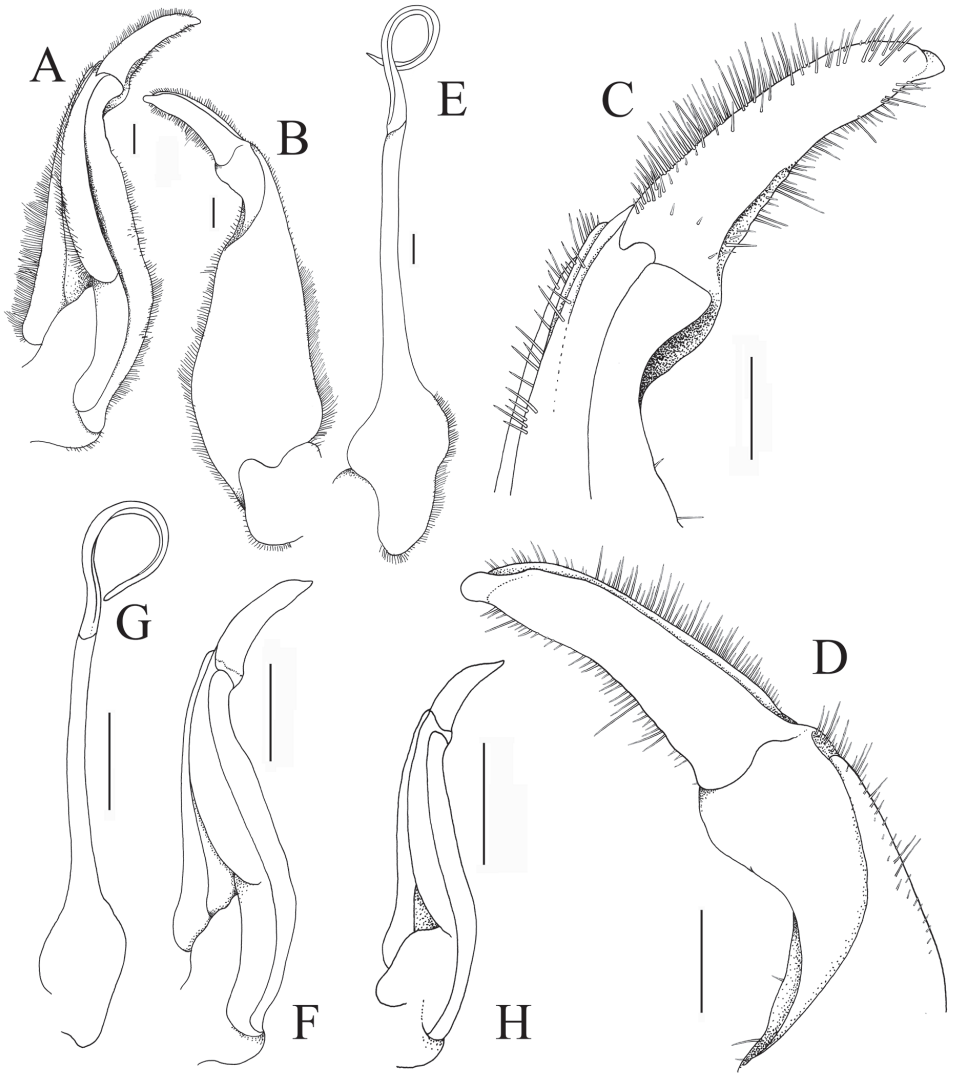

Figure 4. *Indochinamon khinpyae* sp. n. **A–E** holotype male (57.1×43.2 mm) (ZRC 2018.0713); **F, G** paratype male (47.2×36.4 mm) (ZRC 2018.0714) **H** paratype male (34.3×26.6 mm) (ZRC 2018.0714). **A** left G1 (ventral view) **B** left G1 (dorsal view) **C** terminal segment of left G1 (ventral view) **D** terminal segment of left G1 (dorsal view) **E** left G2 **F, H** left G1 (ventral view, setae not drawn) **G** left G2 (setae not drawn). Scale bar: 1.0 mm.

tains), in what is today Myanmar and Yunnan (China). One site, Ponsee, which is the type locality of *I. edwardsii* and *I. hispidum* (and where *I. andersonianum* has also been found), does not appear in most modern maps but this village is in the Dehong, Longchuan area in Yunnan, China (ca. 24°25'34.5"N, 97°53'57.3"E) (cf. Anderson 1876). Until the present record of *I. khinpyae*, no species had been reported from the mountains north of Bhamo and Myitkyina in Myanmar.

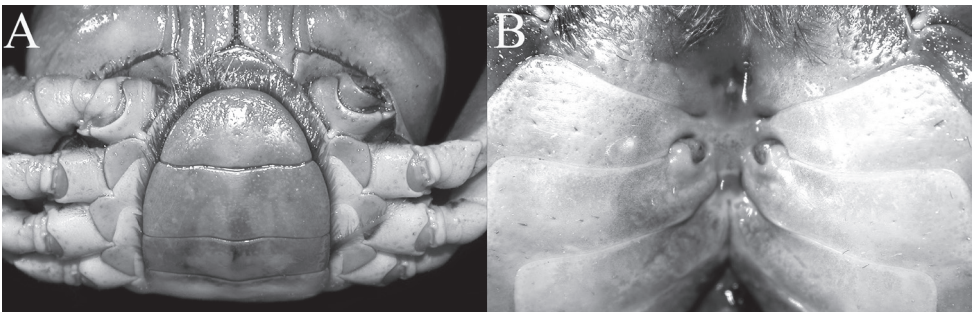

Figure 5. *Indochinamon khinpyae* sp. n., paratype female (39.3×31.1 mm) (ZRC 2018.0714). **A** anterior thoracic sternum and pleon **B** sternopleonal cavity and vulvae.

Adult male specimens of *I. khinpyae* have a strongly sculptured and very rough carapace (Fig. 2F), the G1 terminal segment is relatively long, gently curved, distally bent and the dorsal margin has no trace of a flap (Fig. 4A–D, F, H). In *I. andersonianum*, even large males (50 mm carapace width) have the gastric regions relatively smooth with the rest of the surfaces also less rugose and granulose, and the male pleon is proportionately more narrow (Wood-Mason 1871: pl. 27 figs 16, 17, 20; Bott 1970: pl. 44 fig. 14; unpublished data). The G1 of *I. andersonianum* is also quite different with the terminal segment straight, slender and tapering towards the tip (Bott 1970: pl. 37 fig. 16). The taxonomy of *I. andersonianum* has been confused and many species previously referred to it have turned out to be other taxa (see Ng and Naiyanetr 1993). The figure of *I. andersonianum* by Alcock (1910: pl. 10 fig. 40) is actually a separate species, *Potamiscus rangoonensis* (Rathbun, 1904) (unpublished data). The G1 of the smaller paratype male of *I. khinpyae* (34.3×26.6 mm, ZRC 2018.0714) superficially resembles that of *I. edwardsii* (the type of which is about the same size) but in *I. edwardsii*, the anterolateral margins are prominently serrated even in smaller specimens (Wood-Mason 1871: pl. 27 figs 11, 12; Alcock 1910: pl. 14 fig. 43; unpublished data) (versus anterolateral margins finely granulated or weakly serrated in *I. khinpyae*; Fig. 2F, G); the upper part of the palm of the chela has many large tubercles (Wood-Mason 1871: pl. 27 figs 11, 14; Alcock 1910: pl. 14 fig. 43; unpublished data) (versus with no large tubercles present in *I. khinpyae*; Figs 2A–C, 3H–I); and the lateral margins of the male telson are concave (Wood-Mason 1871: pl. 27 fig. 14; unpublished data) (versus lateral margins gently sinuous to almost straight in *I. khinpyae*; Fig. 3A, C, D). These differences also apply for *I. hirtum* (cf. Alcock 1919: pl. 10 fig. 42; unpublished data). Compared to *I. tritum*, known only from a 35.8×27.4 mm female from the Shitee Hills in the Kakhyen Hills in Yunnan (just north of Ponsee, cf. Anderson 1876: 420), the lateral margin of the postorbital crista of *I. khinpyae* is less clearly marked (Fig. 2F, G) (versus distinctly formed and clearly demarcated from the lateral branchial region in *I. tritum*; cf. Alcock 1910: pl. 14 fig. 69); and the propodus of the last ambulatory leg is proportionately longer (Fig. 2A–C) (versus much shorter in *I. tritum*; cf. Alcock 1910: pl. 14 fig. 69). Compared to *I. hispidum*, described from a male 43.0×31.0 mm from Ponsee, *I. khinpyae* can easily be distinguished by its more rugose dorsal carapace surface (Fig. 2A, B,

F) (versus smooth dorsal carapace surface in *I. hispidum*; cf. Wood-Mason 1871: pl. 27 figs 1, 2); rugose outer surface of the chela (Fig. 3H, I) (versus smooth in *I. hispidum*; cf. Wood-Mason 1871: pl. 27 fig. 4); and the male pleon is proportionately broader with the telson more broadly triangular (Fig. 3A, C, D) (versus male pleon more narrow with the telson acutely triangular in *I. hispidum*; cf. Wood-Mason 1871: pl. 27 fig. 5).

With regards to the other species of *Indochinamon*, they can be separated into several groups on the basis of their G1s. The type species, *I. villosum*, has a relatively short and stout G1 terminal segment which is gently bent and is conical to subconical in shape without an obvious dorsal flap, a character shared with *I. ahkense*, *I. bavi*, *I. bhumibol*, *I. boshanense*, *I. changpoense*, *I. chinghungense*, *I. dangi*, *I. daweishanense*, *I. flexum*, *I. guttum*, *I. jianchuan*, *I. jinpingense*, *I. kimboiense*, *I. menglaense*, *I. mieni*, *I. orleansi*, *I. ou*, *I. parpidum*, *I. phongnha*, *I. tannanti*, *I. xinpingense*, and *I. yunlongense* (including *I. edwardsii* and *I. hispidum*) (cf. Bott 1970; Yeo and Ng 1998; Dai 1999; Naruse et al. 2011, 2018; unpublished data). The other species have G1 terminal segments which are slender, elongate, and straight or curved; or relatively short and strongly bent (cf. Ng and Naiyanetr 1993; Dai 1999; Do et al. 2016; Naruse et al. 2018; unpublished data). The G1 of *I. khinpyae* closely resembles that of *I. changpoense* and *I. daweishanense* (both from Yunnan) but these two species have only a shallow cleft on the outer margin of the subdistal part of the subterminal segment, and the terminal segment is proportionately shorter and straighter (Dai 1999: figs 85–4, 5; 87–4, 5), even though the types are comparable in size to the holotype of *I. khinpyae*. Similarly, *I. yunlongense* (described from a small male 19.0×16.1 mm from Yunnan) has a superficially similar G1 structure to *I. khinpyae*, except that the terminal segment is much straighter (Dai 1999: fig. 84–4, 5). The strongly sculptured and rugose carapace of large *I. khinpyae* allies it with large species like *I. kimboense* and *I. bavi* (both from Vietnam) but in these species, the cleft on the outer margin with of the G1 subterminal segment is shallow and not distinct (cf. Naruse et al. 2011: fig. 3a, b, d, e), even for specimens larger than the holotype of *I. khinpyae*, which has a prominent broad cleft (Fig. 4A–D). The G1 terminal segment of *I. kimboense* and *I. bavi* (as well as *I. cua*, *I. orleansi*, *I. ou* and *I. tannanti*) are also distinctly tapering towards the tip (Naruse et al. 2011: fig. 3a, b, d, e), unlike the subtruncate condition in *I. khinpyae* (Fig. 4A–D). Compared to *I. phongnha* (from Vietnam), which also has the carapace regions distinct, the surfaces are smoother, notably the median and posterior parts which are smooth, even in large specimens (Naruse et al. 2011: fig. 7) (strongly rugose in large *I. khinpyae*; Figs 1A, 2A, F); and the G1, while it has a strong cleft on the outer margin of the subterminal segment, the terminal segment is sharply tapering (Naruse et al. 2011: fig. 9a, b) (terminal segment subcylindrical in large *I. khinpyae*; Fig. 4A–D). The strong cleft on the outer margin of the G1 subterminal segment of *I. khinpyae* is character also shared with *I. cua* from Thailand, but in this species, the cleft is relatively broader and the terminal segment is tapering distally (Yeo and Ng 1998: fig. 4B, C, E, G); and the carapace regions are proportionately much smoother (Yeo and Ng 1998: fig. 7A). In *I. lipkei* from Thailand, the dorsal carapace surface, even in large specimens, is less well marked with the median parts much less rugose (Ng and Naiyanetr 1993: fig. 12A);

pleonal somite 6 is distinctly trapezoidal in shape (Ng and Naiyanetr 1993: fig. 12C); and the G1 terminal segment is strongly bent at about 60° along the longitudinal axis (Ng and Naiyanetr 1993: fig. 47B–E) (versus the dorsal carapace regions are more rugose, pleonal somite 6 is weakly trapezoidal, and the G1 terminal segment is bent at about 45° in *I. khinpyae*; Figs 2F, 3A, C, D, 4A–D).

Indochinamon khinpyae is not known to be threatened by any developments, and the forests and streams where it has been found are isolated and not easily assessible by man. As such, the species is classified under taxa of Least Concern for the moment (cf. Cumberlidge et al. 2009, 2012).

A note on *I. manipurense* (Alcock, 1909) is necessary. Takeda et al. (2012: 207) noted that specimens they had of this species did not possess a flagellum on the exopod of the third maxilliped, and as such, the species should be transferred to *Potamiscus* Alcock, 1909. However, the types of this species do have a flagellum (Yeo and Ng 2007; unpublished data), so Takeda et al.'s (2012) specimens will need to be checked to ascertain their identity. As such, for the moment, we retain the species in the genus *Indochinamon*.

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New species of *Idris* Förster (Hymenoptera, Platygastroidea) from southeast Asia, parasitoids of the eggs of pholcid spiders (Araneae, Pholcidae)

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Abstract

Four new species of the genus *Idris* Förster (Hymenoptera: Platygastroidea), reared from the eggs of pholcid spiders (Araneae: Pholcidae) in southeast Asia are described on the basis of external morphology and the barcode region of the mitochondrial COI gene. The new species and their hosts are: *I. badius* Johnson & Chen, **sp. n.** (ex *Nipisa phyllicola* (Deeleman-Reinhold), *Panjange hamiguitan* Huber), *I. balteus* Johnson & Chen, **sp. n.** (ex *Panjange camiguin* Huber), *I. curtus* Johnson & Chen, **sp. n.** (ex *Calapnita nunezae* Huber, *Panjange camiguin* Huber, *Tissahamia bukittimah* (Huber), *Uthina luzonica* Simon), and *I. fusciceps* (ex *Belisana khaosok* Huber).

Keywords

Araneomorphae, Baeini, Scelioninae, taxonomy, wasps

Introduction

Egg parasitoid wasps of the tribe Baeini (Hymenoptera: Platygastridae) are one of the major biotic sources of mortality among their spider hosts (Austin 1985), and these wasps are notable both for their abundance and diversity of species. The concept of this tribe has been revised as a consequence of phylogenetic analyses (Carey et al. 2006).

There are four core genera that make up the vast majority of species: *Ceratobaeus* Ashmead with 165 described, valid species worldwide; *Idris* Förster with 160 species; *Odontacolus* Kieffer with 55 species; and *Baeus* Haliday with 53 species (Johnson 1992, HOL 2018). While *Odontacolus* appears to be restricted to tropical and subtropical regions, the other genera are widespread throughout the world. Huggert (1979) revised the species of *Idris* and *Ceratobaeus* in the West Palearctic region. This area has a very modest diversity of baeines, only 20 species in total. In contrast, Iqbal and Austin (1997) estimated that in Australia alone the Baeini may total 440 species. Following a focused study of the Australian fauna (Iqbal and Austin 2000) they suggested later that there may be as many as 400 Australian species of *Ceratobaeus* alone. If the genera in tropical Asia, Africa and America are comparably rich, then even a conservative estimate would place the global total in hundreds, if not thousands of species.

The use of the eggs of spiders as hosts among platygastroids is characteristic of baeines, but not limited to them. The genera *Echthrodesis* Masner, *Mirobaeoides* Dodd, and *Neobaeus* Austin also attack these hosts and form a small, separate clade together with *Emibodobia* Ashmead in the analysis of van Noort et al. (2014). *Embidobia* and its close relatives are parasitoids of the eggs of Embiidina (webspinners). Additionally, *Aradophagus* Ashmead has been reported as a spider egg parasitoid (Vetter et al. 2012). According to records summarized in Austin (1985) and Iqbal and Austin (2000) together with those gleaned from specimens in collections, baeines have been reared from 20 families of araneomorph spiders. To date, no baeine has been reared from a host other than a spider. There are no data available to indicate the degree of host specificity within individual wasp species.

The spider hosts in the present paper are all members of Pholcidae, but this is primarily a result of collection trips focused on pholcid spiders and does not imply host specificity of the wasps. Pholcid spider females carry their egg-sacs with their mouthparts until the spiderlings hatch. It is possibly for this direct protection by the female that in most species the eggs are not densely covered by a protective layer of silk but held together by a few turns of silk. This is in contrast to most other spider families where dense and often complex layers of silk are thought to have coevolved with specialized parasitoids and predators (Austin 1985, Hieber 1992). In Pholcidae it seems that few egg parasites have managed to take advantage of the lack of a silk barrier and circumvent the direct protection by the female spider. Only one case has previously been published in Pholcidae (Huber and Wunderlich 2006).

Approximately sixty species of the genera *Idris* and *Ceratobaeus* have been described from tropical Asia, almost entirely from either India or Vietnam (Johnson 1992). Only two species of *Baeus* are known, one from India and the other from Vietnam. There is no comprehensive treatment or identification key for any of the genera, and therefore confident recognition of these species is often next to impossible. The photographic catalogs of primary types of Talamas et al. (2017) and Talamas and Pham (2017) are of limited use in recognition of some of the described species from India and Vietnam respectively. These images are all available at specimage.osu.edu. In most cases, though, the specimens are in such poor condition that positive identification is very difficult.

As a result, it is with some trepidation that we offer the description of new species of *Idris* from southeast Asia.

The problem is that we are dealing with (1) a richly speciose genus, (2) a group without any solid, comprehensive treatment for the region, and (3) a group containing numerous described species many of which are more or less unidentifiable. Would the addition of more isolated species descriptions be a contribution toward progress, or would it simply make the problem larger and more intractable?

If the ultimate goal is a complete documentation of the diversity in such a group, then one can imagine various strategies to achieve that aim. The ideal might be a comprehensive monographic treatment based on the totality of specimens existing in collections, the addition of targeted, newly collected material, a review of all existing primary types, and data sets that incorporate as many independent character sources as possible. For many reasons, this standard may be difficult or impossible to achieve, especially when dealing with a genus comprised of hundreds of species. An alternative could be to work gradually toward that same goal by incrementally planting signposts in the terrain, signposts that are well-defined points of reference to guide for future work. This is our goal here: each species description has host records and COI barcode data to supplement the morphological characters.

Materials and methods

Pholcid spiders were collected manually and egg sacs were checked with a hand-held lens in search of parasitized eggs. Females with parasitized eggs were kept alive in small plastic containers until the wasps emerged. Adult specimens emerged from eight samples. Specimens from these samples were used in both the morphological and molecular analyses:

1. Mal228: SINGAPORE: Dairy Farm Nature Park (1°21.6'N, 103°46.7'E), 50 m a.s.l., 15.ii.2015 (B.A. Huber, J. Koh). Spider: *Uthina luzonica* Simon. 2 specimens sequenced.
2. Mal256: SINGAPORE: Dairy Farm Nature Park (1°21.6'N, 103°46.7'E), 50 m a.s.l., 15.ii.2015 (B.A. Huber, J. Koh). Spider: *Tissahamia bukittimah* (Huber). 2 specimens sequenced.
3. Mal276: MALAYSIA: Perak, Gunung Liang (3°47.7'N, 101°32.0'E), 250 m a.s.l., forest along river, 22.ii.2015 (B.A. Huber, A.R.M. Ghazali, K.A. Braima). Spider: *Nipisa phyllicola* (Deeleman-Reinhold). 1 specimen sequenced.
4. Mal305: MALAYSIA: Perak: Gunung Liang (3°47.7'N, 101°32.0'E), 250 m a.s.l., forest along river, 22.ii.2015 (B.A. Huber, A.R.M. Ghazali, K.A. Braima). Spider: *Tissahamia gombak* (Huber). 2 specimens sequenced.
5. Mal331: THAILAND: Krabi, ~9 km N Krabi town, degraded forest between plantation and rocks (8°09.9'N, 98°51.7'E), 75 m a.s.l., 7.iii.2015 (B.A. Huber, B. Petcharad). Spider: *Belisana khaosok* Huber. 1 specimen sequenced.

6. Phi291: PHILIPPINES: Bohol, near Loboc, above Loboc River (~9.655N, 124.015E), ~250 m a.s.l., forest near caves, 5.iii.2014 (B.A.Huber). Spider: *Panjange camiguin* Huber. 1 specimen sequenced.
7. PSt1226: PHILIPPINES: Mindanao, Davao Oriental, Mount Hamiguitan Wildlife Sanctuary (access Governor Generoso), site 3 (6.6805N, 126.1591E), 580 m a.s.l., 13.ii.2015 (M.A. Responte). Spider: *Panjange hamiguitan* Huber. 1 specimen sequenced.
8. PSt1564: PHILIPPINES: Visayas, Bohol, Bilar, Barangay Riverside, site 5 (9.7052N, 124.1253E), 440 m a.s.l., 15.vi.2015 (M.R.B. Dacar). Spider: *Panjange camiguin* Huber. 1 specimen sequenced.

In an additional five samples the parasitoids grew to the pupal stage, but failed to emerge as adults. Pupae from these samples were used in the molecular analyses.

1. Mal226: SINGAPORE: Upper Selatar Reservoir Park (1°24.0'N, 103°48.4'E), 20 m a.s.l., leaf litter, 15.ii.2015 (B.A. Huber, D. Court). Spider: *Uthina luzonica* Simon. 2 specimens sequenced.
2. Phi271: PHILIPPINES: Mindanao, Mt. Matutum, Kawit Forest, 'site 1'(6.338N, 125.104E), 950 m a.s.l., along brook, on leaves, 13.ii.2014 (B.A. Huber). Spider: *Calapnita nunezae* Huber. 2 specimens sequenced.
3. Phi286: PHILIPPINES: Mindanao, Bukidnon Prov., Santo Domingo (7.782N, 125.397E), 560 m a.s.l., forest remnant along brook, 8–9.ii.2014 (B.A. Huber). Spider: *Teranga domingo* (Huber). 1 specimen sequenced.
4. PSt461: PHILIPPINES: Mindanao, Maguindanao, Camp Abubakar (7.5698N, 124.3198E), 14.xii.2014 (N.U. Elias). Spider: *Nipisa subphyllicola* (Deeleman-Reinhold). 2 specimens sequenced.
5. PSt84: PHILIPPINES: Mindanao, Marawi City, Mt. Mupo (8.0219N, 124.2986E), 19.xi.2014 (N.U. Elias). Spider: *Nipisa subphyllicola* (Deeleman-Reinhold). 2 specimens sequenced.

The wasp specimens are deposited in the C.A. Triplehorn Insect Collection, Ohio State University, Columbus, OH (OSUC). The host spiders are deposited at the Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK).

Abbreviations and morphological terms used in text: A1, A2, A3: antennomere 1, 2, 3; T1, T2, ... T5: metasomal tergite 1, 2, ... 5. Morphological terminology otherwise generally follows Masner (1980) and Mikó et al. (2007). In the Material Examined section the specimens studied are recorded in an abbreviated format, using unique identifiers (numbers prefixed with "OSUC") for the individual specimens. The label data for all specimens are recorded in the Hymenoptera Online database, and details on the data associated with these specimens can be accessed at hol.osu.edu by entering the identifier in the form (note the space between the acronym and the number). All new species names have been prospectively registered with Zoobank (Polaszek et al. 2005, www.zoobank.org). The taxonomic descriptions were generated by a database application,

vSysLab (vsyslab.osu.edu), designed to facilitate the production of taxon by character data matrices and to integrate those data with the existing taxonomic and specimen-level database. The text output for descriptions is in the format of "Character: Character state (s)". Polymorphic characters are indicated by semicolon-separated character states. Comparison with holotypes of species described from India and Vietnam were made using the images in Specimage (specimage.osu.edu) referenced in Talamas et al. (2017) and Talamas and Pham (2017). Images and measurements were made using AutoMontage extended-focus software, using JVC KY-F75U digital camera, Leica Z16 APOA microscope, and 1× objective lens. Images were post-processed with Abobe Photoshop CS3 Extended. The individual wasp images are archived in Specimage (specimage.osu.edu).

Genomic DNA was extracted from ethanol-preserved specimens using the DNeasy Blood & Tissue Kit (Qiagen, Germantown, MD; cat. num. 69506) and following the protocol used by Taekul et al. (2014). A segment of the mitochondrial COI gene region was amplified with PCR using the scelionid-specific primers of Gariepy et al. (2014). PCRs were carried out in 50 μL containing 25 μL GoTaq Green Master Mix, 2× (Promega, USA), 0.5 μL of 100 μM primers and 2.5 μL of genomic DNA. Thermocycling conditions include initial denaturation at 94 °C for 5 min, followed by 35 cycles of 1 min at 94 °C, 1 min at the primers' annealing temperature, and 1.5 min of elongation at 72 °C, and ending with an additional extension of 72 °C for 3 min. Amplicons were directly sequenced in both directions with forward and reverse primers by Genewiz (South Plainfield, NJ). Chromatograms were assembled with Sequencher v4.0 (Gene Codes Corporation, Ann Arbor, MI). All the amplified sequences are deposited in GenBank (Suppl. material 2). Sequences were aligned in Geneious 11.1.4 using the Geneious alignment algorithm. The aligned sequences were then analyzed using the neighbor-joining algorithm and RAxML as implemented in Geneious 1.1.4 with the corresponding sequence from *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygastridae, Telenominae) used as an outgroup to root the tree.

Results

The nucleotide alignment file and GenBank accession numbers are included in Suppl. materials 1, 2 respectively. The results of the RAxML analysis are presented in Figure 1. Both the RAxML and neighbor-joining trees grouped the 20 samples into the same seven groups:

1) Mal305
2) PSt84 + PSt461
3) Mal331 (*Idris fusciceps* sp. n.)
4) Phi286
5) Mal276 + PSt1226 (*Idris badius* sp. n.)
6) Phi 291 (*Idris balteus* sp. n.)
7) Mal228 + Mal256 + PSt1564 + Mal226 + Phi271 (*Idris curtus* sp. n.)

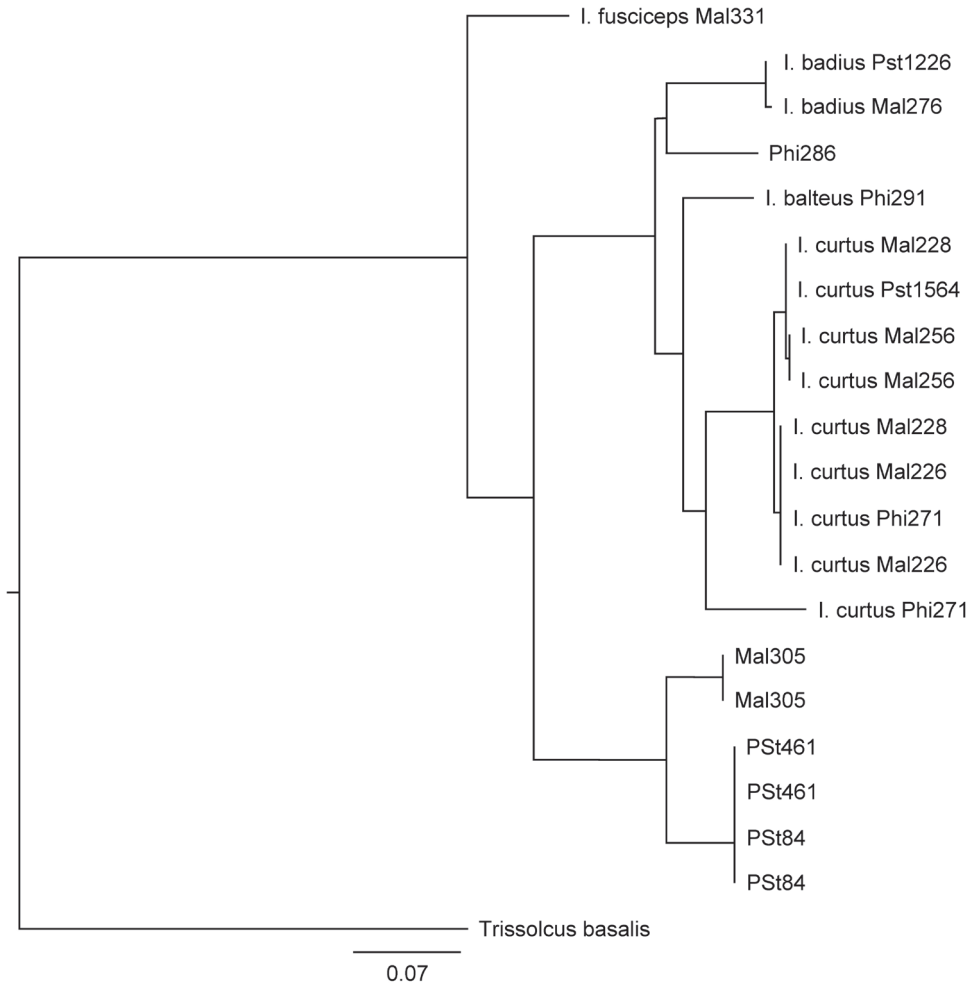


Figure 1. Results of RAxML analysis of COI sequences.

Within each grouping of more than one sequenced sample the average pairwise percentage identity of the sequences was 99.443% (99.142–100%). The average between-group pairwise percentage identity was 88.154% (87.016–90.207%). The average percent identity with the outgroup, *Trissolcus basalis*, was 79.2%. In one egg sac, Phi271, the two specimens sequenced were identical in only 91.3% of the sequence, suggesting either two different species or a relatively high level of intraspecific variation. Unfortunately, no adults emerged from these eggs so it was impossible to distinguish between the two possibilities on the basis of morphological characters.

Five of the seven groupings of molecular samples were represented by adults, and all but one of these are described below as new species. The one not described could not be distinguished on the basis of morphology alone from *I. badius*. The low level of sequence identity (86.5%) strongly suggests that they are not conspecific, but in lieu of finding any morphological distinction, we decided to refrain from describing

it. None of these new species were identifiable on the basis of the key in Lê (2000) nor through examination of images of holotypes in Talamas et al. (2017) and Talamas and Pham (2017).

***Idris badius* Johnson & Chen, sp. n.**
http://zoobank.org/E8EC0A7D-7214-45EE-B0BD-AB8622FF7267
Figures 2, 6, 10

Description. Body length: 0.81 mm. Head color: brown. Mesosoma color: brown. Metasoma color: brown.

Head shape in frontal view: ovoid, distinctly wider than high. Head width/mesosomal width: 1.34–1.44. Sculpture of upper frons, vertex: finely coriaceous reticulate. Position of lateral ocellus: contiguous with inner orbit of compound eye. Central keel of frons: present. Length of central keel of frons: extending dorsally half distance to median ocellus. Speculum: present. Striae on lower frons: absent. Setation of compound eyes: eyes distinctly setose.

Size of A3: subequal in length, width to A2. Shape of A3: length greater than width.

Length/width mesoscutum: 0.74–0.83. Sculpture of mesoscutum: finely reticulate, setal bases pustulate. Notauli: absent. Sculpture of mesoscutellum: finely reticulate, setal bases pustulate. Sculpture of metascutellum: smooth. Propodeal armature: lateral propodeal area produced dorsomedially into small tooth.

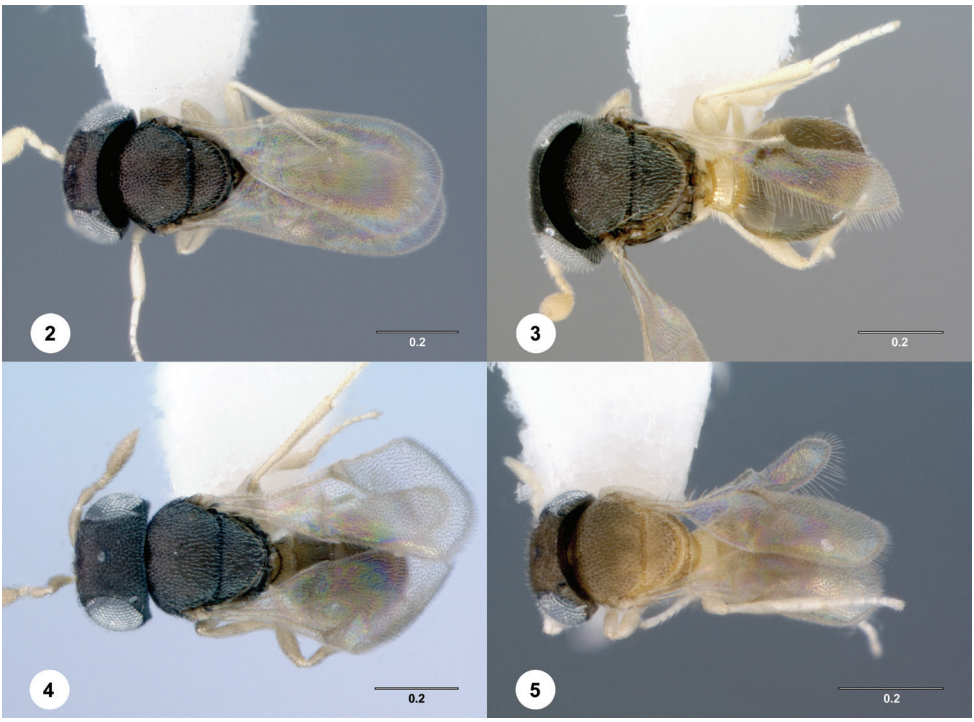
Wing development: fully developed, macropterous. Fore wing patterning: fore wing hyaline throughout. Marginal fringe of fore wing: present, short. Length of bristles on submarginal vein: short, barely reaching beyond costal margin of wing. Basal vein: well-defined, straight, lightly pigmented. Length of stigmal vein: elongate, extending nearly to middle of fore wing. Length of postmarginal vein: extremely short, subequal in length to marginal vein.

Metasoma length/body length: 0.47–0.48. Sculpture of T1: longitudinally costate. Sculpture of T2: longitudinally costate in medial third, finely reticulate along lateral margin, elsewhere smooth. Length T3/length T2: 2.21. Sculpture of T4–T5: finely reticulate basally, smooth apically. Setation of T3: lateral thirds of tergite moderately setose through, median third nearly glabrous, with sparse apical transverse band of setae.

Diagnosis. This species runs to *I. nautalis* Kozlov & Lê in the keys of Kozlov and Lê (1987) and Lê (2000), but differs in the absence of longitudinal striae on T3. It is morphologically indistinguishable from the specimens of sample Mal305 collected at the same time and place, but reared from the eggs of *Tissahamia gombak*. The COI sequences, however, have only 86.5% identity, and this must be used to establish their identity.

Host. Eggs of *Nipisa phyllicola* (Deeleman-Reinhold) (ZFMK, Mal 276) (Fig. 14), *Panjange hamiguitan* Huber (ZFMK, PSt1226 = Ar 13012) (Araneae: Pholcidae).

Etymology. The specific epithet *badius* refers the rich brown color of the body and is intended as an adjective.



Figures 2–5. Dorsal habitus. **2** *Idris badius* sp. n. **3** *I. balteus* sp. n. **4** *I. curtus* sp. n. **5** *I. fusciceps* sp. n. Scale bars in millimeters.

Material examined. Holotype *female*: **MALAYSIA**: Perak, Gunung Liang, forest along river, 250 m a.s.l., 3°47.7'N 101°32.0'E, 22.ii.2015, B. A. Huber, A.R.M. Ghazali & K. A. Braima, ex: egg of *Nipisa phyllicola* (Deeleman-Reinhold), OSUC 270822. **Paratypes**: **MALAYSIA**: 3 females, 1 male with same data as holotype, OSUC 270823, 420837–420838, 627622. **PHILIPPINES**: Mindanao, Davao Oriental, 580 m a.s.l., 6.6805N, 126.1591E, site 3, Mount Hamiguitan Wildlife Sanctuary (access Governor Generoso), 13.ii.2015, M. A. Responte, ex egg of *Panjange hamiguitan* Huber (1 female, OSUC 627625).

Idris balteus Johnson & Chen, sp. n.

http://zoobank.org/04E0C39B-2CAE-4302-8148-413299BE60AE
Figures 3, 7, 11

Description. Body length: 0.85–0.99 mm. Head color: dark brown. Mesosoma color: dark brown. Metasoma color: first segment yellow, second segment brownish yellow, otherwise brown.

Head shape in frontal view: ovoid, distinctly wider than high. Head width/mesosomal width: 1.24–1.31. Sculpture of upper frons, vertex: finely coriaceous reticulate. Position of lateral ocellus: contiguous with inner orbit of compound eye. Central keel

Figures 6–9. Lateral habitus. **6** *Idris badius* sp. n. **7** *I. balteus* sp. n. **8** *I. curtus* sp. n. **9** *I. fusciceps* sp. n. Scale bars in millimeters.

of frons: present. Length of central keel of frons: extending dorsally half distance to median ocellus. Speculum: present. Striae on lower frons: with short striae flanking speculum. Setation of compound eyes: eyes distinctly setose.

Size of A3: distinctly smaller than A2. Shape of A3: length greater than width.

Length/width mesoscutum: 0.72. Sculpture of mesoscutum: finely reticulate, setal bases pustulate. Notauli: absent. Sculpture of mesoscutellum: finely reticulate, setal bases pustulate. Sculpture of metascutellum: smooth. Propodeal armature: lateral propodeal area produced dorsomedially into small tooth.

Wing development: fully developed, macropterous. Fore wing patterning: fore wing hyaline throughout. Marginal fringe of fore wing: present, short. Length of bristles on submarginal vein: short, barely reaching beyond costal margin of wing. Basal vein: well-defined, straight, lightly pigmented. Length of stigmal vein: elongate, extending nearly to middle of fore wing. Length of postmarginal vein: extremely short, subequal in length to marginal vein.

Metasoma length/body length: 0.45–0.48.Sculpture of T1: longitudinally costate. Sculpture of T2: longitudinally costate in medial third, finely reticulate along lateral margin, elsewhere smooth. Sculpture of T3: finely reticulate, with weak irregularly longitudinal rugulae medially. Length T3/length T2: 1.81–2.17. Sculpture of T4–T5: finely reticulate basally, smooth apically. Setation of T3: lateral thirds of tergite moderately setose through, median third nearly glabrous, with sparse apical transverse band of setae.

Diagnosis. In the keys of Kozlov and Lê (1987) and Lê (2000) this species runs to *I. nautalis*, but differs from that species in the lack of longitudinal striae on T3 and the uniform coloration of the metasoma. Distinguished from many species of *Idris* by the xanthic first segment of the metasoma. The COI sequence will serve to help distinguish this species from others with the same character.

Host. *Panjange camiguin* Huber (ZFMK, Phi291) (Araneae: Pholcidae) (Fig. 15).

Etymology. The specific epithet *balteus*, a Latin word for belt, refers to the golden base of the metasoma. It is intended as a noun in apposition.

Material examined. Holotype *female*: **PHILIPPINES**: Bohol, near Loboc, above Loboc River, forest near caves, ~250 m a.s.l., ~9.655N, 124.015E, 5.iii.2014, B. A. Huber, ex egg of *Panjange camiguin* Huber, OSUC 270828. **Paratypes**: **PHILIPPINES**: 3 females, 1 male with same data as holotype, OSUC 270829, 420844–420845, 627631). **Other material**: 1 broken female with same data as holotype, OSUC 270830.

Idris curtus Johnson & Chen, sp. n.

http://zoobank.org/C8DA9FB6-A843-4D33-9475-5E3FE090068C
Figures 4, 8, 12

Description. Body length: 0.83–0.89 mm. Head color: brown. Mesosoma color: brown. Metasoma color: brown

Head shape in frontal view: ovoid, distinctly wider than high. Head width/mesosomal width: 1.20–1.27. Sculpture of upper frons, vertex: finely coriaceous reticulate. Position of lateral ocellus: contiguous with inner orbit of compound eye. Central keel of frons: present. Length of central keel of frons: extending dorsally half distance to median ocellus. Speculum: present. Striae on lower frons: with short striae flanking speculum. Setation of compound eyes: eyes distinctly setose.

Size of A3: distinctly smaller than A2. Shape of A3: length greater than width.

Length/width mesoscutum: 0.65–0.79. Sculpture of mesoscutum: finely reticulate, setal bases pustulate. Notauli: absent. Sculpture of mesoscutellum: finely reticulate, setal bases pustulate. Sculpture of metascutellum: smooth. Propodeal armature: lateral propodeal area produced dorsomedially into small tooth.

Wing development: fully developed, macropterous. Fore wing patterning: fore wing hyaline throughout. Marginal fringe of fore wing: present, short. Length of bristles on submarginal vein: short, barely reaching beyond costal margin of wing. Basal vein: well-defined, straight, lightly pigmented. Length of stigmal vein: elongate, extending nearly to middle of fore wing. Length of postmarginal vein: extremely short, subequal in length to marginal vein.

Metasoma length/body length: 0.52–0.57. Sculpture of T1: longitudinally costate. Sculpture of T2: longitudinally costate in medial third, finely reticulate along lateral margin, elsewhere smooth. Length T3/length T2: 1.87–2.33. Sculpture of T4–T5: finely reticulate basally, smooth apically. Setation of T3: lateral thirds of tergite

Figures 10–13. Head, anterior view. **10** *Idris badius* sp. n. **11** *I. balteus* sp. n. **12** *I. curtus* sp. n. **13** *I. fusciceps* sp. n. Scale bars in millimeters.

moderately setose through, median third nearly glabrous, with sparse apical transverse band of setae.

Diagnosis. Very similar to *I. badius*, distinguished by the distinctly shorter third antennomere (compared with A2). As with *I. badius*, this species runs to *I. nautalis* Kozlov & Lê in the keys of Kozlov and Lê (1987) and Lê (2000). It differs in the absence of longitudinal striae on T3. Distinguished from other species of *Idris* by its COI sequence.

Host. *Calapnita nunezae* Huber (ZFMK, Phi271), *Panjange camiguin* Huber (ZFMK, PSt1564 = Ar 15064), *Tissahamia bukittimah* (Huber) (ZFMK, Mal 256) (Fig. 16), *Uthina luzonica* Simon (ZFMK, Mal228 = Ar 19637 and Mal226) (Araneae: Pholcidae).

Etymology. The name *curtus*, Latin for short, refers to relative length of the first flagellomere of the female antenna. It is intended to be used as an adjective.

Material examined. Holotype *female*: **SINGAPORE**: 50 m a.s.l., 1°21.6'N 103°46.7'E, Dairy Farm Nature Park, 15.ii.2015, B. A. Huber & J. Koh, reared ex egg of *Tissahamia bukittimah* (Huber), OSUC 270831. **Paratypes**: **SINGAPORE**: 6 females, 2 males, with same data as holotype, OSUC 270832, 270833, 420829–420831, 420833, 627623, 627624. 1 female, 2 males with same data as holotype except reared ex egg of *Uthina luzonica* Simon, OSUC 420836, 6217633, 627634. **PHILIPPINES**: Visayas, Bohol, Bilar, Barangay Riverside, 440 m a.s.l., 9.7052N, 124.1253E, 15.vi.2015, M.R.B.

Dacar; reared ex egg of *Panjange camiguin* Huber, 1 female, 1 male, OSUC 420834, 627632. **Other material**: **SINGAPORE**: 50 m a.s.l., 1°21.6'N 103°46.7'E, Dairy Farm Nature Park, 15.ii.2015, reared, B. A. Huber & J. Koh, ex egg of *Tissahamia bukittimah* (Huber), female, OSUC 420832 (broken specimen); ex egg of *Uthina luzonica* Simon, male, OSUC 420835 (broken). The remaining material is based on DNA sequences from pupae. **SINGAPORE**: Upper Selatar Reservoir Park (1°21.3'N, 103°48.4'E), 20 m a.s.l., 15.ii.2015 (B.A. Huber, D. Court). Host: *Uthina luzonica* Simon. **PHILIPPINES**: Mindanao, Mt. Matutum, Kawit Forest, 'site 1', (6.338N, 125.104E), 950 m a.s.l., along brook, on leaves, 13.ii.2014, B. A. Huber, ex egg of *Calapnita nunezae* Huber.

***Idris fusciceps* Johnson & Chen, sp. n.**
http://zoobank.org/F316941C-D414-4DC1-9420-129ADBC8192E
Figures 5, 9, 13

Description. Body length: 0.58–0.66 mm.

Head color: light brown. Mesosoma color: brownish yellow, contrasting with darker color of head. Metasoma color: brownish yellow.

Head shape in frontal view: ovoid, distinctly wider than high. Head width/mesosomal width: 1.17–1.24. Sculpture of upper frons, vertex: pustulate. Position of lateral ocellus: separated from inner orbit of compound eye by approximately 1 ocellar diameter. Central keel of frons: present. Length of central keel of frons: extending dorsally one-third distance to median ocellus. Speculum: present. Striae on lower frons: absent. Setation of compound eyes: eyes distinctly setose.

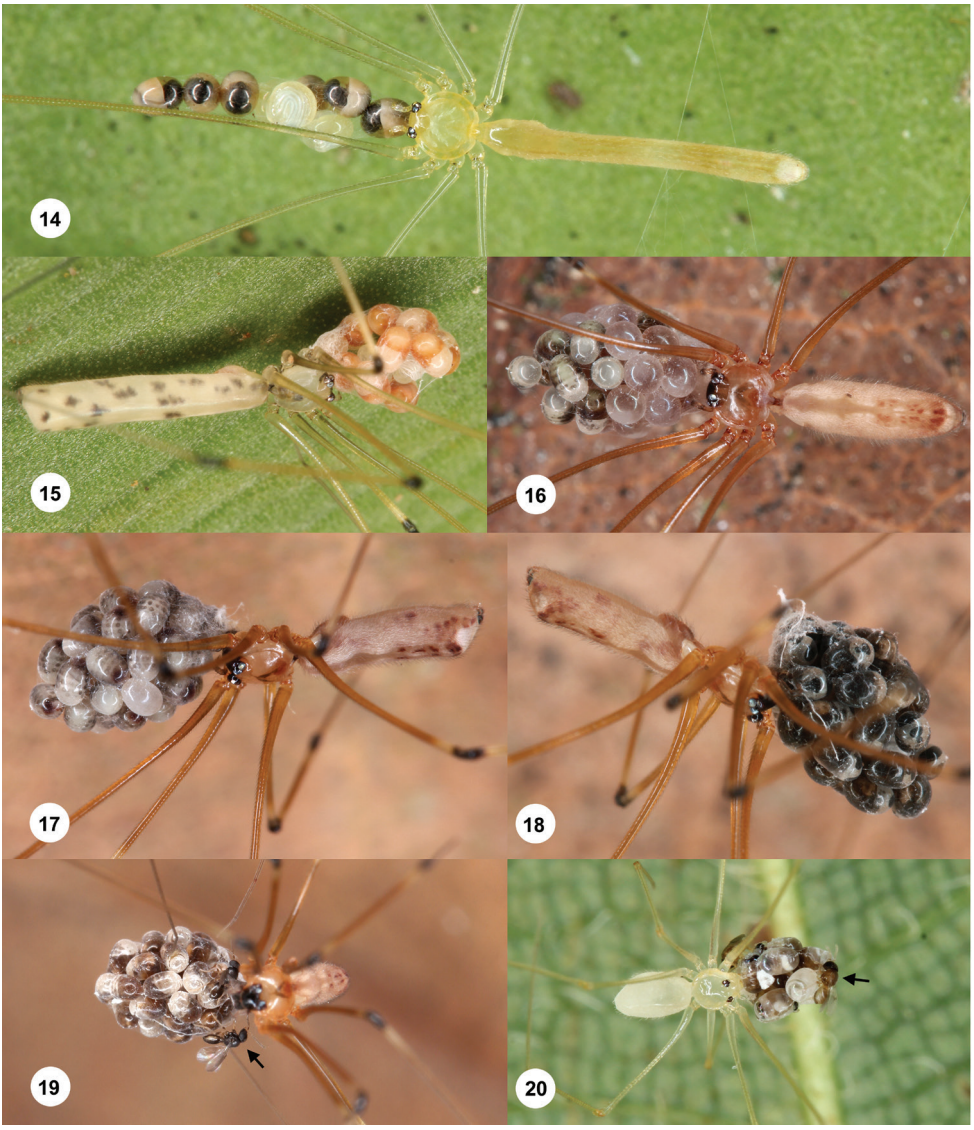
Size of A3: distinctly smaller than A2. Shape of A3: width greater than length.

Length/width mesoscutum: 0.64–0.72. Sculpture of mesoscutum: finely reticulate, setal bases pustulate. Notauli: present, short. Sculpture of mesoscutellum: finely reticulate, setal bases pustulate. Sculpture of metascutellum: rugulose. Propodeal armature: lateral propodeal area produced dorsomedially into small tooth.

Wing development: fully developed, macropterous. Fore wing patterning: fore wing hyaline throughout. Marginal fringe of fore wing: present, short. Length of bristles on submarginal vein: elongate, extending beyond costal margin by distance more than half their length. Basal vein: well-defined, straight, lightly pigmented. Length of stigmal vein: elongate, extending nearly to middle of fore wing. Length of postmarginal vein: extremely short, subequal in length to marginal vein.

Metasoma length/body length: 0.44–53. Sculpture of T1: longitudinally costate. Sculpture of T2: longitudinally costate in medial third, finely reticulate along lateral margin, elsewhere smooth. Sculpture of T3: finely reticulate, with weak irregularly longitudinal rugulae medially. Length T3/length T2: 1.56–1.60. Sculpture of T4–T5: finely reticulate basally, smooth apically. Setation of T3: lateral thirds of tergite moderately setose through, median third nearly glabrous, with sparse apical transverse band of setae.

Diagnosis. In the keys of Kozlov and Lê (1987) and Lê (2000), this species comes closest to *I. oobius* Kozlov & Lê, particularly in the weak sculpture of T3 and the



Figures 14–20. Host spiders with parasitized egg-sacs. **14** *Nipisa phyllicola* (Mal276); note that two eggs are not parasitized **15** *Panjange camiguin* (Phi291) **16** *Tissahamia bukittimah* (Mal256); note that only some of the eggs are parasitized **17–19** *Tissahamia gombak* (Mal305) at different stages of wasp development (6 days lie between **17** and **18** 1 day between **18** and **19**); arrow points at eclosed wasp **20** *Belisana khaosok* (Mal331); arrow points at eclosed wasp.

uniform coloration of the wings. This species is distinguished from *I. oobius* by the extremely short A3 in comparison to the length of A2. It may be distinguished from the other reared species described herein by the presence of notauli and the dark-colored head; among other morphologically similar species of *Idris* it may be recognized by its COI sequence.

Host. *Belisana khaosok* Huber (ZFMK, Mal331= Ar 19649) (Araneae: Pholcidae) (Fig. 20).

Etymology. The specific epithet refers to the darker color of the head in comparison with the mesosoma and metasoma. It is to be treated as a noun in apposition.

Material examined. Holotype, female: **THAILAND**: Krabi, ~9 km N Krabi town, degraded forest between plantation and rocks, 75 m a.s.l., 8°09.9'N 98°51.7'E, 7.III.2015, B. A. Huber & B. Petcharad, ex egg of *Belisana khaosok* Huber. OSUC 270824. **Paratypes**: **THAILAND**: 8 females, 1 male with same data as holotype (OSUC 270825–270827, 420839–420843, 627626).

Acknowledgments

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Supplementary material 1

Fasta file: pholcid Idris

Authors: Norman F. Johnson, Huayan Chen, Bernhard A. Huber

Data type: Fasta file

Link: https://doi.org/10.3897/zookeys.811.29725.suppl1

Supplementary material 2

GenBank accessions: pholcid Idris

Authors: Norman F. Johnson, Huayan Chen, Bernhard A. Huber

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: GenBank Accession numbers for DNA sequences..

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Neotermes costaseca: a new termite from the coastal desert of Peru and the redescription of *N. chilensis* (Isoptera, Kalotermitidae)

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Abstract

The imago and soldier castes of a new *Neotermes* species, *N. costaseca*, are described. It is only the third termite species known from the Pacific coastal desert of Peru. *Neotermes costaseca* **sp. n.** is compared with the allopatric *Neotermes chilensis* from the arid central and southern coastal plain of Chile.

Keywords

New species, Neotropics, Chile, imago, soldier

Introduction

The coastal desert of Peru and Chile (Atacama) spans approximately 3,000 km from -5° to -27° latitude. Only two termite species are recorded from this region, *Cryptotermes brevis* (Walker) (widespread, Scheffrahn et al. 2009) and *Amitermes lunae* in the north (Trujillo, Peru; Scheffrahn and Huchet 2010). Another species in the genus *Neotermes* Holmgren, 1911, *N. chilensis* (Blanchard), extends northward to the steppe transition zone of the Atacama (Copiapo, Chile) and ranges southward along the coastal plain to Santa Cruz, Chile (Camousseight and Vera 2005). Herein, a new *Neotermes* species is described, *N. costaseca*, the third species of termite from the Peruvian coastal desert, and it is compared with the Chilean *N. chilensis*.

Materials and methods

Microphotographs were taken as multi-layer montages using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software. Preserved specimens were taken from 85% ethanol and suspended in a pool of Purell® Hand Sanitizer to position the specimens on a transparent Petri dish background.

Taxonomy

***Neotermes costaseca* sp. n.**
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Figures 1A–C, 2, 3A–D, 4; Tables 1, 2

Diagnosis. The imago of *N. costaseca* has larger eyes and ocelli than *N. chilensis* and the former possesses arolia. The soldier mandible of *N. chilensis* has much more pronounced basal humps than *N. costaseca* and the former has more protruding genal horns.

Description. *Imago* (Figs 1A–C, 2; Table 1). Head capsule and pronotum orange-brown. Compound eye nearly circular; ocellus yellowish orange, large, and roundly ellipsoid; nearly touching eye margin. Head vertex and frons slightly depressed, without rugosity; covered with dozens of long (0.25 mm), variously directed setae. Pronotum wider than head capsule; anterior margin evenly concave; anterior margin very weakly emarginate. Pronotum covered with shorter and many long (0.3 mm) setae, especially along lateral margins. Antennae with 17–22 articles, basal article relative lengths 1>2=3>4. Anterior margin of fore wing scale convex; margin lined with 12–15 setae. Fore wing with subcosta joining costal margin at ca. one-fifth of wing length from suture. Radius joining costal margin at two-fifths wing length; radial sector with ca. seven anterior branches. Median vein sclerotised and running very close to and parallel radial sector. Arolium present.

Soldier (Fig. 3A–D, Table 2). Head capsule in dorsal and lateral aspect orange-brown; ventrally yellowish orange; pronotum yellowish orange. Eye spot yellow; small, narrow ellipsoid. Head and pronotum covered with shorter and moderately long (0.15–0.25 mm) setae; seta denser and longer on frontal lobes. Head capsule with lateral margins nearly parallel, slightly converging at anterior; genal horns not protruding in ventral view. Frons roundly sloping 45° from vertex; depressed and slightly rugose from width of postclypeus to anterior vertex. Y-suture distinct, narrow. Pronotum width 2.5× length, posterior margin slightly concave, posterolateral corners rounded 90°. Antennae with 14–16 articles, basal article relative lengths 1>2<3>4. Mandibles with shallow basal hump more than 4/5th length from apical points. Mandibles evenly curved ca. 80° along apical third.

Holotype: Perú: Lurin, Rio Lurin, (-12.275, -76.879), 23OCT2007, J Křeček (JK); labelled soldier (University of Florida Termite collection no. PE131).

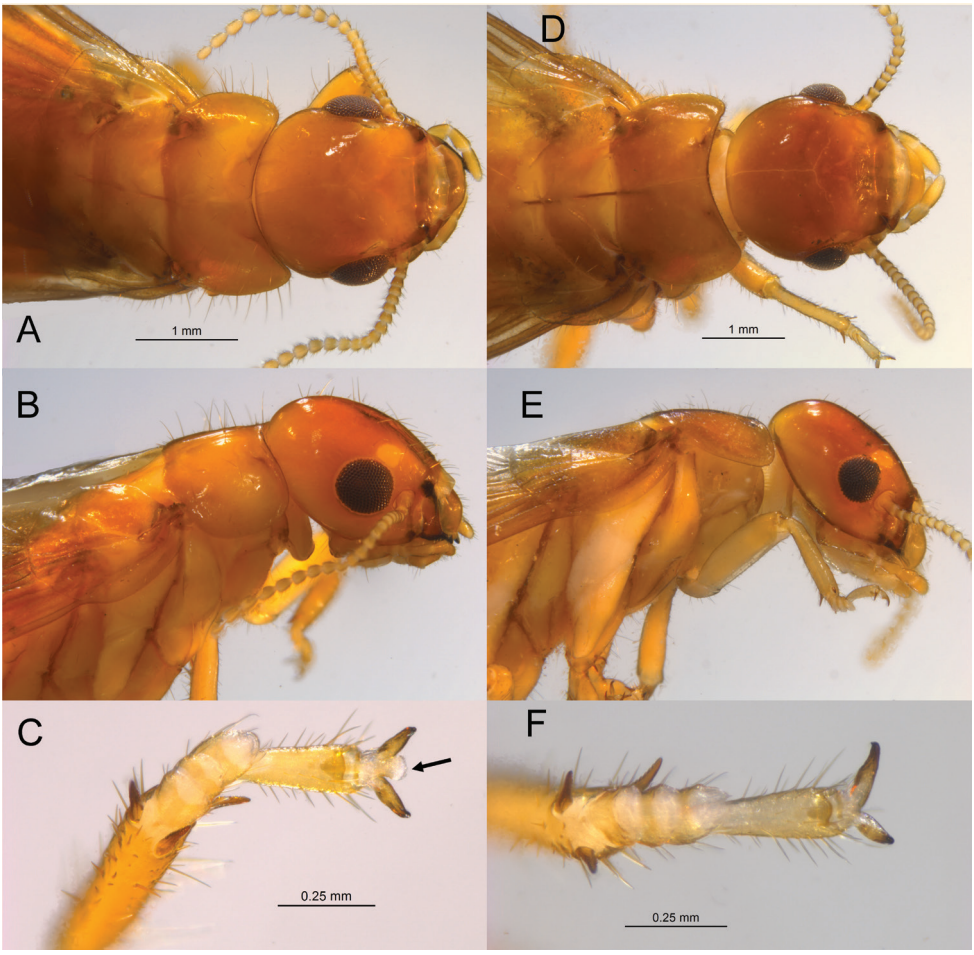

Figure 1. Dorsal and lateral views of head and pronotum and fore tarsi of *Neotermes* alates. **A–C** *N. ostaseca* (arrow = arolium) **D–F** *N. chilensis*.

Material examined. Perú: Lurin, Rio Lurin (-12.275, -76.879), 23OCT2007, J. Křeček (JK); winged imagos, soldiers, pseudergates (UF no. PE131). Perú: Lima, Rio Chillon (-11.979, -77.090), 20OCT2007, JK; winged imagos (UF no. PE107). Perú: Lima, Rio Lurin, Quebrada Verde bridge (-12.237, -76.856), 23OCT2007, JK, Gerardo; winged imagos (UF no. PE117). Perú: Lima, Rio Lurin, Quebrada Verde bridge (-12.237, -76.856), 23OCT2007, JK, Gerardo; winged imagos (UF no. PE119). Perú: Lima, Huaral (-12.275, -76.879), 23OCT2007, JK, Gerardo; winged imagos (UF no. PE131). Perú: Lima, Rio Lurin (-11.521, -77.239), 25OCT2007, JK, C. Torres; winged imagos (UF no. PE145). Perú: Lima, Chacra y Mar (-11.60804, -77.23939), 25OCT2007, T. Carrijo R. Constantino, J. Chase, J. Křeček, E. Kuswanto, J. Mangold, A. Mullins, T. Nishimura, R. Scheffrahn (CCCKKMMNS); winged imagos (UF no. PU1012). Perú: Ancash, Huaylas (-8.872, -77.894), 9MAY2014, CCCKKMMNS;

Table 1. Measurements (mm) of *Neotermes* imagos' characters.

Characters	Females, 3 colonies (n = 8)		Males, 5 colonies (n = 10)	
***Neotermes costaseca*, sp. n.**	**mean**	**range**	**mean**	**range**
Head width, maximum (w/out eyes)	1.7	1.60–1.90	1.69	1.66–1.72
Head width, maximum (with eyes)	1.84	1.76–1.96	1.85	1.78–1.94
Pronotum, maximum width	2.07	1.98–2.13	2.02	1.97–20.9
Eye diameter, maximum	0.56	0.50–0.60	0.57	0.50–0.61
Body length	8.56	7.14–13.17	8.47	6.80–9.40
Right forewing length	14.67	14.00–16.35	15.41	13.00–16.19
Body length with wings	17.43	16.51–17.94	17.59	16.30–18.73
Number of antennal articles	18.9	17–21	19.75	17–22
Neotermes chilensis	**Females, 1 colony (n = 1)**		**Males, 2 colonies (n = 2)**	
	mean	**range**	**mean**	**range**
Head width, maximum (w/out eyes)	1.74	1.70–1.78	1.64	1.63–1.66
Head width, maximum (with eyes)	1.82	1.82–1.82	1.79	1.78–1.80
Pronotum, maximum width	2.04	1.95–2.13	1.97	1.91–2.03
Eye diameter, maximum	0.47	0.44–0.51	0.46	0.44–0.47
Body length	8.57	6.51–10.63	7.2	6.40–8.00

Table 2. Measurements (mm) of *Neotermes* soldier characters.

Characters	***Neotermes costaseca* (n = 10)**		***Neotermes chilensis* (n = 10)**	
	mean	**range**	**mean**	**range**
Head length to lateral mandible base	3.46	2.66–3.92	3.25	2.80–3.84
Head width, maximum	2.44	2.25–2.66	2.63	2.31–2.97
Head height with gula, maximum	2.04	1.72–2.30	1.94	1.75–2.13
Pronotum length	1.38	1.20–1.69	1.54	1.25–1.84
Pronotum width	2.60	2.38–3.06	2.74	2.38–3.19
Number of antennal articles	15	14–16	16.22	14–18
3rd antennal article length	0.17	0.14–0.19	0.23	0.19–0.28

soldiers (UF no. PU1019). Perú: Parque Nat. Lachay (-11.363, -77.371), 9MAY2014, CCCKKMMNS; soldiers (UF no. PU1007). Perú: Lima, Chacra y Mar (-11.608, -77.239), 3JUN14, CCCKKMMNS; soldiers (UF no. PU1011). Perú: Lima, Huaral, Pueblo Libre, Rio Chancay bridge (-11.514, -77.230), 23OCT2007, JK, C. Torres; soldiers (UF no. PE135). Perú: Lima, Rio Lurin, Quebrada Verde bridge (-12.237, -76.856), 23OCT2007, JK, Gerardo Torres; soldiers (UF no. PE120). Perú: Lima, Pachacamac (-12.243, -76.864), 23OCT2007, JK, Gerardo; soldiers (UF no. PE126). *Neotermes fulvescens,* Paraguay: Dry Chaco Mariscal Estigarribia (-22.078, -60.552), 1JUN2012, J. Chase; soldiers and queen (UF no. PA742).

Etymology. From Spanish, meaning "dry coast" and describing the species' habitat; to be treated as a noun in apposition.

Comparisons. Although climatically isolated, some character overlap is possible with other neotropical *Neotermes*. A revision of Neotropical *Neotermes* is needed to identify diagnostic characters. The imago of *N. costaseca* has longer head and pronotal setae

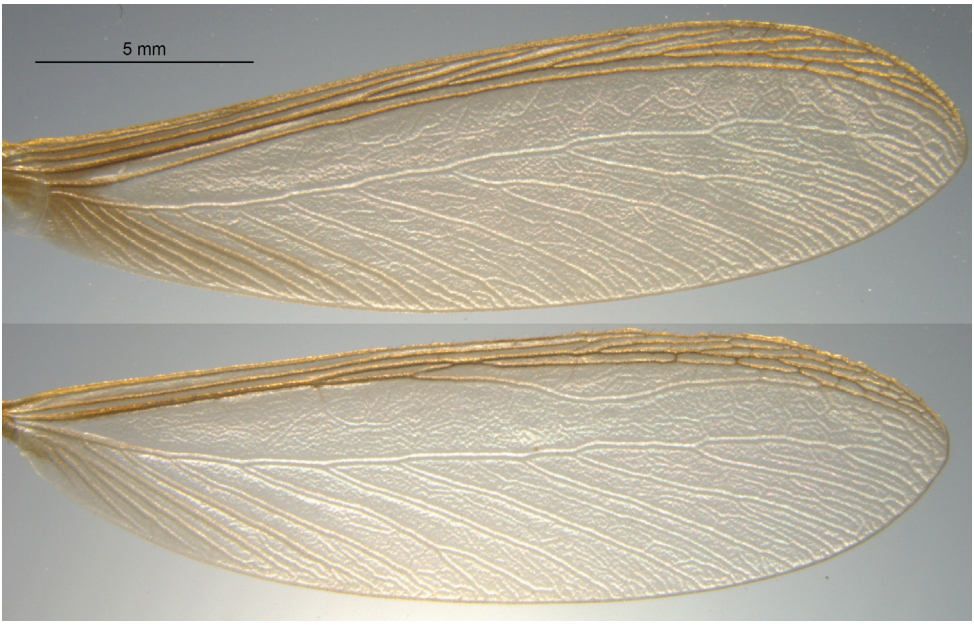

Figure 2. Fore and hind wing of the *Neotermes costaseca* alate.

and larger eyes and ocelli than *N. chilensis. Neotermes costaseca* has an arolium which is lacking in *N. chilensis*. The soldier mandible of *N. chilensis* has much more pronounced basal humps, more sinuate marginal teeth, and more sharply curved apical teeth than *N. costaseca*. The anterolateral corners of *N. chilensis* constrict more than those of *N. costaseca* and, unlike *N. costaseca*, the genal horns of *N. chilensis* protrude. The pronotum of the *N. chilensis* soldier is crescent-shaped with that of *N. costaseca* resembles a bow tie. The soldier eye spot of *N. costaseca* is hyaline while that of *N. chilensis* is almost always pigmented. The soldier of *N. castaneus* differs from both *N. costaseca* and *N. chilensis* in having shorter, thicker mandibles with larger, more rounded basal humps.

The arid-adapted *N. costaseca* and *N. chilensis* are most comparable with non-Amazonian congenerics from Argentina (Torales et al. 2008), Bolivia, Paraguay, and southern Brazil (Krishna et al. 2013). Compared to *N. chilensis*, the soldiers of *N. hirtellus* (Silvestri), *N. fulvescens* (Silvestri), and *N. modestus* (Silvestri) all have more reduced madibular basal humps (Silvestri 1903). Compared to *N. costaseca* and *N. chilensis*, the *N. hirtellus* soldier has a shorter third antennal article relative to the second, the head converging toward the front, and the ocellus separated from eye (Costa Lima 1941). The imago and soldier of *N. fulvescens* are smaller, the imago lacks an arolium, and the solder mandibles are shorter and thicker than both *N. chilensis* and *N. costaseca*. The *N. modestus* soldier and imago are smaller than both *N. chilensis* and *N. costaseca* (Silvestri 1903). Compared to *N. chilensis* and *N. costaseca*, the imago wings of *N. arthurimuelleri* (Rosen) are more darkly pigmented, shorter (12 mm long), and the ocelli are more separated from the eye (Costa Lima 1942).

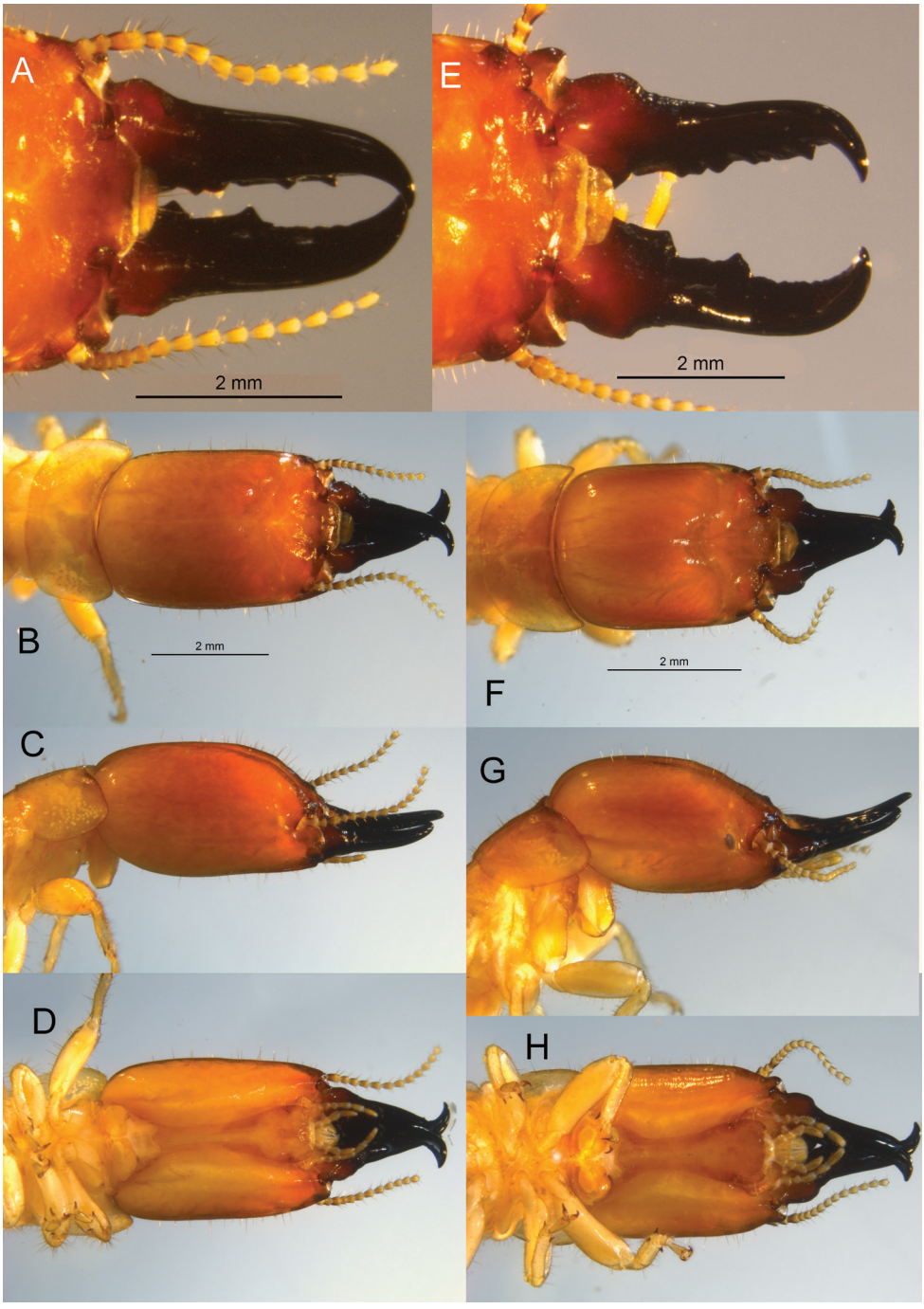

Figure 3. Open mandible, dorsal, lateral, and ventral views of soldier head capsule and pronotum of *Neotermes* soldiers. **A–D** *Neotermes costaseca* and **E–H** *N. chilensis*.

Figure 4. Live habitus photographs of *Neotermes costaseca*; **A** physogastric queen and pseudergate, colony 1 **B** soldier, colony 1 **C** various castes, colony 2 **D** exposed galleries of live tree from where colony 2 was removed.

The *N. glabriusculus* Oliveira imago has smaller ocelli than both *N. costaseca* and *N. chilensis* and are more removed from the eye while the soldier dentition in the former is less robust and the tips are not as curved and have almost no basal humps (Oliveira 1979). The *N. magnoculus* (Snyder) imago is smaller (Snyder 1926) than *N. chilesnsis* and N. costaseca. The *N. wagneri* (Desneux) soldier has proportionally shorter mandibles and no enlargement of the third antennal article compared with *N. chilesnsis* and *N. costaseca* (Costa Lima 1941, 1942). Finally, the *N. zanclus* Oliveira soldier has a more elongated and sub rectangular head capsule (Oliveira 1979).

Biology. *Neotermes costaseca* colonies were collected from both dead branches attached to live trees and directly from sapwood within live trees (Fig. 4). Alates were present in October, but were not collected in June suggesting the latter as part of the likely flight season. The greater tergite separation and mottling in the queen depicted in Fig. 4A suggest that this queen is older than the queen in Fig. 4C

***Neotermes chilensis* (Blanchard, 1851)**
Figures 1D–F, 3E–4; Table 1, 2

Synonyms. See Krishna et al. 2013: 538–539 for complete synonymic list. Camousseight and Alehandro 2005: 39–45, synonymy; measurements; soldier, worker mandibles figured. Ripa and Luppichini 2004: 69–71, Chile termite key; 84, alate and soldier illustrated and photographed.

Description. *Imago* (Fig. 1D–F; Table 1). Head capsule and pronotum reddish brown. Anterodorsal margin of compound eye straight; ocellus yellowish orange, reniform; touching eye margin. Head vertex and frons slightly depressed, slightly rugose; covered with scattered short setae (0.15–0.2 mm) directed forward on head, variably directed on pronotum. Pronotum wider than head capsule; anterior margin evenly concave; anterior margin emarginate giving "bow tie" resemblance. Pronotum covered with short and medium-long (0.15–0.25 mm) setae. Anterior margin of fore wing scale convex; margin lined with 15–20 setae of same length. Arolium absent.

Soldier (Fig. 3E–H, Table 2). Head capsule in dorsal and lateral aspect orange-brown; ventrally lighter; pronotum yellowish orange. Eye spot dark; small, ellipsoid. Head and pronotum covered with short (0.1–0.15 mm) setae; seta more dense and longer on frontal lobes. Head capsule with lateral margins parallel, converging to ~ 85% of width at anterior; genal horns protruding in ventral view. Frons sloping gradually ~ 30° from vertex; depressed from width of postclypeus to middle of vertex. Pronotum crescent-shaped, posterior margin evenly rounded to the anterolateral corners. Antennae with 14–18 articles, basal article relative lengths 1>2<3>4. Mandibles with robust basal hump more ~ 3/4th length from apical points. Mandibles abruptly curved ca. 90° along apical fourth. Dentition robust, undulating.

Material examined. Chile: La Serena, Road 5, Ovalle-Quebrada Seca intersection (-27.356, -70.659), 6OCT2007, JK, R. Ripa, P. Luppichini; imago (UF no. CL26). Chile: Atacama, 3km E PN Llanos de Challe (-30.518, -71.484), 5OCT2007, JK, R. Ripa, P. Luppichini; soldier (UF no. CL21). Chile: La Serena, PN Borque Fray Jorge (-30.667, -71.675), 6OCT2007, JK, R. Ripa, P. Luppichini; soldier (UF no. CL30). Chile: Valparaiso, La Cruz (-32.852, -71.183), 9OCT2007, JK, R. Ripa, P. Luppichini; soldier (UF no. CL33). Chile: Valparaiso, La Cruz (-32.852, -71.183), 9OCT2007, JK, R. Ripa, P. Luppichini; soldier (UF no. CL34). Chile: Santiago de Chile, Mallarauco (-33.459, -70.635), 11MAR1997, M. Rust; soldier (UF no. CL49). Chile: Santiago de Chile (-33.459, -70.635), 15FEB1999, J. Hughes; imago (UF no. SA158). Syntypes deposited in the Muséum National d'Histoire Naturelle, Paris, were unavailable and not examined.

Biology. *Neotermes chilensis* colonies were collected from fence posts, dead branches, and dead tree trunks. An alate was collected in mid-February suggesting a late summer flight season.

Discussion. The lack of termite diversity in the Neotropical coastal desert can be attributed to its climate and geographical barriers of the Pacific Ocean and the Andes. The entire coast of Peru and much of the Chilean coast is arid, but profound aridity (≤ 20 mm/yr) begins near Pacasmayo, Peru, and extends southward to approximately Copiapo, Chile (Fig. 5, climate data from http://www.weatherbase.com/). Although

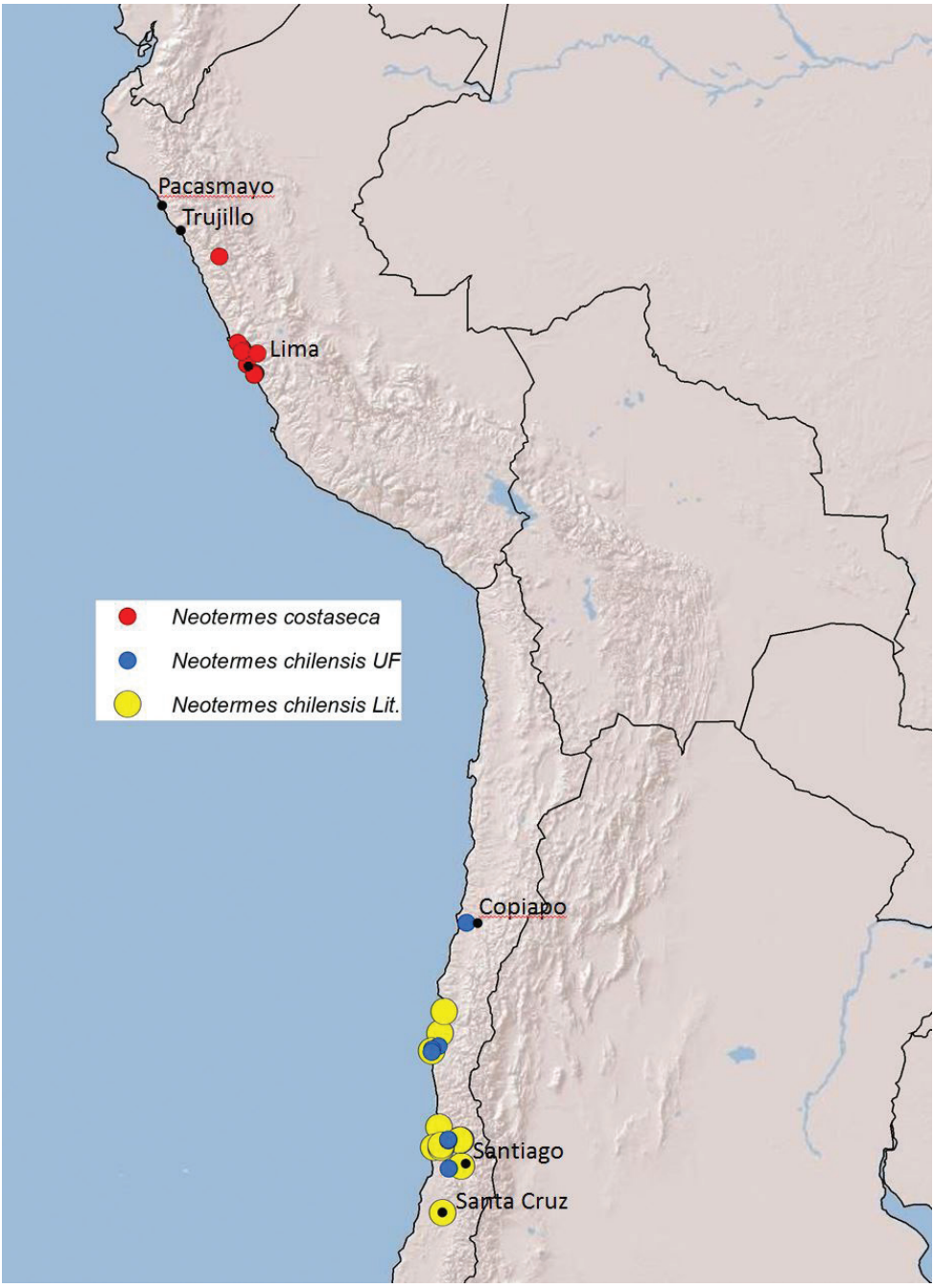

Figure 5. Map of *Neotermes costaseca* and *N. chilensis* localities.

hyperarid as a result of Humboldt Current cooling, this region is transected by many wooded riparian habitats fed by rain and snowmelt runoff from the Andes, providing food (wood) for only three termite species.

With the addition of *N. costaseca*, there are now 27 *Neotermes* species (Krishna et al. 2013). With only *N. costaseca* and two other termite species known from the coastal desert of Peru and Chile, it is unlikely that *N. costaseca* will be found outside of this unique Neotropical biome.

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An annotated checklist of the Cook Islands psyllids with keys to the species and two new records (Hemiptera, Psylloidea)

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Abstract

An annotated checklist of the psyllids of the Cook Islands is presented. The presence of *Syntomoza tahuata* (Klyver, 1932) and *Trioza alifumosa* Klyver, 1932 in the archipelago, based on new material collected, is reported for the first time. This is the first record from these islands of the genus *Syntomoza* and the family Liviidae. An identification key to the psyllid species known from the Cook Islands is provided, and their origin and provenance are discussed in relation to their biogeographic implications.

Keywords

Jumping plant lice, Pacific Islands, Polynesia, Rarotonga, Sternorrhyncha

Introduction

The superfamily Psylloidea (Hemiptera: Sternorrhyncha) is composed of almost 4000 described species worldwide (Ouvrard 2018). These include taxa used for biological control, such as *Arytainilla spartiophila* (Förster, 1848) released in New Zealand to control Scotch broom, *Cytisus scoparius* (L.) Link (Fabaceae) (Syrett et al. 2007), and also a number of species listed as pests (EPPO/CABI 1997). Among these, a few taxa are known to vector plant pathogenic bacteria (e.g. Munyaneza 2007, 2014). Such a

broad range of ecological functions ensures that psyllids' movement between countries is of interest. For example, a recent study implemented modelling analyses to assess the risk and predict the spread of the pest species *Russelliana solanicola* Tuthill, 1959, the South American potato psyllid, to several countries where it is not yet present (Syfert et al. 2017). Similarly, the recent establishment of the tomato/potato psyllid *Bactericera cockerelli* (Šulc), vector of *Candidatus* Liberibacter solanacearum and agent of the zebra chips disease, has caused great economic losses in New Zealand (Vereijssen et al. 2018). Therefore, understanding psyllid distributions is fundamental to assess the risk associated with new invasions. In recent years, research on psyllid biodiversity has been conducted in a number of regions and islands of the Austro-Pacific. These include the description of taxa in Australia (Taylor et al. 2016, Taylor 2018), the reclassification of *Pariaconus* Enderlein, 1926 and *Swezeyana* Caldwell, 1940 in the Hawaiian Islands (Percy 2017, 2018) and reports of the arrival of alien species in Australia (Taylor and Kent 2013), New Zealand (Thorpe 2013, Martoni et al. 2016, Martoni et al. 2018) and French Polynesia (Claridge et al. 2014). However, the psyllid fauna of most other Pacific Islands has not been updated for many years (Ouvrard 2018).

The first report on the psyllid fauna of the Cook Islands appears in Hodkinson's checklist of the Austro-Oriental and Pacific area that listed three species: *Mesohomotoma hibisci* (Froggatt, 1901); *Leptynoptera sulfurea* Crawford, 1919; and *Trioza vitiensis* Kirkaldy, 1907 (Hodkinson 1983). An additional species, *Heteropsylla cubana* Crawford, 1914, was reported a few years later (Muddiman et al. 1992). The most recent addition was a *Trioza* species similar to *T. zimmermani* Tuthill, 1942, identified by P. Dale and recorded in the online Cook Island Biodiversity and Natural Heritage database (McCormack 2007).

The geographical location of the Cook Islands puts them in a central position between French Polynesia and other countries such as Samoa, Tonga, Fiji, and New Zealand. This makes this small archipelago important for evaluating biogeographic hypotheses and testing theories of biological dispersal within the Pacific. Additionally, due to the high movement of people and produce between the Cook Islands, New Zealand and Australia, understanding the biodiversity of the Cook Islands allows evaluation of potential biosecurity risks for New Zealand or Australian agriculture.

For these reasons, recent field collections from the Cook Islands presented in this work have contributed to updating our knowledge of the psyllid biodiversity of the Islands, with the discovery of two additional taxa: *Syntomoza tahuata* (Klyver, 1932), and *Trioza alifumosa* Klyver, 1932, both originally described from French Polynesia (Marquesas) (Klyver 1932).

Materials and methods

Specimens were collected by SDJB on the island of Rarotonga, Cook Islands, in March and April 2017. Collections were made by beating host foliage over a beating tray. Insects were stored in propylene glycol until morphological identification was per-

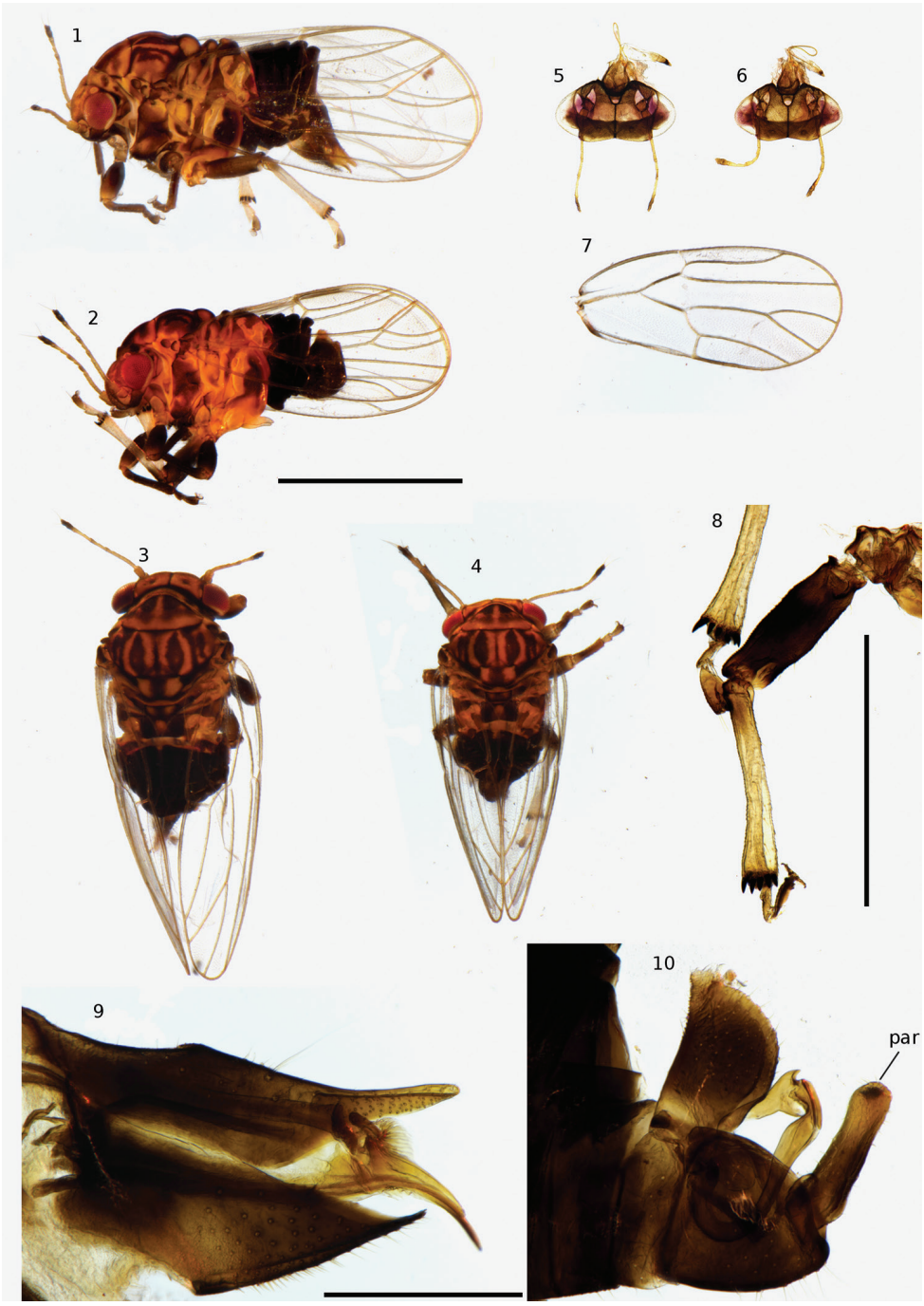
formed. Photographs were taken using a Nikon DS-Ri2 camera connected to a Nikon SMZ25 microscope. Pictures presented in the plates are the result of stacking photographs using the software Nikon NIS-Elements D v4.5 resulting in a single image with an extended depth of field. Plates were prepared using GIMP version 2.8.14. For closer examination, two specimens of each species (male and female) were mounted on microscope slides following the protocol of Taylor et al. (2016). Morphological terms follow Taylor et al. (2011) and wing venation follows Hodkinson and White (1979) and Hollis (1984). Psyllid specimens from the recent field collection have been deposited in the New Zealand Arthropod Collection (**NZAC**, Manaaki Whenua Landcare Research, Tamaki, Auckland), and the Lincoln University Entomology Collection (**LUNZ**, Canterbury). Plants were identified by SDJB using Sykes (2016). Specimens of the host plants collected at the same time as insect specimens were deposited in the Allan Herbarium (Landcare Research, Lincoln, New Zealand), with catalogue numbers CHR644589 (*Homalium acuminatum*), CHR644590 (*Weinmannia samoensis*), and CHR644584 and CHR644585 (*Metrosideros collina*). Paratype specimens of *T. alifumosa* and *T. alipellucida* Klyver, 1932 were examined in the Bernice Pauahi Bishop Museum (**BPBM**, Honolulu, Hawaii).

Identification of the newly reported species

***Syntomoza tahuata* (Klyver, 1932)**
Figures 1–10, 23

Material examined. 4 females, 10 males. This species was collected on two separate occasions on Rarotonga: on 15 April 2017 on Te Manga at elevations between 540 m and 560 m, collected from two host plants: from *Weinmannia samoensis* A.Gray (Cunioniaceae) (five specimens) and from *Freycinetia wilderi* Martelli ex Wilder (Pandanaceae, plant specimens not collected) (two specimens), and on 17 April 2017 in the Avana Valley around 70 m elevation, from the foliage of a fallen *Homalium acuminatum* Cheeseman (Salicaceae) (seven specimens collected, with several more observed). Three additional specimens collected around Avatiu in November 1979 by NLH Krauss were located in the Bishop Museum.

Measurements. Measurements are in mm (n = 3 ♂, 2 ♀ unless reported differently in brackets). Length of body (vertex to terminalia) ♂ 0.98–1.30 (n = 2), ♀ 1.17–1.53; length of body (vertex to apex of folded wings) ♂ 1.72–1.88 (n = 2), ♀ 2.21–2.22; width of head (HW) ♂ 0.53–0.60 (n = 2), ♀ 0.63–0.65; length of genal processes (GCL) ♂ 0.10 (n=1), ♀ 0.12; length of vertex (VL) ♂ 0.12–0.18 (n = 2), ♀ 0.18–0.19; width of vertex (VW) ♂ 0.30–0.35 (n = 2), ♀ 0.34–0.38; length of antenna (AL) ♂ 0.40–0.49 (n = 2), ♀ 0.44–0.57; length of fore wing ♂ 1.40–1.49, ♀ 1.71–1.77; width of fore wing ♂ 0.63–0.68, ♀ 0.75–0.85; length of vein Rs ♂ 0.82–0.87, ♀ 1.02–1.04; length of vein M (M) ♂ 0.44–0.46, ♀ 0.52–0.53; length of vein M1+2 (M1) ♂ 0.36–0.40, ♀ 0.48–0.51; marginal width of cell m1 ♂ 0.18–0.20, ♀ 0.26–0.27; marginal



Figures 1–10. *Syntomoza tahuata*. **1** lateral habitus of female **2** lateral habitus of male **3** dorsal habitus of female **4** dorsal habitus of male **5** head of female, dorsal view **6** head of male, dorsal view **7** wing of male **8** mesotibia of male **9** terminalia of female, lateral view of left side **10** terminalia of male, lateral view of left side. Abbreviation: par = paramere. Scale bars: 1 mm (**1–7**); 0.5 mm (**8**); 0.25 mm (**9, 10**).

width of cell cu1 ♂ 0.50–0.54, ♀ 0.62–0.63; length of vein Cu1b ♂ 0.11–0.14, ♀ 0.13–0.16; length (height) of proctiger (PL) ♂ 0.21–0.24 (n = 2); length of paramere ♂ 0.17–0.19 (n = 2); length of proximal aedeagal segment ♂ 0.19 (n = 1); length of distal aedeagal segment ♂ 0.09 (n = 1); length of proctiger (PL) ♀ 0.44–0.52; length of circum-anal ring (CL) ♀ 0.16–0.20; length of subgenital plate (SL) ♀ 0.35–0.46.

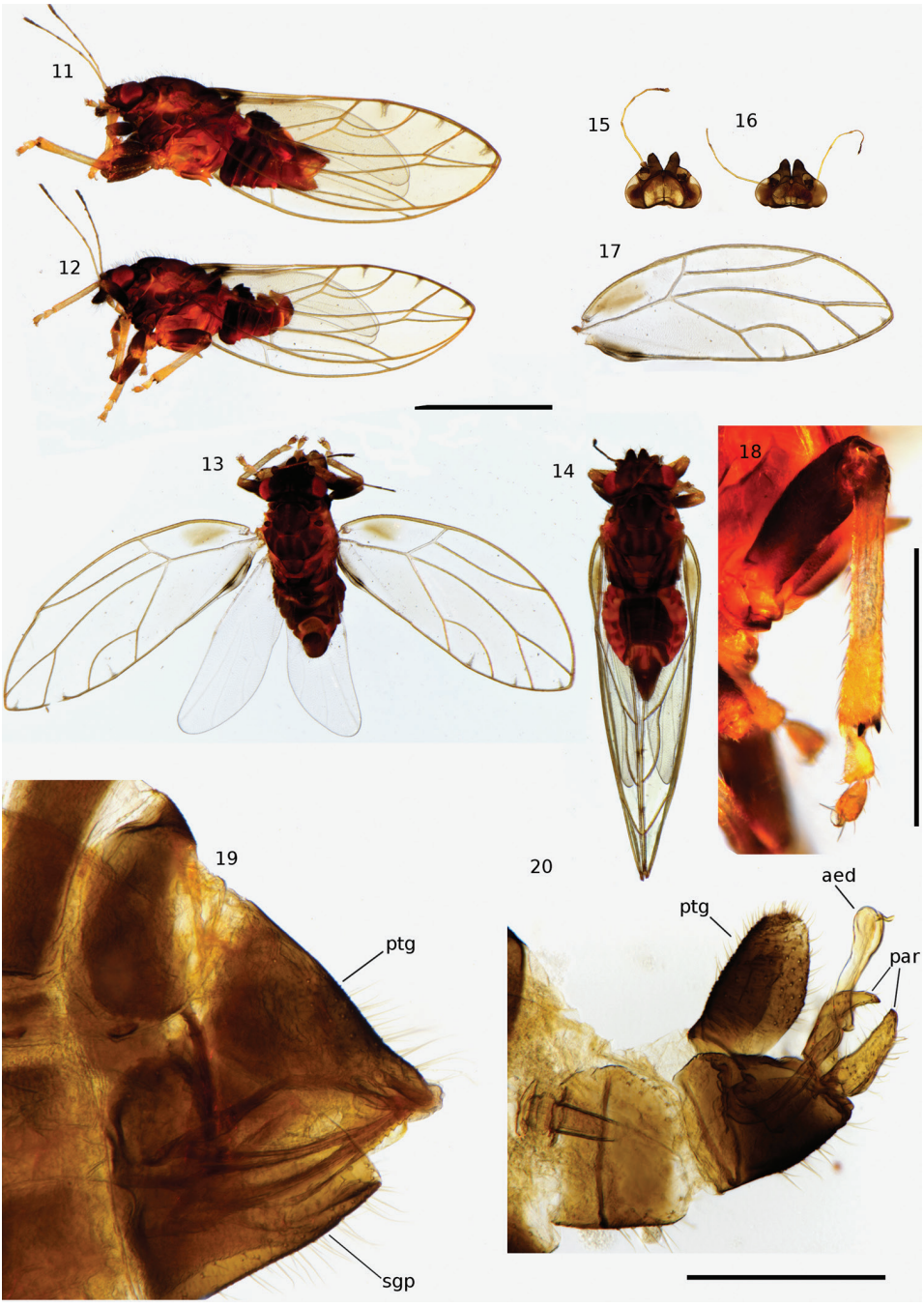
Description. The stout body shape, and the distinct dorsal patterning of orange stripes on a black background makes this psyllid readily recognised within the Cook Island fauna. This psyllid was identified using the original description (Klyver 1932) and the subsequent reclassification that attributed this species to the genus *Syntomoza* Enderlein, 1921 (Burckhardt and Mifsud 2003). Other features that allow it to be placed in *S. tahuata* include the greatly modified tergites and the secondary groups of small teeth at the apex of the posterior tibiae in both sexes (Figure 8), which are characteristic of this genus, together with the strongly inclined head (at about 90° to the longitudinal body axis; Figures 1, 2). Furthermore, the female terminalia which are pronouncedly down-turned at about 45° (Figure 1), the shape of the male parameres (Figure 10), and wing shape and venation (Figure 7) allowed identification of this species as per the description and figures presented by Klyver (1932).

***Trioza alifumosa* Klyver, 1932**
Figures 11–20, 26

Material examined. 11 females, 8 males. A single population of this species was collected on Rarotonga, on the summit of Raemaru at an elevation of 380 m. On 16 March 2017 all 19 individuals were collected from a single plant of *Metrosideros collina* (J.R.Forst. and G.Forst.) A.Gray.

Measurements. Measurements are in mm (n = 2 ♂, 3 ♀ unless reported differently in brackets). Length of body (vertex to terminalia) ♂ 1.30–1.45, ♀ 1.60–1.78; length of body (vertex to apex of folded wings) ♂ 2.57–2.81, ♀ 2.86–3.10; width of head (HW) ♂ 0.50–0.53, ♀ 0.52–0.57 (n = 2); length of genal processes (GCL) ♂ 0.09–0.14 ♀ 0.10–0.13 (n = 2); length of vertex (VL) ♂ 0.21, ♀ 0.20–0.25 (n = 2); width of vertex (VW) ♂ 0.31–0.32, ♀ 0.32–0.33 (n = 2); length of antenna (AL) ♂ 0.78–0.79, ♀ 0.81–0.85 (n = 2); length of fore wing ♂ 2.27–2.28, ♀ 2.38–2.57 (n = 2); width of fore wing ♂ 0.83–0.86, ♀ 0.85–0.96 (n = 2); length of vein Rs ♂ 0.91–0.99, ♀ 1.00–1.08 (n = 2); length of vein M (M) ♂ 1.11–1.12, ♀ 1.15–1.24 (n = 2); length of vein M1+2 (M1) ♂ 0.44–0.48, ♀ 0.54–0.56 (n = 2); marginal width of cell m1 ♂ 0.28–0.32, ♀ 0.38 (n = 2); marginal width of cell cu1 ♂ 0.40–0.42, ♀ 0.42–0.44 (n = 2); length of vein Cu1b ♂ 0.23–0.25, ♀ 0.21–0.25 (n = 2); length (height) of proctiger (PL) ♂ 0.15–0.20; length of paramere ♂ 0.11–0.13; length of proximal aedeagal segment ♂ 0.17 (n = 1); length of distal aedeagal segment ♂ 0.16 (n = 1); length of proctiger (PL) ♀ 0.30–0.51; length of circum-anal ring (CL) ♀ 0.10–0.13; length of subgenital plate (SL) ♀ 0.29–0.34.

Description. This psyllid can be identified by the following combination of characters: habitus as in Figures 11–14, with a dark brown colour, fore wings with an infuscate



Figures 11–20. *Trioza alifumosa*. **11** lateral habitus of female **12** lateral habitus of male **13** dorsal habitus of male **14** dorsal habitus of female **15** head of female, dorsal view **16** head of male, dorsal view **17** wing of male **18** mesotibia of male **19** terminalia of female, lateral view of left side **20** terminalia of male, lateral view of left side. Abbreviations: aed = aedeagus, par = paramere, ptg = proctiger, sgp = subgenital plate. Scale bars: 1 mm (**11–17**); 0.5 mm (**18**); 0.25 mm (**19, 20**).

spot in the apical costal cell as in Figures 13, 17, female proctiger short and bearing setae on the subgenital plate (Figure 19); male parameres elongate, slightly back-turned apically and bearing setae (Figure 20). Both this species and *T. alipellucida* Klyver, 1932, were described from material collected on *Metrosideros collina*. The evenly dark colouration of the dorsal surface and head, the presence of an infuscate spot in the apical costal cell (c+sc), the rounded but elongated shape of the aedeagus, the elongated shape of the male proctiger and the slightly back-turned parameres lead us to place it in *T. alifumosa*. *Trioza alipellucida* differs from *T. alifumosa* by most specimens having a wide lighter brown stripe on the pronotum, not having an infuscate spot at the base of the forewing, and for a shorter male proctiger associated with parameres that are not as back-turned. The morphological distinction between *T. alifumosa* and *T. zimmermani* appears more immediate, with the latter presenting light stripes dorsally on a dark brown abdomen and having hyaline wings without any dark spot in the cell c+sc (Tuthill 1942).

Checklist of the Cook Islands psyllids

The following checklist includes all species known to be present in the Cook Islands. Information on their taxonomy is reported together with their worldwide distribution and host plant associations. For species of socio-economic interest, such as pests, basic information on their biology is summarised.

Family Carsidaridae

***Mesohomotoma hibisci* (Froggatt, 1901)**
Figures 21, 28

Tyora hibisci Froggatt, 1901: 287.
Udamostigma hibisci (Froggatt); Enderlein 1910: 138.
Mesohomotoma hibisci (Froggatt); Crawford 1925: 32.

Distribution. Reported on the Cook Islands by Hodkinson (1983). Known from Rarotonga and Mangaia. Other locations include: Australia (Hollis 2004), Africa [Cameroon, Democratic Republic of the Congo, Kenya, Madagascar, Seychelles, South Africa, Tanzania, Uganda and Zimbabwe (Yana et al. 2015; Burckhardt and Van Harten 2006)], Asia [Chagos archipelago, China, India, Japan, Malaya, Malaysia, Mauritius, Philippines, Ryukyu Islands, Singapore, Yemen (Hodkinson 1983, Hodkinson 1986, Burckhardt and Van Harten 2006, Percy 2017)], Pacific Islands [Bismarck Archipelago, Caroline Islands, Fiji, French Polynesia (Australs, Societies, Marquesas), Gilbert Islands, New Caledonia, Palau, Tonga, Solomon Islands, Vanuatu (Hodkinson 1983)].

Host plant. *Hibiscus* species, especially *H. tiliaceus* L. (Malvaceae).

Common name. Hibiscus (woolly) psyllid (David Hockings 2013).

Figure 21. *Mesohomotoma hibisci* nymphs and adult on *Hibiscus tiliaceus* on Rarotonga, showing white waxy exudates formed by the nymphs.

Remarks. the genus *Mesohomotoma* Kuwayama was reviewed by Hollis (1987). The species included in the genus have a lot of variation between populations, and subtle differences between species. Although Hollis (1987) suspected all nominal taxa may represent a single species, he did not formally synonymise them, recommending that further research into their biology and hostplants be undertaken to further investigate species boundaries in the genus. This species breeds in the tips of *Hibiscus tiliaceus* branches. The nymphs produce filamentous exudates, which forms a woolly coating on the leaves and stem of the plant (Figure 21). *Mesohomotoma hibisci* is considered a pest (David Hockings 2013).

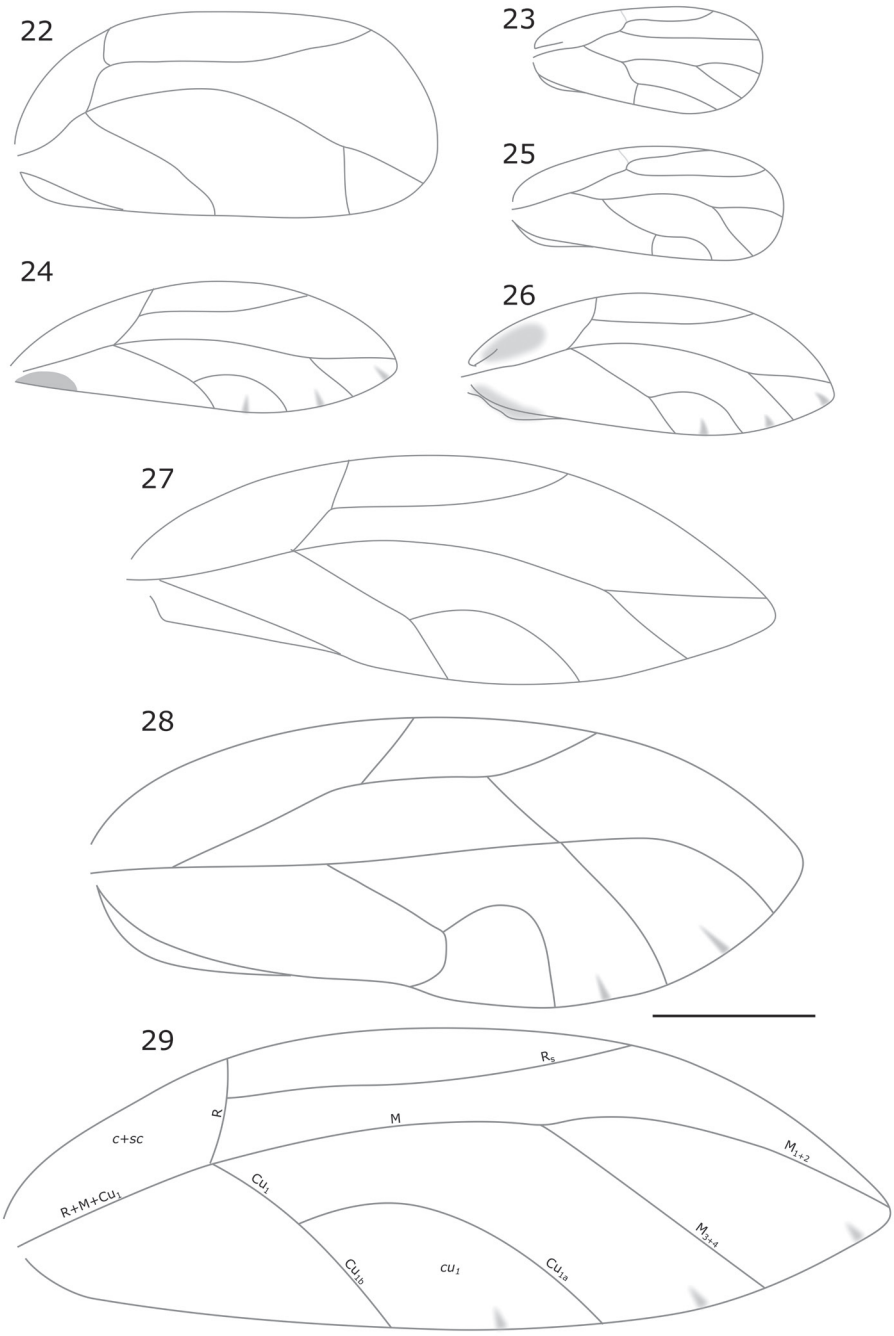
Family Liviidae

Syntomoza tahuata (Klyver, 1932)

Figures 1–10, 23

Anomoterga tahuata Klyver, 1932: 94.
Syntomoza tahuata (Klyver); Burckhardt and Mifsud 2003: 17.

Distribution. Reported on the Cook Islands in the present study. Known only from Rarotonga. Other locations include: French Polynesia (Marquesas) (Klyver 1932).



Figures 22–29. Wings, schematic. **22** *Leptynoptera sulfurea* (after Crawford 1919) **23** *Syntomoza tahuata* (from slide-mounted Rarotonga specimen) **24** *Trioza* cf. *zimmermani* (from photograph of Rarotonga specimen by G. McCormack) **25** *Heteropsylla cubana* (after Tuthill 1959) **26** *Trioza alifumosa* (from slide-mounted Rarotonga specimen) **27** *Trioza zimmermani* (after Tuthill 1942) **28** *Mesohomotoma hibisci* (after Froggatt 1901) **29** *Trioza vitiensis* (after Klyver 1932). Scale bar: 1 mm.

Host plant. No host plants have been previously proposed (Burckhardt and Mifsud 2003; Ouvrard 2018). In June 2002, however, Percy (pers. comm.) collected a high number of adult specimens (> 30) from *Weinmannia parviflora* in French Polynesia (Marquesas) with no specimens found on surrounding plants.

Family Psyllidae

***Heteropsylla cubana* Crawford, 1914**
Figure 25

Heteropsylla cubana Crawford, 1914.

Distribution. Reported on the Cook Islands by Hodkinson (1983). Known only from Rarotonga. Other locations include: Australia (Muddiman et al. 1992), America [Bahamas, Bermuda, Brazil , Central America, Chile, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, El Salvador, Guatemala, Jamaica, Mexico, Nicaragua, Panama, Peru, Suriname, Trinidad and Tobago, USA (Brown and Hodkinson 1988, Burckhardt and Queiroz 2012, Hodkinson and White 1981, Hodkinson 1988, Hodkinson and Muddiman 1993, Muddiman et al. 1992, Olivares and Burckhardt 2002, Percy et al. 2012)], Africa [Burundi, Cameroon, Kenya, KwaZulu-Natal, Mauritius, Mpumalanga, Reunion, Tanzania, Uganda, Zimbabwe (FAO 1994, Dzokou et al. 2009, Matimati et al. 2009, Muddiman et al. 1992, Olckers 2011)], Asia [Bangladesh, Cambodia, China, Christmas Islands, India, Indonesia, Japan, Malaysia, Mariana Islands, Nepal, Ryukyu Islands, Philippines, Sri Lanka, Taiwan, Thailand, Vietnam (Muddiman et al. 1992, Martin and Lau 2011, Inoue and Miyatake 2001, Geiger and Gutierrez 2000)], Pacific Islands [Fiji, French Polynesia (Australs), Guam, Haiti, Hawaiian Islands, New Caledonia, Niue, Papua New Guinea, Samoa, Solomon Islands, Tonga (Beardsley and Uchida 1990, Claridge et al. 2014, Muddiman et al. 1992, FAO 1994)], Europe [Ireland (Muddiman et al. 1992)].

Host plant. *Leucaena leucocephala* (Lam.) de Wit (Fabaceae).

Common name. Leucaena psyllid (Asadi et al. 2011).

Remarks. *Heterpsylla cubana* is considered an agricultural pest both in the Asia-Pacific area and in Africa (FAO 1994). The biological control agent that has been used most and with better results is the parasitoid *Psyllaephagus yaseeni* Noyes, 1990 (Encyrtidae), but *Curinus coeruleus* Mulsant, 1850 (Coccinellidae) and *Tamarixia leucaenae* Boucek, 1988 (Eulophidae) have been used as well (Geiger and Gutierrez 2000).

Biology. The biology and life cycle of *H. cubana* is reported here with the intent of summarising information (mostly from Showler and Melcher 1995 and CABI 1990) that may be relevant for a better understanding of this pest species. The incubation period for eggs is generally 2–5 days. Immature stages grow from the egg

through five instars to adulthood in 10–20 days. Nymphs feed at first gregariously near the oviposition site and then, more and more solitarily, they colonise and feed on other parts of stems, branches, and petioles of young leaves. Generations are overlapping, and longevity of adults is on average 14.5 days for females and 9.7 days for males. Mating can occur more than once for both males and females (Rauf et al. 1990) and eggs are laid in groups on very young shoots, often covering the whole leaflet. Each female can produce 300–500 eggs throughout a lifetime and can lay as many as 60 eggs in one day. *Heteropsylla cubana* is diurnal, and flight of adults can occur in the morning and afternoon.

Family Triozidae

***Leptynoptera sulfurea* Crawford, 1919**
Figure 22

Leptynoptera sulfurea Crawford, 1919: 147.

Distribution. Reported on the Cook Islands by Hodkinson (1983). Known only from Rarotonga. Other locations include: Australia (Hollis 2004), Asia [China, Chagos Islands, Cocos Islands, India, Indonesia, Japan, Malaysia, Philippines, Ryukyu Islands, Singapore, Sulawesi, Taiwan, Thailand (Martin and Hollis 1992, Hodkinson 1983, 1986, Neville et al. 2015)], Pacific Islands [Caroline Islands, Fiji, French Polynesia (Australs), Guam, Hawaiian Islands, Mariana Islands, New Caledonia, Palau, Papua New Guinea, Tonga (Hodkinson 1983, Martin and Hollis 1992, Percy 2017].

Host plant. *Calophyllum inophyllum* L. (Calophyllaceae).

Remarks. *Leptynoptera sulfurea* forms galls along the leaf margins of *Calophyllum inophyllum* (Neville et al. 2015), a tree of particular significance for Cook Islanders in that the trunks were preferentially used for building canoes (Hiroa 1927).

***Trioza alifumosa* Klyver, 1932**
Figures 11–20, 26

Trioza alifumosa Klyver, 1932: 96.

Distribution. Reported on the Cook Islands in the present study. Known only from Rarotonga. Other locations include: French Polynesia (Marquesas, Fatu Hiva) (Klyver 1932).

Host plant. *Metrosideros collina* (J.R. Forst. & G. Forst.) A. Gray (Myrtaceae).

***Trioza vitiensis* Kirkaldy, 1907**
Figure 29

Trioza vitiensis Kirkaldy, 1907: 103.
Megatrioza vitiensis (Kirkaldy); Crawford 1919: 195.
Phyllopecta vitiensis (Kirkaldy); Klyver 1932: 99.
Trioza vitiensis Kirkaldy, 1907 combinatio revivisco according to Mathur (1975): 348.

Distribution. Reported on the Cook Islands by Hodkinson (1983). Known only from Rarotonga. Other locations include: Asia [China, India, Indonesia, Malaya, Malaysia, Philippines, Singapore, Sri Lanka (Hodkinson 1983, 1986)], Pacific Islands [Caroline Islands, Fiji, French Polynesia (Societies, Marquesas), Samoa (Kirkaldy 1907, Hodkinson 1983)].

Host plant. *Syzygium malaccense* (L.) Merr. & L.M.Perry, 1938 (Myrtaceae).

***Trioza* cf. *zimmermani* Tuthill, 1942**
Figure 24

Distribution. Reported on the Cook Islands by P.J. Dale (McCormack 2007). Known only from Rarotonga.

Host plant. *Metrosideros collina* (J.R. Forst. & G. Forst.) A. Gray (Myrtaceae).

Remarks. no specimens of this psyllid were collected by the authors. Photographs provided by G McCormack were consistent with the morphology of *T. zimmermani*, with the greatest difference shown in the wings (Figures 24, 27), with the Rarotongan specimens being shorter and with a less acute apex (Figure 24), than those from Raivaevae drawn by Tuthill (1942, Figure 27). However, since no specimens could be examined in person, this taxon is reported here based on the identification made by Dale. The distribution of *T. zimmermani* includes French Polynesia (Australs) (Tuthill 1942, Percy 2017).

Key to the Cook Islands psyllids

1 Forewing with vein R+M+Cu1 bi-furcating to form R and M+Cu1 (Figures 23, 25, 28).....**2**
– Forewing with vein R+M+Cu1 tri-furcating to form R, M and Cu1 (Figures 24, 29).....**4**
2 Forewing with veins R and M+Cu1 equally long or M+Cu1 slightly longer than R (Figures 7, 23). Body colour black with orange stripes on the dorsum.....***Syntomoza tahuata* (Klyver, 1932)**
– Forewing with vein R longer than M+Cu1 (Figures 25, 28). Body colour light green.....**3**

3 Forewing with vein Rs very short (♂ 0.91, ♀ 1.14), strongly bent towards margin at apex, with a transverse vein crossing from centre of Rs to the bifurcation between M1+2 and M3+4 (Figure 28) ..... ***Mesohomotoma hibisci* (Froggatt, 1901)**

– Forewing with vein Rs not turning upward and no transverse vein crossing the wing (Figure 25) ..... ***Heteropsylla cubana* Crawford, 1914**

4 Forewing with vein Cu1 not bi-furcating and therefore not forming cell cu1 (Figure 22). Body colour light brown..... ***Leptynoptera sulfurea* Crawford, 1919**

– Cell cu1 present (Figures 24, 29). Body colour darker brown/black..... **5**

5 Forewing with dark spot on cell c+sc (Figures 17, 26). Body colour black with subtle brown patterning..... ***Trioza alifumosa* Klyver, 1932**

– Forewing with no spots (Figures 24, 29). Body colour brown with tan pattern or black with pale stripe on the abdomen..... **6**

6 Male genitalia with parameres pointing forward at apex and proctiger bearing long setae on the apical part facing the parameres. Female genitalia extremely short, approximately ¼ of abdomen. Length of psyllid to tip of folded wings between 5 mm and 6 mm. Body colour brown, with tan patterning..... ***Trioza vitiensis* Kirkaldy, 1907**

– Male parameres pointing backward at apex, proctiger bearing short setae uniformly, female terminalia longer (half of the rest of abdomen). Length of the psyllid to tip of folded wings only 3.5mm. Body colour black with pale stripe at base of abdomen ..... ***Trioza* cf. *zimmermani* Tuthill, 1942**

Discussion

Based on the similarity of the samples analysed with the description and the drawings provided by the literature, the presence of the psyllids *Syntomoza tahuata* and *Trioza alifumosa* is reported on the Cook Islands for the first time. Host plants for these two species in the Cook Islands are hypothesised to be *Weinmannia samoensis* or *Homalium acuminatum* and *Metrosideros collina* respectively, based on collection data. Percy's collection of a large number of individuals of *S. tahuata* from *Weinmannia parviflora* suggests this genus could be a true host plant (Percy, personal communication). However, we consider that *H. acuminatum* should remain under consideration as a possible host. No specimens of *W. samoensis* were seen near the Avana Valley site where *S. tahuata* was collected from *H. acuminatum*, and the elevation of the site is well below the lower elevational limit of *W. samoensis* (Sykes 2016). The number of *S. tahuata* observed during this collecting event was much greater than were captured, and were much more abundant than on the occasions when *S. tahuata* was beaten from *W. samoensis*. A search for immature stages of *S. tahuata* on both *H. acuminatum* and *W. samoensis* should be undertaken to differentiate between these host plant hypotheses or confirm whether *S. tahuata* is a generalist (Burckhardt et al. 2014).

We consider these two species to be indigenous to the Cook Islands, despite their not having been recorded here previously. The Cook Islands are underexplored entomologically, with relatively little collecting having been done in indigenous vegetation in particular. Moreover, these species were found in areas of relatively intact vegetation, with little human modification, which tend to be more resistant to invasive species (Brockerhoff et al. 2010). We hypothesise that further investigation of the psyllid fauna in other islands of Eastern Polynesia will locate these species there also, in areas where *Metrosideros collina* and *Homalium* species may be found. However, this in itself would not provide sufficient evidence to distinguish between hypotheses of recent or distant arrival in the Cook Islands. In the absence of past collections, analysis of rapidly evolving DNA regions would be necessary to provide further data to infer the arrival of these species in the Cook Islands.

The psyllid fauna of the Cook Islands now includes seven psyllid taxa from five genera and four families. The addition of *S. tahuata* is not only the first report for the genus in the Cook Islands, but also for the family Liviidae.

Compared with the psyllid fauna of other nearby archipelagos, the Cook Islands appear to have a very similar psyllid biodiversity. In fact, the single taxon present in Niue (*H. cubana*) and three of the four taxa present in Tonga (*H. cubana*, *M. hibisci*, and *L. sulfurea*) are also present in the Cook Islands (Ouvrard 2018). Similarly, the psyllid fauna of French Polynesia lists eight species, four of which are in common with the Cook Islands: *M. hibisci*, *T. zimmermani*, *T. alifumosa*, and *S. tahuata* (Ouvrard 2018). On the other hand, the Cook Islands do not share any of the three taxa present in American Samoa (Ouvrard 2018). A recent review indicates that the biota of the Society islands in many cases show close sister-taxon relationships with the Cook, Austral, and Marquesas Islands (Hembry and Balukjian 2016). They also found that many taxa showed patterns of multiple colonisation of the islands, indicating high species turnover in the Eastern Polynesian region (Hembry and Balukjian 2016). We believe that the records of the two psyllid species reported here for the first time from the Cook Islands provides further evidence of the recognition of a distinctive Eastern Polynesian fauna.

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Twenty six new species of *Leioproctus* (*Colletellus*): Australian Neopasiphaeinae, all but one with two submarginal cells (Hymenoptera, Colletidae, *Leioproctus*)

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Abstract

Twenty six new species of Australian *Leioproctus* (subgenus *Colletellus*) (Hymenoptera, Colletidae) are described: *aberrans* Leijs, **sp. n.**, *alatus* Leijs, **sp. n.**, *albipilosus* Leijs, **sp. n.**, *albiscopis* Leijs, **sp. n.**, *aliceafontanus* Leijs, **sp. n.**, *altispinosus* Leijs, **sp. n.**, *aratus* Leijs, **sp. n.**, *auricorneus* Leijs, **sp. n.**, *bidentatus* Leijs, **sp. n.**, *centralis* Leijs, **sp. n.**, *ciliatus* Leijs, **sp. n.**, *claviger* Leijs, **sp. n.**, *consobrinus* Leijs, **sp. n.**, *constrictus* Leijs, **sp. n.**, *laciniosus* Leijs, **sp. n.**, *longivultu* Leijs, **sp. n.**, *lucidus* Leijs, **sp. n.**, *nitidifuscus* Leijs, **sp. n.**, *pectinatus* Leijs, **sp. n.**, *pilotapilus* Leijs, **sp. n.**, *quadripinnatus* Leijs, **sp. n.**, *rubicundus* Leijs, **sp. n.**, *rubricinctus* Leijs, **sp. n.**, *similis* Leijs, **sp. n.**, *splendens* Leijs, **sp. n.**, *submetallicus* Leijs, **sp. n.** High resolution images of diagnostic characters for all type specimens are included. Identification keys are provided.

Keywords

Bush Blitz surveys, colletid bees, identification keys, *Leioproctus* (*Colletellus*)

Introduction

The monotypic subgenus *Leioproctus* (*Colletellus*) was established by Michener (1965) for *L. velutinellus,* an unusual species of Australian neopasiphaeine bee with two submarginal cells and ciliate, rather than pectinate, inner hind tibial spurs. Formerly *Leioproctus* was classified under the Colletinae (Michener 2007), but recent phylogenetic analyses of the world's Colletidae indicated its position under Neopasiphaeinae (Almeida et al. 2011). Now, more than 50 years later, examination of numerous specimens collected by T.F. Houston (WA-Museum) and others, as well as specimens collected on a number of Bush Blitz surveys in remote locations of Australia indicates that *L.* (*Colletellus*), is a rather speciose group of bees. The latter surveys are the result of a partnership between the Australian Government, BHP Billiton and Earthwatch Australia to document fauna and flora from selected national reserves. These surveys regularly result in the discovery of new invertebrate species (e.g., true bugs: Symonds and Cassis 2014; spiders: Baehr et al. 2013; bees: Hogendoorn et al. 2015, Leijs and Hogendoorn 2016; review of new described species: Taylor et al. 2017a, b).

Below, we describe 26 new species. Morphologically, the bees treated here key out to *L.* (*Colletellus*) when using Michener's (2007) identification key to the subgenera of *Leioproctus* of the Australian Region, with the exception of a single character: not all females have a ciliate hind tibial spur. Removing the latter character, the distinctive characters for the subgenus are a combination of two submarginal cells, convex clypeus and supra clypeal area, a large, parallel-sided stigma and the jugal lobe of the hind wing long, i.e. extending well below the level of cu-v.

Materials and methods

For descriptions of the new species the terminology used by Michener (2007) was followed. A Leica stereomicroscope with auto-montage imaging stacking software was used to obtain high-resolution images of all species. A compound microscope (Nikon, Eclipse 50i) and Zerene Stacker was used to image male genitalia and metasomal sterna seven and eight. Head measurements were taken from high-resolution frontal head images using the Leica auto-montage software. All measurements were converted relative to the head width, which was set to 50 units (following Houston 1990).

Abbreviations for these relative measurements are as follows:

AOD antennocular distance;
ASD antennal socket diameter;
HL head length;
HW head width;
IAD interantennal distance;
LFW lower face width, measured between lowest eye margins;
OOD ocellocular distance;
OAD ocellantennal distance;
UFW upper face width, measured between upper eye margins;
OW width of ocellar cluster.

Abbreviations for wing measurements are:

MSR ratio of stigma length and marginal cell length measured on wing costa;
FSR ratio of the lengths of the first submarginal cell and second submarginal cell;
SFR ratio of the lengths of the stigma and first submarginal cell.

Other abbreviations used are:

T1, T2, etc. first, second metasomal terga, etc.;
S1, S2, etc. first, second metasomal sterna, etc.;
F1, F2, etc. first, second flagellar segment, etc;
BTP basitibial plate.

The terminology for integument sculpture, grades of pit and pubescence density and pit size follows Houston (1975; Fig. 1). Integument sculpture was observed using 40× magnification and YK-B144T LED ring elimination.

Some of the specimens treated here were also submitted to BOLD (Barcode of Life Database) for DNA barcoding using the cytochrome c oxidase subunit 1 gene. Specimen details, including DNA sequence, collecting dates and locality information can be accessed in BOLD under the project Australian Bee Survey, e.g., http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS145-12. AUSBS-numbers are presented under material examined.

Repositories:

AM Australian Museum, Sydney
ANIC Australian National Insect Collection, Canberra
SAMA South Australian Museum, Adelaide
QM Queensland Museum, Brisbane
WAM Western Australian Museum, Perth

Results and discussion

Twenty-six new species of *Leioproctus* are described. All specimens of these species key out to subgenus *Colletellus* when using Michener's (2007: 148) identification key to the subgenera of *Leioproctus* of the Australian region. The type species of *L.* (*Colletellus*)*, L. velutinellus* Michener, 1965 was unique amongst *Leioproctus* species due to its possession of a combination of two, rather than three, submarginal cells, convex clypeal and supraclypeal area, large parallel-sided stigma, long jugal lobe of the hind wing and ciliate rather than pectinate inner hind tibial spurs and long and pointed basitibial plates in females. The 26 additional species described here all conform to these characters with the exception of the hind tibial spurs in females and the shape of the basitibial plates. While 10 of the newly described species have ciliate spurs, 9 have pectinate spurs, and

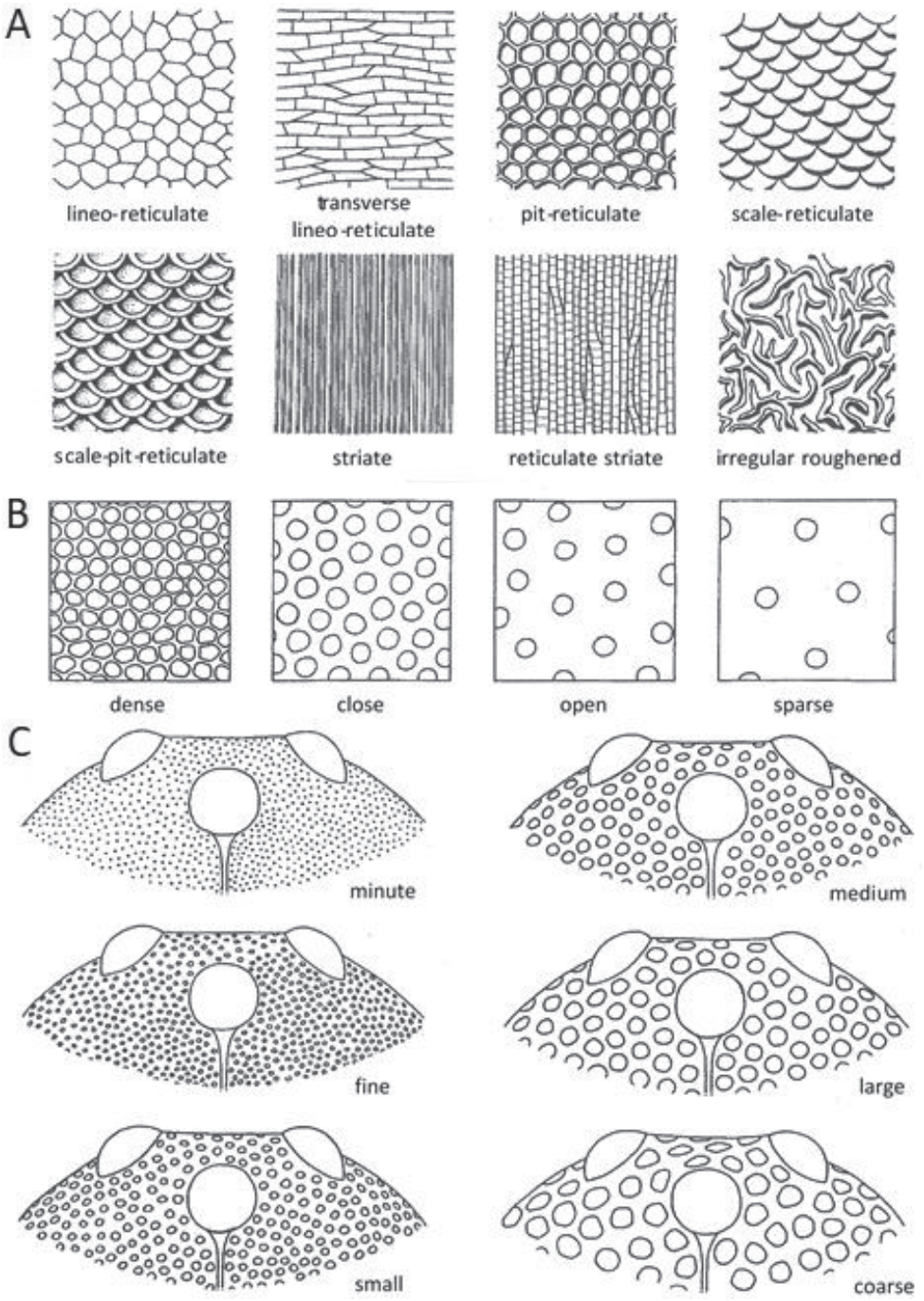


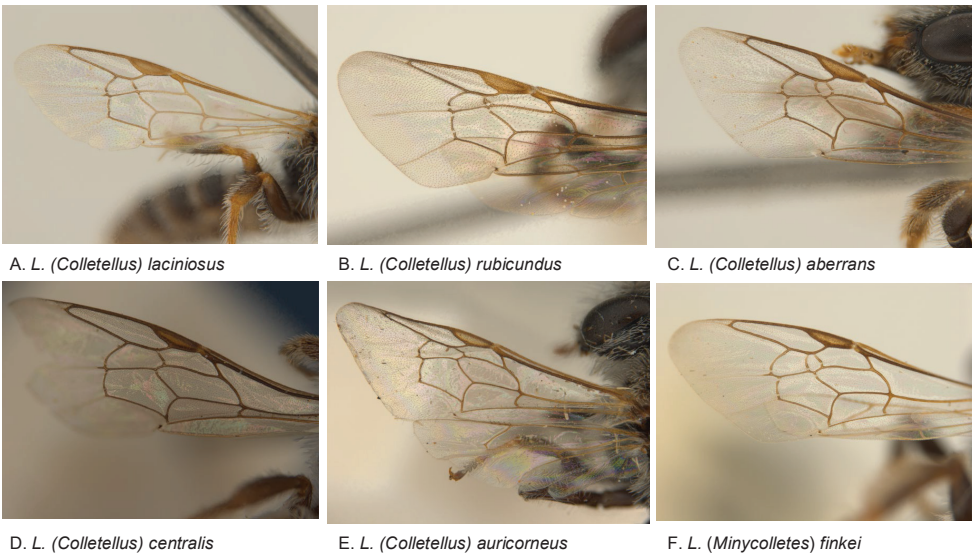
Figure 1. A Various kinds of integument sculpture **B** Grades of pit density **C** Grades of pit size. Reproduced from Houston (1975), with permission from CSIRO Publishing.

16 of the additional species have short and rounded basitibial plates. Morphological characters as well as molecular data indicate that these species are almost certainly not a monophyletic group, but multivariate analyses of a large number of body size measurements as well as characters with discrete states did not result in clear clusters of species.

Although it may be possible to separate species groups based on wing venation, we hesitate to do so without the inclusion of independent molecular data for the majority of the species. Until now fresh tissue is only available from four of the *L.* (*Colletellus*) species, mainly from specimens collected at Bush Blitz surveys, and these have been DNA barcoded. Neighbour joining analyses using PAUP* (Swofford 2001) based on the DNA sequence data available from BOLD that include 22 other Australian *Leioproctus* species showed two independent groups of *L.* (*Colletellus*) species amongst other *Leioproctus*. Although this analysis is preliminary and only based on four *L.* (*Colletellus*) species it supports the idea that *L.* (*Colletellus*) as it stands now is paraphyletic. One of the groups, consisting of three South Australian species (*L. aberrans*, *L. laciniosus* and *L. rubicundus*) have pectinate inner hind tibial spurs in females and have a wing venation that differs from all other species described here. If corroborated, this would also indicate that a reduction of the number of submarginal cells has happened multiple times independently within *Leioproctus*.

Wing vein reduction

Wing vein reduction is a common phenomenon with reduction in body size in Hymenoptera (Danforth 1989). In *L.* (*Colletellus*) this seems to have occurred in two different ways. In the majority of the *Leioproctus* species with three submarginal cells, the first recurrent vein is distal to the first submarginal cross vein, as is also the case for most *L.* (*Colletellus*) species. It therefore seems that the majority of the *L.* (*Colletellus*) species lost the second submarginal cross vein (e.g., *L. centralis*: Fig. 2D). This is also demonstrated in species where the second submarginal cross vein is rudimentary (e.g., *L. auricorneus*: Fig. 2E). However, in the South Australian species *L. rubicundus* and *L. laciniosus* the first recurrent vein is basal to or meeting the submarginal cross vein (Fig. 2A, B), suggesting that in these species the first submarginal cross vein was lost. Regaining lost veins may be possible when considering the venation of *L. aberrans* (Fig. 2C), a species that has three submarginal cells and which is phylogenetically very close to *L. rubicundus* and *L. laciniosus*, uncorrected pairwise sequence divergence 6.0–8.3% (sequences available in BOLD). The same explanations are possible for other *Leioproctus* subgenera with two submarginal cells. In *L.* (*Andrenopsis*) and *L.* (*Euryglossidia*) the position of the first recurrent vein is distal to the first submarginal cross vein and it is therefore likely that these taxa lost the second submarginal cross vein, while *L.* (*Baeocolletes*) and *L.* (*Filiglosssa*) have possibly lost the first submarginal cross vein, because the position of the recurrent vein is basal or meeting the submarginal cross vein. Examination of Almeida's Colletidae phylogeny suggest independent losses of submarginal cross veins for each of these above mentioned *Leiproctus* subgenera (Almeida et al. 2011).



A. *L. (Colletellus) laciniosus* B. *L. (Colletellus) rubicundus* C. *L. (Colletellus) aberrans*

D. *L. (Colletellus) centralis* E. *L. (Colletellus) auricorneus* F. *L.* (*Minycolletes*) *finkei*

Figure 2. Variation in wing venation.

Distribution and phenology

Leioproctus (*Colletellus*) are widespread in arid and semi-arid environments of Western Australia, Northern Territory and South Australia west of approximately 138 degrees longitude (Fig. 3). The majority of the specimens were collected during the months August, September and October (Table 1), with a significant negative correlation between latitude and collection date ($r^2 = 0.4044$; $p < 0.001$), Fig. 4), indicating a response in activity to temperature. The two outliers represent species *L. albipilosus* collected north of Broome in April, WA and a single male of *L. claviger* collected at Dawesville, WA in May. These records are at odds with most other records of these species, which show collecting dates between the end of July and late October.

Flower visitation

Leioproctus (*Colletellus*) were collected on 26 genera of plants belonging to 17 families (178 records). Eighty-five percent of the records involve only five plant families: Portulacaceae (24%), Proteaceae (22%), Stylidiaceae (17%), Asteraceae (13%) and Myrtaceae (8%). The Proteaceae and Myrtaceae species represent small shrubs, however the remaining 70 % of the records were from herbaceous plants, which seem to be preferred by *L.* (*Colletellus*) species. Five *L.* (*Colletellus*) species were collected on *Calandrinia* (Montiaceae).

Those species that have a multitude of flower records visited a multitude of plant families and genera, indicating that they are generalist flower visitors. However, lecty is often classified according to the number of plant genera and families from which

Table 1. Phenology data of *L.* (*Colletellus*) in approximately 15-day periods per month.

Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
0	0	0	0	0	0	0	1	1	0	0	0	1	23	44	46	26	25	51	51	1	3	0	0

Figure 3. Distribution data of all *Leioproctus* (*Colletellus*) species combined.

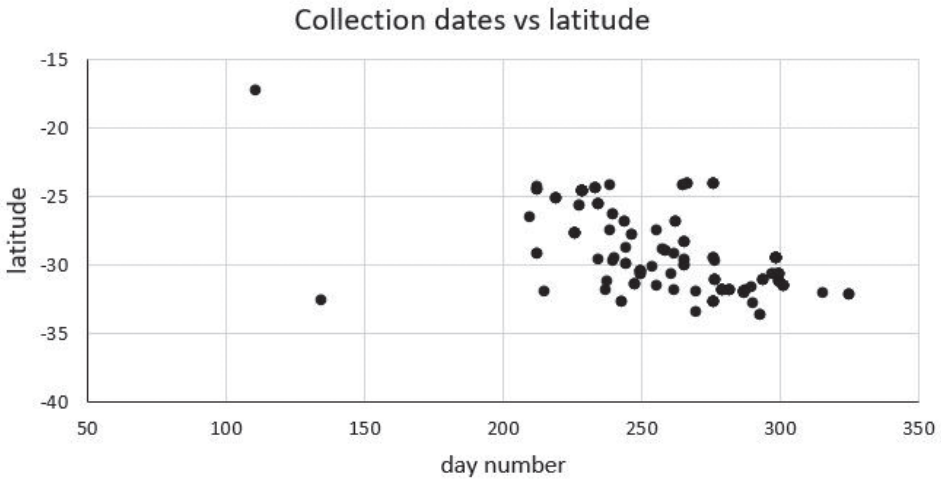


Figure 4. *Leioproctus* (*Colletellus*) collection dates plotted against the latitude of the collection sites.

pollen is collected (Cane and Sipes 2006) – information that is usually not recorded on the specimen labels. Therefore, we conclude that, currently, there is no evidence that *L.* (*Colletellus*) species are oligolectic.

Systematics

Revised identification key to the subgenera of *Leioproctus* for species with two submarginal cells (modified from Michener 2007)

N.B. Specimens of *L. aberrans* have three submarginal cells. While this species keys out to *Leioproctus* s. str. when using Maynard's (2013) key to the subgenera of *Leioproctus* with three submarginal cells, it does not meet the other diagnostic characters for *Leioproctus* s. str., because the female facial fovea is absent, the antennal scape does not reach the median ocellus, apical hair bands are present on T2–4, and the male flagellum is short. Hence, the species is included here.

1 Jugal lobe of hind wing extending well beyond level of cu-v.....***L.* (*Colletellus*)**
– Jugal lobe of hind wing short, not attaining level of cu-v **2**
– Jugal lobe of hind wing meeting level of cu-v. **4**
2 First recurrent vein basal to first submarginal cross vein (fig. 39–5h); clypeus and supraclypeal area usually flat, depressed, shining, largely impunctate; hind tibial spurs robust, curved apically, outer one nearly as coarsely toothed as inner .....***L.* (*Baeocolletes*)**
– First recurrent vein distal to or meeting first submarginal cross vein; clypeus and supraclypeal area convex, the latter elevated above level of antennal sockets; hind tibial spurs not strongly curved apically, pectinate, outer one not coarsely toothed.....**3**
3 Galea with several very long apical hairs and labial palpus filamentose, about as long as face .....***L.* (*Filiglossa*)**
– Mouthparts not modified ..... ***L.* (*Euryglossidia*)**
4 Female: facial fovea broad, only slightly depressed. Male: S5 without apparent apical fringe, clypeus yellow ..... ***L.* (*Andrenopsis*)**
– Female: facial fovea absent. Male: S5 with strong apical fringe, clypeus dark. Specimens of this species have been found with three submarginal cells..... .....***L.* (*Minycolletes*) *abnormis***

Leioproctus Subgenus *Colletellus* Michener, 1965

Leioproctus (*Colletellus*) Michener, 1965: 70.

Type species. *Andrenopsis velutinus* Cockerell, 1929 (not *Paracolletes velutinus* Cockerell, 1929, homonym in *Leioproctus*) = *Leioproctus velutinellus* Michener, 1965, by original designation.

Diagnosis. Two submarginal cells. Jugal lobe of hind wing extending well beyond level of cu-v. Antennal scape short, not reaching median ocellus. Facial fovea absent.

Description. The original description of *L.* (*Colletellus*) by Michener (1965), based on the type species *L. velutinellus* is no longer accurate with the addition of numerous species to this subgenus. Body length of 5–6.7 mm; eyes converging below; clypeus not protuberant; facial fovea absent; scape short, not approaching level of anterior ocellus, antenna as a whole short, median segments of flagellum much broader than long, with the exception of *L. aratus* which has an elongated flagellum with median segments longer than wide; two submarginal cells, however some species show incomplete or complete additional submarginal cross veins; stigma large, not parallel sided, more than half of length of costal edge of marginal cell; jugal lobe exceeding cu-v; metanotum not tuberculate; propodeum in profile with subhorizontal surface, curving onto vertical surface without sharp differentiation; inner hind tibial spur ciliate or pectinate; basitibial plate elongated and pointy or short and rounded; scopa plumose; claws cleft; metasoma in most species without distinct hair bands, but occasionally faint apical hair bands laterally, with the exception of *L. aberrans* and *L. laciniosus* which have distinct apical hair bands on T2–4; post gradular areas often depressed, especially in males, with orange-brown integumental colouring; large variation in the shape of male S7, especially with regard to the shape , the number of lateral lobes and the placement of setae.

The species in this subgenus are not difficult to identify because there are clear differences among species in integumental structure, especially on the clypeus, frons, scutum, metapostnotum and metasoma, as well as remarkable diversity of shapes of the male S7.

Identification keys

The following keys are based on our current knowledge of the species. Considering the low numbers of specimens and localities of several species, as well as the fact that for a number of species only a single sex is known, one should be aware, when using the keys, of the high likelihood of encountering undescribed sexes of species or even new species not treated in this paper.

Identification key to the females of *Leioproctus* (*Colletellus*) (20)

The number in brackets shows the number of species relevant to the character choices in each couplet.

1 Basitibial plate pointed (Fig. 31F), (11 spp.) **2**
– Basitibial plate rounded (9 spp.) **12**
2 Inner hind tibial spur pectinate, teeth longer than spur diameter (2 spp.) **3**
– Inner hind tibial spur ciliate, teeth shorter than spur diameter (9 spp.) **4**

3 Basitibial plate short, circa 1/5 of the tibial length; propodeum smooth, shiny, almost wholly vertical; T1 smooth, openly punctate, T2–4 closely punctate with underlying transverse reticulation.....***albipilosus* sp. n.**
– Basitibial plate long, about 1/3 of the tibial length; metapostnotum triangular shaped, dull, pit-reticulate; T1–4 closely punctate .....***longivultu* sp. n.**
4 Thorax and head with faint metallic shine..... ***submetallicus* sp. n.**
– Thorax and head without metallic shine (8 spp.).....**5**
5 Scutum shiny and smooth, openly to closely punctate (5 spp.) **6**
– Scutum dull, densely punctate (3 spp.) **10**
6 Ventral margin of clypeus with two tubercles.....***bidentatus* n. sp**
– Ventral margin of clypeus without tubercles (4 spp.).....**7**
7 T1 smooth with sparse, minute punctures .....***splendens* sp. n.**
– T1 sculpture with open, fine punctures or lineo-reticulate (3 spp.) **8**
8 Ocellocular area irregularly roughened near ocellus and shiny towards eye; frons coarsely reticulate striate (Fig. 8C); antenna long, scape reaching ocellus (Fig. 8E) .....***albiscopis* sp. n.**
– Ocellocular area not as above; frons not striate; antenna short, scape not reaching ocellus (2 spp.).....**9**
9 Ocellocular area pit-reticulate, shallower and shiny towards eye; frons coarsely pit-reticulate (Fig. 16C) .....***claviger* sp. n.**
– Ocellocular area dull, with dense minute punctures; frons with dense small punctures (Fig. 17C).....***consobrinus* sp. n.**
10 Scutum, scutellum and metanotum with dense short light brown pubescence; clypeus somewhat shiny, openly punctate with minute depressions between punctures (Fig. 31E) .....***velutinellus* Michener**
– Scutum, scutellum and metanotum pubescence short to medium length, openly to closely spaced; clypeus dull, finely reticulate (Figs 15E, 28E) (2 spp.) **11**
11 Scutum, scutellum and metanotum pubescence short and white; T1–4 predominantly orange (Fig. 16A)..... ***ciliatus* sp. n.**
– Scutum, scutellum and metanotum pubescence of medium length, light brown; T1–4 dark brown with transparent posterior margins (Fig. 28A) ....***similis* sp. n.**
12 Inner hind tibial spur ciliate, teeth shorter than spur diameter (2 spp.).....**13**
– Inner hind tibial spur pectinate, with robust teeth (7 spp.) **14**
13 Terga depressed anteriorly; T1 shiny and openly punctate; basitibial plate less than 1/5 of tibial length; inner hind tibial spur with less than 10 slender teeth .....***constrictus* sp. n.**
– Terga not depressed anteriorly, T1 shiny and very sparsely punctate; basitibial plate elongated and slightly pointed, more than 1/4 of tibial length; inner hind tibial spur with more than 10 tiny teeth ..... ***nitidifuscus* sp. n.**
14 Scutum punctation near parapsidal lines sparse to open (4 spp.).....**15**
– Scutum punctation close to dense (3 spp.).....**18**

15 T1 smooth and sparsely punctate; T2–4 transparent posterior margins wide, through which adpressed pubescence on anterior margin of following terga are visible as hair bands ..... ***lucidus* sp. n.**
– T1 dull and densely punctate; T2–4 no hair bands on anterior margins. (3 spp.) **16**
16 T2–4 without dense adpressed hair bands on posterior margins, only semi erect hairs present; clypeus closely punctate ..... ***rubicundus* sp. n.**
– T2–4 with adpressed hair bands on posterior margins, T2 laterally only; clypeus openly punctate (2 spp.) **17**
17 Scape black, shiny anteriorly (ventrally) almost without punctures; 2 submarginal cells ..... ***laciniosus* sp. n.**
– Scape dark brown, dull with microsculpture and punctures; 3 submarginal cells (Fig. 2C) ..... ***aberrans* sp. n.**
18 Ocellocular area openly punctate (Fig. 23C); scutum pubescence medium length and open (Fig. 23A) ..... ***pectinatus* sp. n.**
– Ocellocular area impunctate, smooth or minutely reticulate (Figs 14C, 24C); scutum pubescence short (Figs 14A, 24A) (2 spp.) **19**
19 Ocellocular area dull, finely pit-reticulate (Fig. 24C); terga brown-black with transparent orange posterior margins and open semi erect hair bands on T3–4 ..... ***pilotapilus* sp. n.**
– Ocellocular area shiny, almost without punctures (Fig. 14C); terga predominantly orange with close semi erect hair bands on T3–4..... ***centralis* sp. n.**

Identification key to the males of *Leioproctus* (*Colletellus*) (17)

1 Ocellocular area dull, finely to coarsely roughened (6 spp.) **2**
– Ocellocular area shiny, openly to sparsely punctate and/or with microsculpture (11 spp.) 7
2 Scutum dull, densely punctate or reticulate (4 spp.) **3**
– Scutum shiny, openly to closely punctate (2 spp.) **5**
3 F1 longer than F2; clypeus punctation open to sparse; terga anteriorly with strongly depressed pregradular grooves, orange (Fig. 31G, H) ..... ***velutinellus* Michener**
– Length F1 equal to or shorter than F2; clypeus punctation close; terga anteriorly depressed (Figs 6B, 27B) or not depressed. (2 spp.) **4**
4 Terga anteriorly depressed; posterior margin of terga transparent orange; head and scutum without faint metallic shine. (2 spp.) **5**
– Terga anteriorly not depressed; posterior margin of terga opaque brown; head and scutum with faint metallic shine..... ***submetallicus* sp. n.**
5 T1 shiny, posteriorly on disc with fine reticulation; supraclypeal area shiny; inner hind femur convex..... ***alatus* sp. n.**
– T1 dull, posterior on disc with dense reticulation; supraclypeal area dull; inner hind femur concave ..... ***rubricinctus* sp. n.**

6 Ocellocular area coarsely reticulate (Fig. 11C); metapostnotum smooth with shallow microsculpture (Fig. 11D) ..... ***aratus* sp. n.**
– Ocellocular area reticulate (Fig. 16I); metapostnotum dull and finely reticulate (Fig. 16J) ..... ***claviger* sp. n.**
7 Metapostnotum dull, alveolate or coarsely reticulate (2 spp.) **8**
– Metapostnotum shiny, completely smooth or with microsculpture (9 spp.) **9**
8 Basitibial plate pointed; metapostnotum regularly pit-reticulate; T2–3 dull with fine punctation and reticulation, pregradular areas strongly depressed..... ..... ***bidentatus* sp. n.**
– Basitibial plate rounded; metapostnotum irregularly coarsely reticulate; T2–3 shiny with close punctation, pregradular areas depressed..... ***altispinosus* sp. n.**
9 Ocellocular area smooth, almost without punctures (4 spp.) **10**
– Ocellocular area punctate or with microsculpture (5 spp.) **13**
10 T1 openly punctate, T2–3 anteriorly strongly depressed..... ***constrictus* sp. n.**
– T1 densely punctate or with microsculpture; T2–3 not anteriorly depressed (3 spp.) **11**
11 T1 shiny, finely lineo-reticulate..... ***rubicundus* sp. n.**
– T1 dull, densely punctate (2 spp.)..... **12**
12 S2–4 apical hair bands with dense, short hairs, 2 submarginal cells (Fig. 2A).... ..... ***laciniosus* sp. n.**
– S2–4 apical hair bands with longer, openly placed hairs, often 3 submarginal cells (Fig. 2C) ..... ***aberrans* sp. n.**
13 Metapostnotum entirely smooth (2 spp.) **14**
– Metapostnotum with microsculpture (3 spp.) **15**
14 Flagellum F1–5(6) orange; T1–2 dull, densely reticulate.. ***auricorneus* sp. n.**
– Flagellum entirely dark; T1–2 smooth openly punctate .... ***quadripinnatus* sp. n.**
15 T2–4 anteriorly depressed, orange; ocellocular area smooth with open punctures..... ***centralis* sp. n.**
– T2–4 anteriorly moderately depressed, same colour as disk; ocellocular area with microsculpture (2 spp.) **16**
16 Propodeal triangle bordered by coarsely alveolate groove (Fig 24J) .... ***pilotapilus* sp. n.**
– Propodeal triangle bordered by fine alveolate groove (Fig. 9D)..... ..... ***aliceafontanus* sp. n.**

***Leioproctus* (*Colletellus*) *aberrans* Leijs, sp. n.**
http://zoobank.org/7D5CDCA8-90E4-4EC8-A0D6-DD1086550DBA
Figures 2C, 5A–O

Specimens examined. (1♂, 1♀): Female holotype: Bon Bon Stn (30.7789S; 135.3841E), 27 Oct. 2010, Leijs, R., on *Angianthus brachypappus*, SAMA 32-033494, BOLD: AUSBS124-12/RL1629A.

Male allotype: Bon Bon Stn (30.7789S; 135.3841E), 27 Oct. 2010, Leijs, R., on *Angianthus brachypappus*, SAMA 32-033495, BOLD: AUSBS125-12/RL1629B.

Diagnosis. Three submarginal cells, distinct posterior hair bands on T2–4.

Description. Holotype, female, body length: 6.2 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 2.7, AOD 8.5, HL 36, IAD 9.4, LFW 29, OAD 15, OOD 9.7, OW 17, UFW 35, HW/HL 1.4, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.56, FSR 1.76, SFR 0.83.

Structure: terga not depressed anteriorly; BTP rounded; BTP/tibial length ratio 0.2; inner hind tibial spur pectinate with 8 strong teeth.

Sculpture: scutum smooth with sparse punctures; metapostnotum smooth, shiny, horizontal part as long as vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate, orange anterior rim; supraclypeal area shiny, closely punctate; labrum smooth orange-brown; ocellocular area smooth, shiny; frons smooth openly to sparsely punctate; scape shiny, almost no punctures.

Coloration: terga anterior brown-orange, posterior margins transparent white, T2–4 with white adpressed hair bands; scopa white; mandibles orange with brown tip; scape black, flagellum F1–3 black, F4–10 orange-brown below.

Pubescence: scutum: dispersed, short, branched; scutellum: dispersed, short, branched; metanotum: dispersed, short, branched; T2–4 with hair bands, long, branched.

Description. Allotype male, body length: 5.2 mm; head width: 1.8 mm. *Relative head measurements*: HW 50, ASD 3.5, AOD 7.6, HL 38, IAD 9.4, LFW 27, OAD 14, OOD 9.4, OW 19, UFW 36, HW/HL 1.3, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.61, FSR 1.76, SFR 0.83.

Structure: terga not depressed anteriorly; BTP rounded; flagellum F1–3 black, F4–10 brown below, shorter than wide; *S7*: dorsal apical lobe small, ventral apical lobe large, branched setae present on dorsal subcentral apical ridge and apical lobe of ventral apical lobe.

Sculpture: scutum smooth with sparse punctures; metapostnotum smooth, shiny, horizontal part little shorter than vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate, anterior rim orange; supraclypeal area shiny, closely punctate; ocellocular area smooth, shiny, almost no punctures; frons smooth openly to sparsely punctate.

Coloration: terga anteriorly brown-orange; mandibles brown at base, orange medially with brown tip.

Pubescence: scutum: dispersed, short, branched; scutellum: dispersed, short, branched; metanotum: dispersed, short, branched; S5 with dense hair band, short, branched, S2–4 erect and open hair band; scape black, shiny, almost no punctures.

Remarks. Both examined specimens have been DNA barcoded, accessible through the following links:

http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS124-12
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS125-12

Flower records. *Angianthus brachypappus* (Asteraceae).

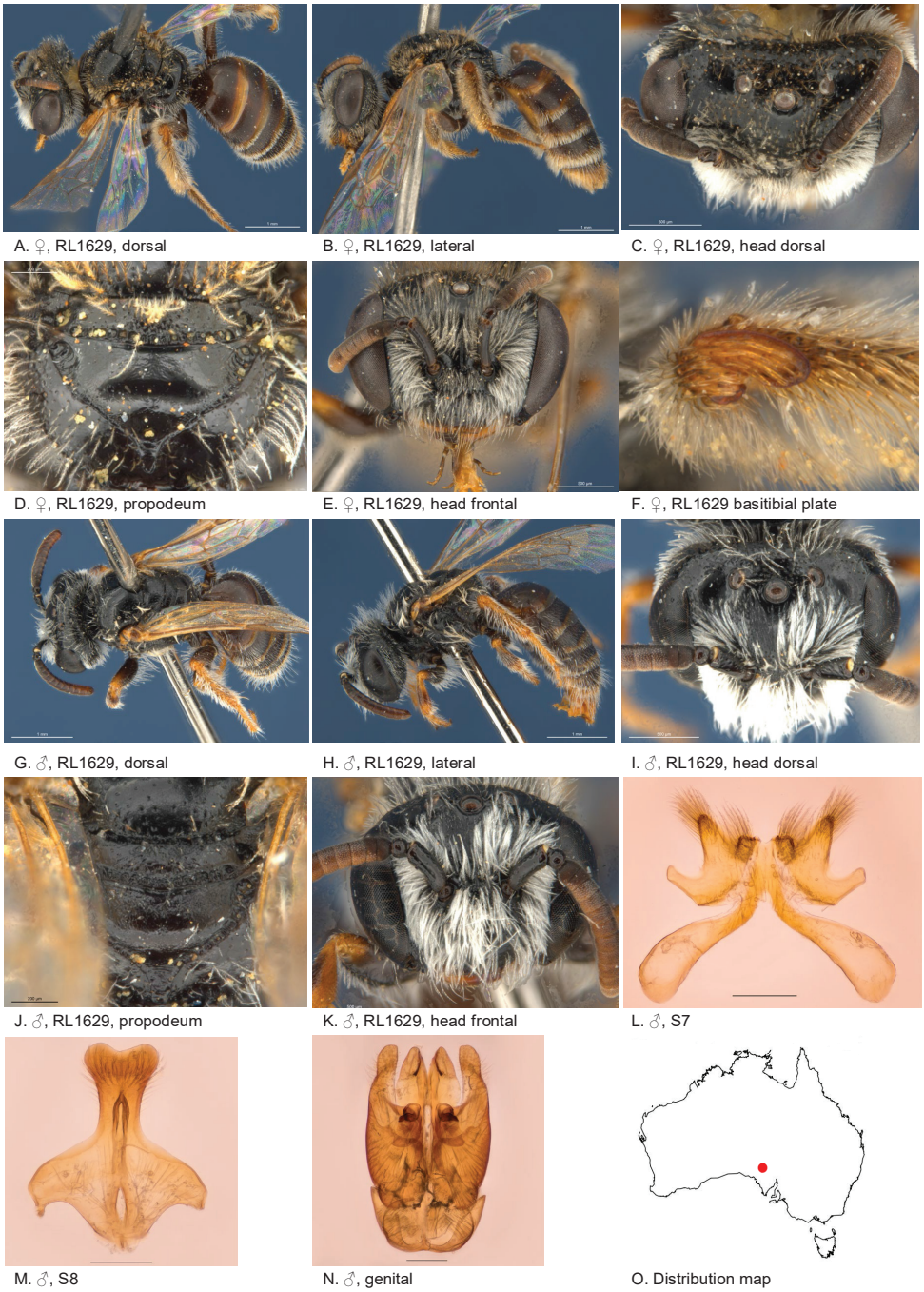


Figure 5. *Leioproctus* (*Colletellus*) *aberrans* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**L, M, N**).

Distribution. Figure 5O.

Etymology. The specific epithet '*aberrans*' refers to abnormal wing venation: this species has three submarginal cells instead of two (Fig. 2).

***Leioproctus* (*Colletellus*) *alatus* Leijs, sp. n.**
http://zoobank.org/51F9E4E1-F6A8-4AE0-8E52-FBD4A323316D
Figure 6A–I

Specimens examined. (3♂): Holotype male, Kalbarri NP (27.8333S; 114.4667E), 14 Aug. 2003, Bickel, D., yellow pan trap, AM, K447299. Paratypes 2 males, same locality data as holotype, AM, K447298, K447306.

Diagnosis. Head and thorax dull and densely reticulate, S7 with large wing shaped ventral apical lobes.

Female unknown.

Description. male holotype: body length: 5.1 mm; head width: 1.5 mm. *Relative head measurements*: HW 50, ASD 4.0, AOD 6.9, HL 42, IAD 11.4, LFW 28, OAD 15, OOD 10.2, OW 19, UFW 38, HW/HL 1.2, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.45, FSR 1.41, SFR 1.00.

Structure: terga anteriorly slightly depressed; BTP rounded, short; BTP/tibial length ratio 0.11; flagellum F1 = F2, other segments longer than wide; male S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on apico-medial area of ventral apical lobe.

Sculpture: scape dull, densely reticulate; scutum dull, anteriorly with transverse reticulation, densely punctate; metapostnotum pit-reticulate, some striae in lateral corners; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus dull with dense reticulation; supraclypeal area dull with dense reticulation; ocellocular area concave, dull; frons densely sculptured.

Coloration: terga anterior dark brown, posterior margins transparent orange; mandibles and, F1–2 black, F3–11 orange-brown below.

Pubescence: scutum: open, short and scattered, long; scutellum: open, short and scattered, long; metanotum: open, short and scattered, long.

Flower records. No data.

Distribution. Figure 6I.

Etymology. The specific epithet refers to wing shaped lateral lobes of the male S7.

***Leioproctus* (*Colletellus*) *albipilosus* Leijs, sp. n.**
http://zoobank.org/751F411E-DBB3-46DF-9199-473971F65D74
Figure 7A–F

Specimens examined. (1♀): Holotype female, 8 km S of Cape Bertholet (17.3167S; 122.1667E), WA, 21 Apr. 1977, Colless, D.H., ANIC 32-111660.

Diagnosis. Short white pubescence on thorax and head, integument abdomen red, metapostnotum smooth and shiny.

Male unknown.

Description. Female holotype: body length: 5 mm; head width: 1.7 mm. *Relative head measurements*: HW 50, ASD 3.2, AOD 7.9, HL 39, IAD 10.2, LFW 29, OAD

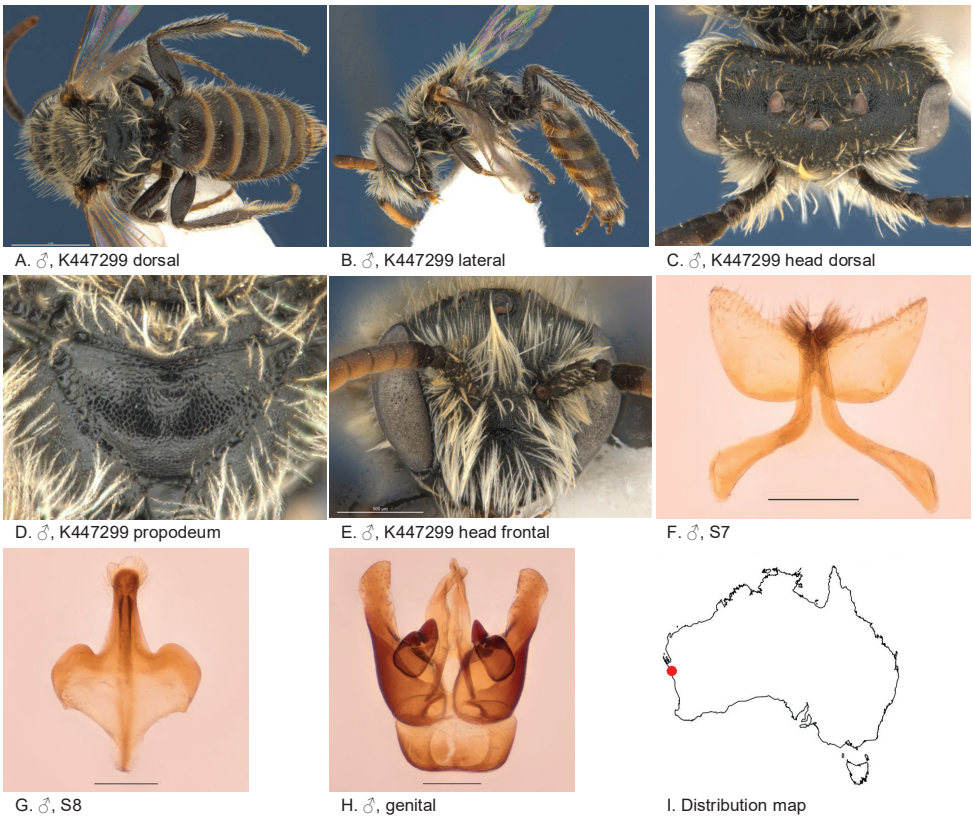


Figure 6. *Leioproctus* (*Colletellus*) *alatus* Leijs, sp. n. ♂ holotype. Scale bar: 0.1 mm (**F, G, H**).

16, OOD 8.5, OW 19, UFW 33, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.09, FSR 0.95, SFR 0.86.

Structure: terga anteriorly not depressed; BTP pointed, short; BTP/tibial length ratio 0.2; inner hind tibial spur pectinate with 7 strong teeth.

Sculpture: scutum smooth, closely punctate; metapostnotum smooth, shiny, almost wholly vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, closely punctate, ventral margin width 1/3 of ocellar diameter; supraclypeal area smooth, closely punctate; labrum dull, orange; ocellocular area smooth, openly to sparsely punctate; frons smooth closely punctate.

Coloration: terga anteriorly orange, posterior margins transparent orange; scopa white; mandibles orange with brown tip; scape brown with orange base; flagellum orange.

Pubescence: scutum: short, dense, white; scutellum: short, dense, white; S1–4 with fringes of long, branched hairs; scape, open, pubescence of white branched hairs.

Flower records. No data.

Distribution. Figure 7F.

Etymology. The specific epithet refers to short white pubescence on the scutum.

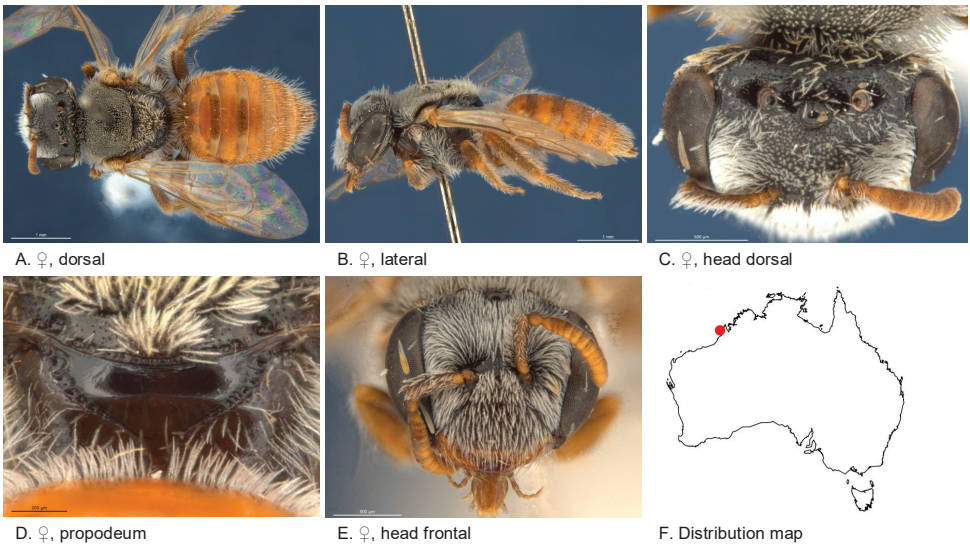


Figure 7. *Leioproctus* (*Colletellus*) *albipilosus* Leijs, sp. n. ♀ holotype ANIC 32-111660.

***Leioproctus* (*Colletellus*) *albiscopis* Leijs, sp. n.**
http://zoobank.org/B99A0ECC-6B1B-4665-9732-7B40A139A826
Figure 8A–F

Specimens examined. (2♀): Holotype female, Arrowsmith River (29.6166S; 115.2881E), WA, 03 Oct. 1997, Houston, T.F., on *Allocasuarina campestris*, WAM 19109; paratype female, same locality data as holotype, WAM 19108.

Diagnosis. Integument mostly black, scopa white, ocellocular area shiny near eye, coarsely irregular roughened near ocellus; frons coarsely reticulate striate.

Male unknown.

Description. Female holotype: body length: 6.2 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 3.4, AOD 10.2, HL 36, IAD 8.4, LFW 32, OAD 12, OOD 8.8, OW 17, UFW 33, HW/HL 1.4, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.88, FSR 1.00, SFR 1.00.

Structure: terga anteriorly not depressed; BTP pointed, broad; BTP/tibial length ratio 0.29; inner hind tibial spur ciliate; flagellum long, F4–9 slightly longer than wide; scape long, reaching ocellus, smooth.

Sculpture: scutum anteriorly transverse lineo-reticulate, remainder openly punctate; metapostnotum smooth, shallow lineo-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, with medium to large sparse punctures; supraclypeal area shiny, with medium to large sparse punctures; labrum brown-black; ocellocular area shiny near eye, coarsely irregular roughened near ocellus; frons coarsely reticulate striate.

Coloration: terga anteriorly brown black, posterior margins brownish, not transparent; scopa grey-white with darker pubescence towards BTP; mandibles brown.

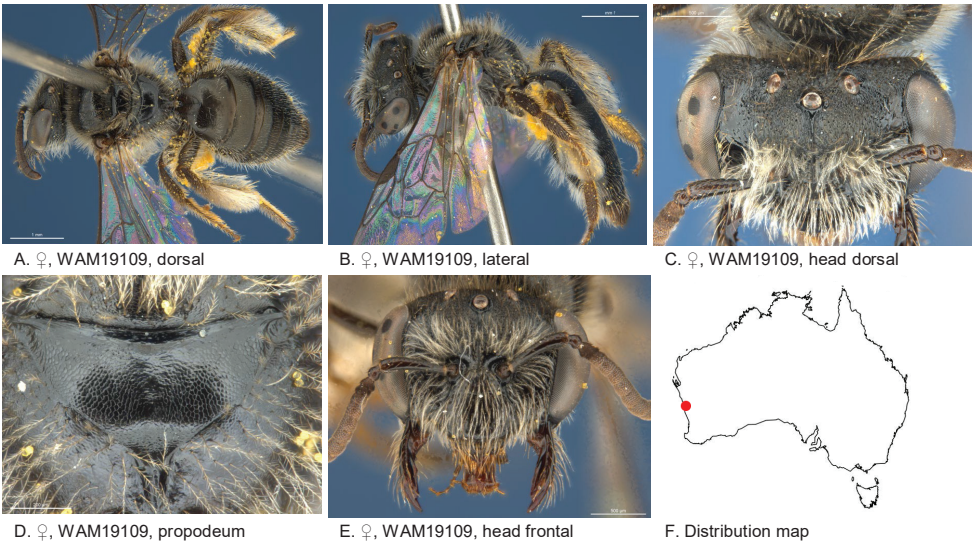


Figure 8. *Leioproctus* (*Colletellus*) *albiscopis* Leijs, sp. n. ♀ holotype.

Pubescence: scutum: medium length with sparse, long, grey brown hairs; scutellum: sparse, long, grey brown along edges; sterna white-grey fringe at S5.

Flower records. *Allocasuarina campestris* (Casuarinaceae).

Distribution. Figure 8F.

Etymology. The specific epithet refers to the white scopa pubescence on the hind tibia of the female.

Leioproctus (*Colletellus*) *aliceafontanus* Leijs, sp. n.

http://zoobank.org/873313DC-5CD5-4FCE-8432-EFE2565E699C
Figure 9A–I

Specimens examined. (7♂): Holotype male, James Ranges (24.25S; 133.43E), 22 Sep. 1978, Cardale, J., ANIC 32-111659;

Paratypes: 2 males, 56 km SE of Alice Springs (24.1833S; 134.0167E), 24 Sep. 1978, Cardale, J., ANIC 32-111667–68; 1 male, James Ranges (24.25S; 133.43E), 22 Sep. 1978, Cardale, J., ANIC 32-111669; 3 males, 45 km NE of Welbourn Hill (27.05S; 134.37E), 20 Sep. 1978, Cardale, J., ANIC 32-111670–72.

Diagnosis. Ocellocular area smooth with some punctures near eye margin, metapostnotum shiny with microsculpture, posterior margins of terga transparent.

Female unknown.

Description. Male holotype: body length: 5.1 mm; head width: 1.62 mm. *Relative head measurements*: HW 50, ASD 2.8, AOD 7.1, HL 38, IAD 9.2, LFW 27, OAD 13, OOD 10.5, OW 17, UFW 34, HW/HL 1.3, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.15, FSR 0.96, SFR 1.00.

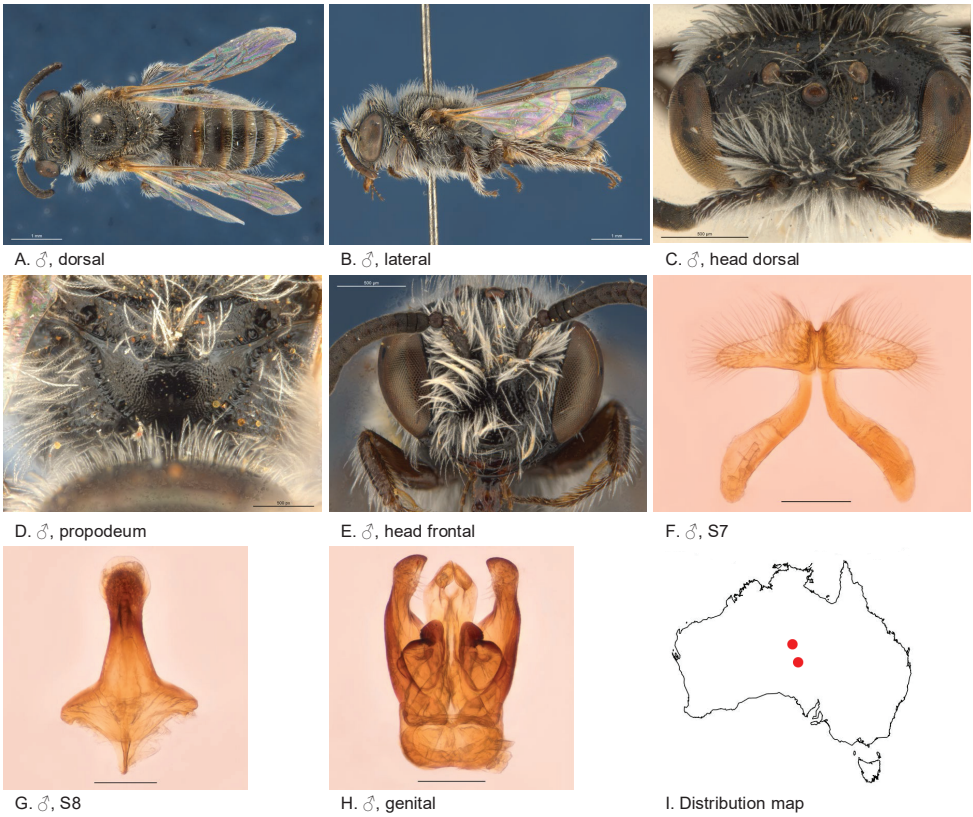


Figure 9. *Leioproctus* (*Colletellus*) *aliceafontanus* Leijs, sp. n. ♂ holotype ANIC 32-111659. Scale bar: 0.1 mm (**F,G,H**).

Structure: terga anteriorly moderately depressed; BTP rounded. S7: dorsal apical lobe absent, ventral apical lobe large, robust simple setae present on dorsal subcentral apical ridge and ventral apical lobe.

Sculpture: scutum smooth, with sparse fine punctures; metapostnotum dullish, finely reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate; supraclypeal area smooth, openly punctate; labrum smooth; scape dull; ocellocular area shiny, minutely reticulate, with sparse punctures; frons smooth closely punctate.

Coloration: terga anteriorly dark brown, posterior margins transparent brown; mandibles brown with reddish tip; labrum brown; scape and flagellum brown.

Pubescence: scutum: medium length, open; scutellum: medium length, open.

Flower records. No data.

Distribution. Figure 9I.

Etymology. The specific epithet refers to the distribution of this species around Alice Springs.

***Leioproctus* (*Colletellus*) *altispinosus* Leijs, sp. n.**
http://zoobank.org/4E3CAA6B-279D-400E-B179-65167BBC06D4
Figure 10A–I

Specimens examined. (28♂): Holotype male, 25 km SW of Tangadee (24.5688S; 118.7636E), 22 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Dicrastylis flexuosa*, WAM 12368;

Paratypes: 24 males, 24 km NNE of Beyondie (24.7055S; 120.2558E), 17 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Calandrinia*, WAM 12305–28; male, Tangadee (24.5688S; 118.7636E), 22 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Calandrinia*, WAM 12330; male, 10 km NNW of Meedo (25.6991S; 114.7175E), 23 Aug. 1980, Howard, C.A. & Houston, T.F., on *Calandrinia polyandra*, WAM 19839; male, 5 km SSE of Eurardy HS (27.5472S; 114.6247E), 27 Aug. 1999, Houston, T.F., on *Calandrinia* , WAM 27540.

Diagnosis. Ocellocular area shiny and openly punctate, metapostnotum coarsely reticulate, S7 lateral lobes very small relative to apodemes and with robust setae.

Female unknown.

Description. Male holotype: body length: 5.8 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 3.1, AOD 7.6, HL 40, IAD 8.7, LFW 28, OAD 15, OOD 8.8, OW 19, UFW 35, HW/HL 1.2, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.43, FSR 0.97, SFR 0.89.

Structure: terga anteriorly depressed; BTP rounded; S7: dorsal apical lobe absent, ventral apical lobe small, very robust simple setae present on ventral apical lobe; scape roughened.

Sculpture: scutum closely punctate; metapostnotum dull, roughened; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, closely punctate; supraclypeal area shiny, closely punctate; ocellocular area smooth openly punctate; frons densely punctate.

Coloration: terga anteriorly black, posterior margins orange, transparent; mandibles brown, orange tip; flagellum dark brown.

Pubescence: scutum: open, medium length, branched; scutellum: open, medium length, branched; metanotum: open, medium length, branched; sterna 5 with row of dense long straight hairs; scape with pubescence.

Remarks. There is some variation in body size. There are a few exceptionally large males. Several specimens are carrying Strepsiptera.

Flower records. *Calandrinia polyandra, Calandrinia* sp. (Montiaceae), *Dicrastylis flexuosa* (Lamiaceae).

Distribution. Figure 10I.

Etymology. The specific epithet refers to the robust setae on the tip of the ventral apical lobe of male sterna 7. It also is a translation of the name of our linguistic advisor Wiebe Hogendoorn.

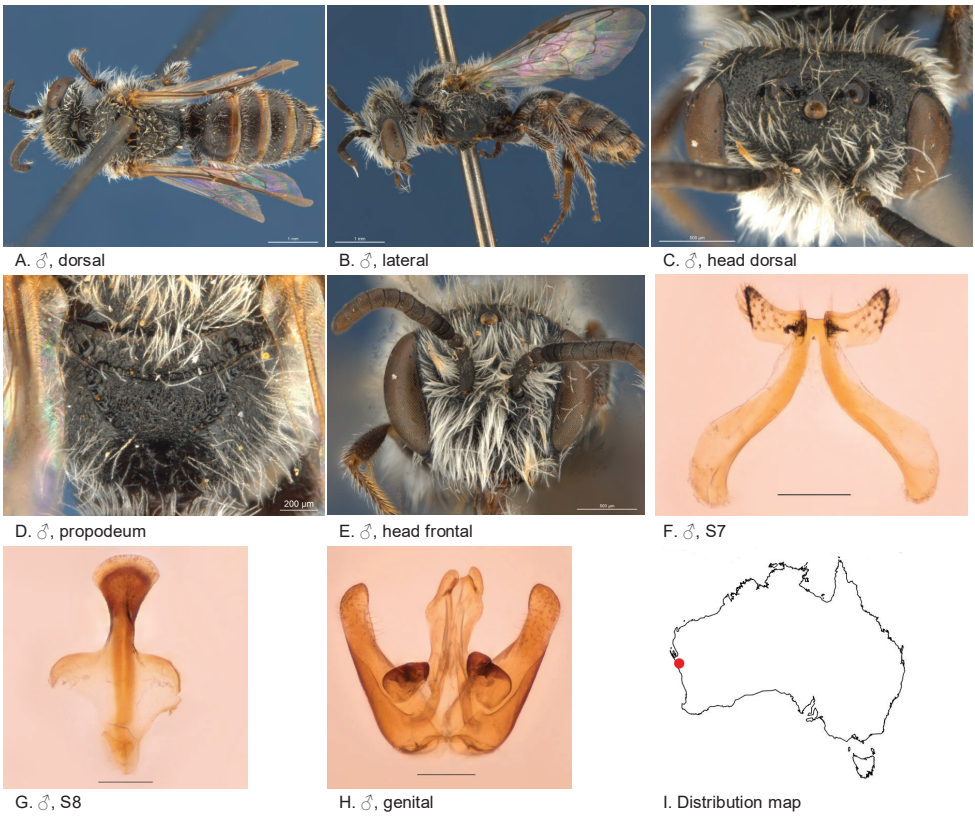


Figure 10. *Leioproctus* (*Colletellus*) *altispinosus* Leijs, sp. n. ♂ holotype WAM12368. Scale bar: 0.1 mm (**F, G, H**).

***Leioproctus* (*Colletellus*) *aratus* Leijs, sp. n.**
http://zoobank.org/71D12BE5-DFCD-4AA8-86F7-CA18F5F86FFB
Figure 11A–I

Specimens examined. (1♂): Holotype male, Orange Grove (32.0233S; 116.0253E), 03 Aug. 1986, Peakall, R., on *Prasophyllum fimbria*, WAM 12365.

Diagnosis. Antennae long, ocellocular area very roughly sculptured, metapostnotum smooth with shallow microsculpture, S7 with small and narrow dorsal and ventral lobes bearing robust simple setae.

Female unknown.

Description. Male holotype: body length: 6 mm; head width: 1.85 mm. *Relative head measurements*: HW 50, ASD 3.1, AOD 6.1, HL 41, IAD 9.9, LFW 24, OAD 13, OOD 9.0, OW 17, UFW 34, HW/HL 1.2, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.94, FSR 0.93, SFR 1.19.

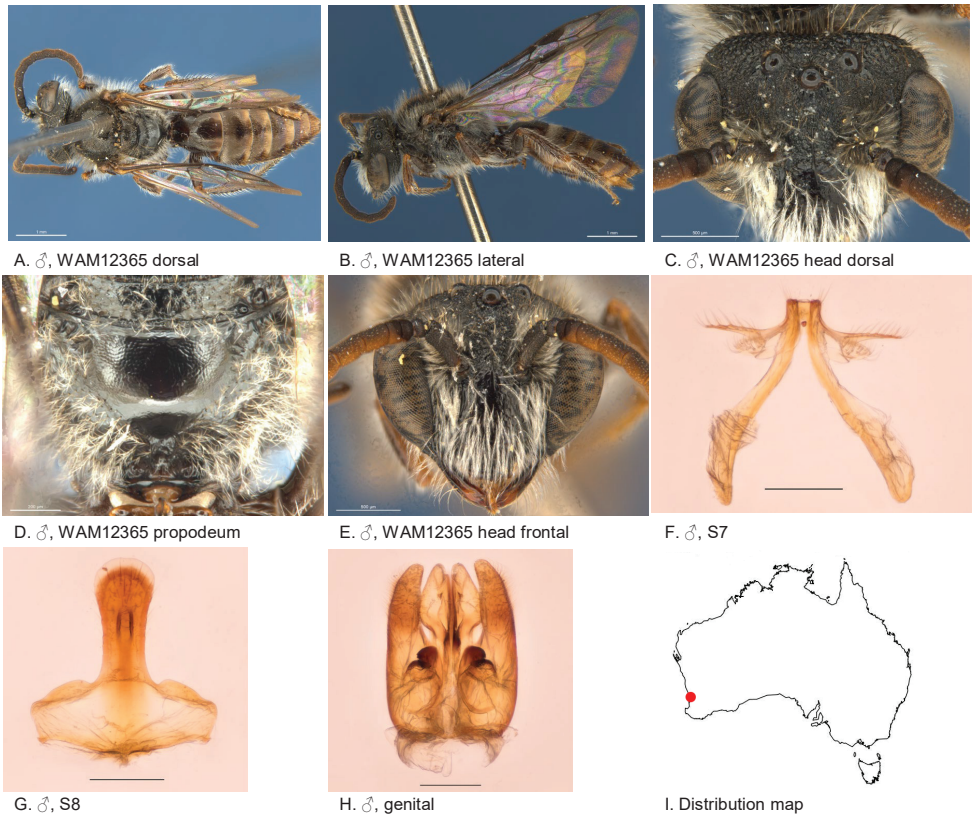


Figure 11. *Leioproctus* (*Colletellus*) *aratus* Leijs, sp. n. ♂ holotype. Scale bar: 0.1 mm (**F, G, H**).

Structure: terga anteriorly little depressed; BTP rounded, elongated; flagellum elongated: F3–11 little less than twice as long as wide, light-brown below; S7: dorsal apical lobe of medium size, ventral apical lobe slender, robust simple setae present on dorsal and ventral apical lobes.

Sculpture: scutum smooth, open, small punctures, posteriorly denser; metapostnotum smooth, shallow micro-sculpture; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate; supraclypeal area smooth, openly punctate, medially without punctures; labrum black; ocellocular area coarsely pit-reticulate; frons coarsely pit-reticulate; scape closely punctate.

Coloration: terga anteriorly brown, posterior margins transparent orange; mandibles black with brown tip; scape black; F3–11 light-brown below.

Pubescence: scutum: medium length, open, brown; scutellum: medium length, open, brown.

Flower records. *Prasophyllum fimbria* (Orchidaceae).

Distribution. Figure 11I.

Etymology. The specific epithet refers to very coarse pit-reticulate sculpture on the head.

***Leioproctus* (*Colletellus*) *auricorneus* Leijs, sp. n.**
http://zoobank.org/58AC9DC5-F331-4D55-A84C-5225A8049ABA
Figures 2E, 12A–I

Specimens examined. (1♂): Holotype male, 56 km SE of Alice Springs (24.1833S; 134.0167E), 03 Oct. 1978, Cardale, J., Malaise trap, ANIC 32-111658.

Diagnosis. Ocellocular area smooth shiny openly punctate, metapostnotum shiny, but T1–2 dull and densely reticulate, flagellum orange. S7 ventral lobe large with long branched setae.

Female unknown.

Description. Male holotype: body length: 4.9 mm; head width: 1.7 mm. *Relative head measurements*: HW 50, ASD 3.1, AOD 6.5, HL 40, IAD 10.8, LFW 26, OAD 16, OOD 9.2, OW 19, UFW 35, HW/HL 1.2, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.22, FSR 0.96, SFR 0.96.

Structure: terga anteriorly almost not depressed; BTP rounded, elongated almost pointy; flagellum F1–7 orange, 8–11 brown; S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on posterior area of ventral apical lobe.

Sculpture: scutum smooth, with open small punctures; metapostnotum entirely smooth; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, closely punctate; supraclypeal area smooth, closely punctate; ocellocular area smooth, openly punctate; frons smooth, openly to closely punctate.

Coloration: terga anteriorly black, posterior margins transparent brown; mandibles black with reddish tip; scape brown, dull.

Pubescence: scutum: long, open; scutellum: long, open; S5 posteriorly with very dense fringe of long white hairs.

Flower records. No data.

Distribution. Figure 12I.

Etymology. The specific epithet refers to the orange coloured antennae.

***Leioproctus* (*Colletellus*) *bidentatus* Leijs, sp. n.**
http://zoobank.org/9FE5BCA4-3E48-4DFB-A381-C4D035345763
Figure 13A–N

Specimens examined. (8♂, 9♀): Holotype female, Gooseberry Hill (31.9541S; 116.0469E), 07 Oct. 1994, Houston, T.F., on *Verticordia acerosa*, WAM 14412.

Allotype male, Cockleshell Gully (30.15S; 115.10E), 23 Sep. 1998, Houston, T.F., on *Stylidium*, WAM 20312.

Paratypes: 2 males, Cockleshell Gully (30.15S; 115.10E), 23 Sep. 1998, Houston, T.F., on *Stylidium*, WAM 20311, WAM 20313; male, Peak Charles National Park (32.8833S; 121.1608E), 18 Oct. 1985, Houston, T.F., on *Thryptomene*? , WAM 12400; male, Gooseberry Hill (31.9541S; 116.0469E), 07 Oct. 1994, Houston, T.F., on *Verticordia acerosa*, WAM 14413; female, Arrowsmith River (29.6166S;

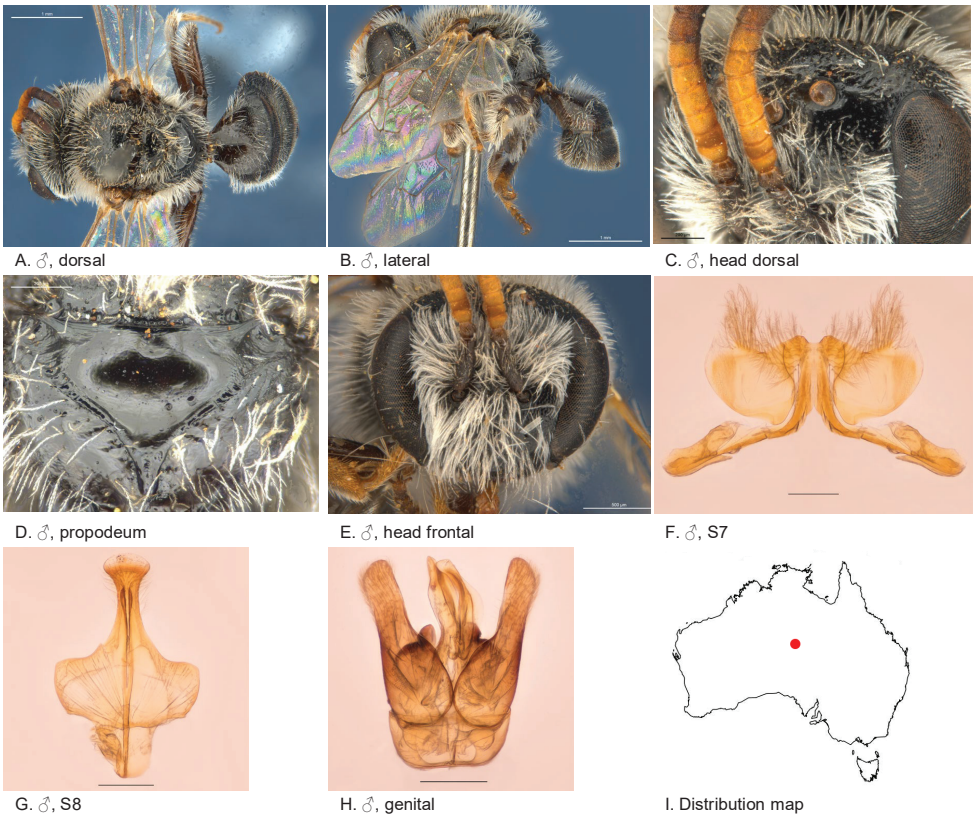


Figure 12. *Leioproctus* (*Colletellus*) *auricorneus* Leijs, sp. n. ♂ holotype ANIC 32-111658. Scale bar: 0.1 mm (**F, G, H**).

115.2881E), 03 Oct. 1997, Houston, T.F., on *Thysanotus*, WAM 19107; male, Mcdermid Rock (32.0222S 120.7339E), 27 Sep 1978, Houston, T.F., et al., *on Leptospermum erubescens*, WAM 19114; male, female, Lesmurdie (32.1300S; 116.0328E), 14 Oct. 2009, Batley, M., on *Stylidium bulbiferum*, AM 359765, 359755; 2 females, Yallingup (33.6938S; 115.0358E), 20 Oct. 1983, Stoutamire, W.P., on *Agrostocrinum*, WAM 12381–2; 2 males, 3 females, Boorabbin Rock (31.2036S; 120.2856E), 04 Oct 1981, Houston, T.F., on *Baeckea*, WAM 12394–7, WAM 14421; male, Boorabbin Rock (31.2036S; 120.2856E), 04 Oct. 1981, Houston, T.F., on *Thryptomene australis*, WAM 12398; female, Eneabba (29.8213S; 115.2692E), 04 Oct. 1985, McMillan, R.P., on *Thryptomene*, WAM 12399.

Diagnosis. Clypeus of female with two small teeth at ventral margin, ocellocular area and clypeus smooth with open punctation, metapostnotum dull micro-alveolate.

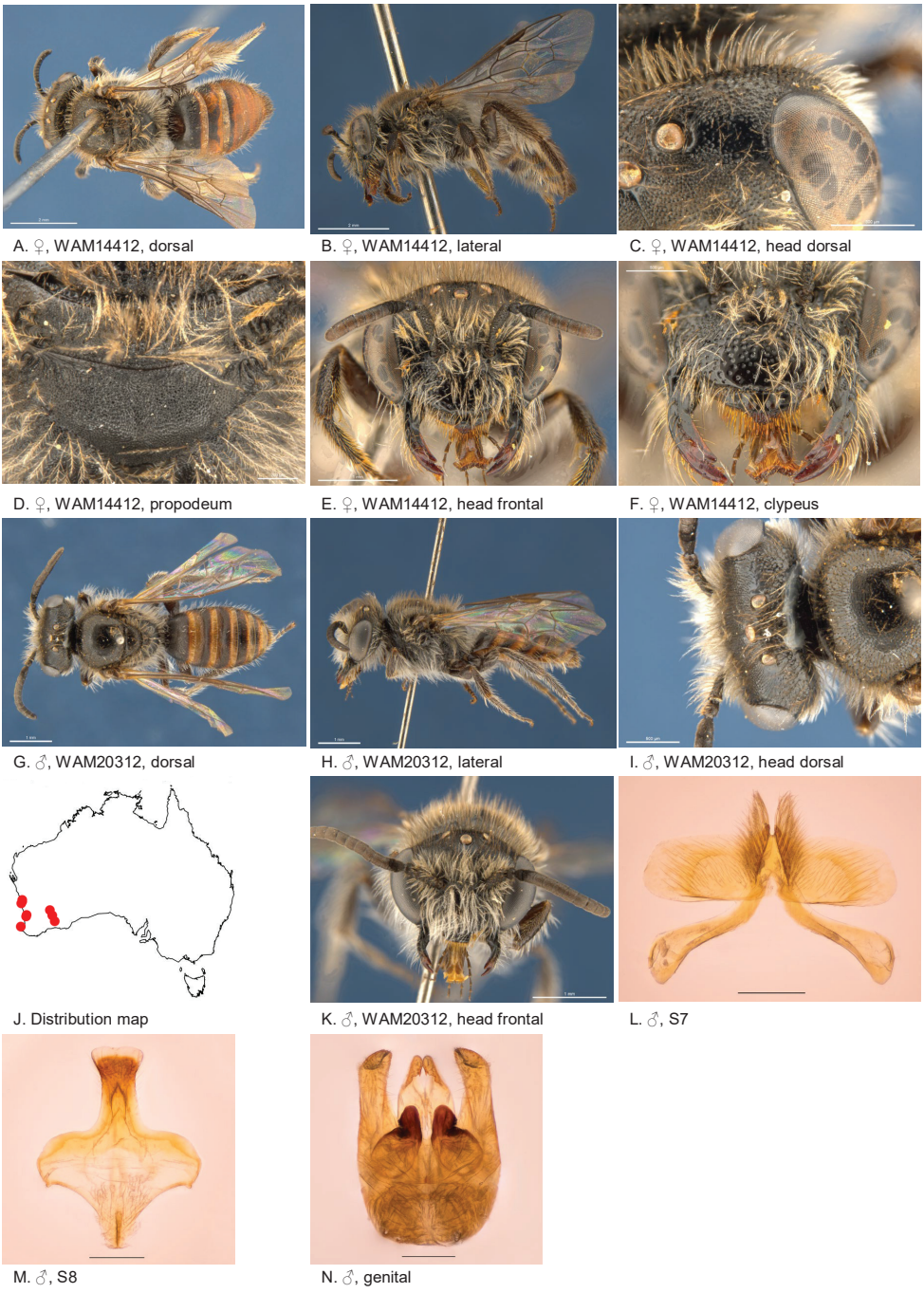


Figure 13. *Leioproctus* (*Colletellus*) *bidentatus* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**L, M, N**).

Male terga anteriorly strongly depressed, S7 ventral apical lobe large, branched setae present on dorsal subcentral apical ridge.

Description. Female holotype: 6.6 mm; head width: 2.3 mm. *Relative head measurements*: HW 50, ASD 2.7, AOD 8.6, HL 35, IAD 10.5, LFW 29, OAD 14, OOD 10.6, OW 15, UFW 36, HW/HL 1.4, LFW/UFW 0.8. *Relative wing measurement*: MSR 1.26.

Structure: terga anteriorly little depressed; BTP pointed, long; BTP/tibial length ratio 0.33; inner hind tibial spur ciliate with circa 18 little teeth.

Sculpture: scutum smooth openly punctate; metapostnotum microalveolate, striate in lateral corners; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate, smooth between punctures, ventral margin drawn in thin plate with two teeth; supraclypeal area smooth, shiny; labrum smooth; ocellocular area smooth openly punctate; frons densely punctate; vertex roughened with punctures; scape dullish openly coarsely punctate.

Coloration: terga anteriorly dark, posterior margins transparent orange; scopa brown; mandibles black with brown tip; flagellum F1–3 black, F4–10 orange/brown below.

Pubescence: scutum: medium length, open; scutellum: medium length, open; metanotum: medium length, open; sterna 1–5 with fringes of long simple hairs, S5 not dense; scape with medium length grey pubescence.

Description. Male allotype: body length: 5.8 mm; head width: 2.1 mm. *Relative head measurements*: HW 50, ASD 2.4, AOD 6.1, HL 36, IAD 10.2, LFW 26, OAD 15, OOD 11.9, OW 15, UFW 36, HW/HL 1.4, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.26, FSR 1.08, SFR 0.69.

Structure: terga anteriorly strongly depressed; BTP pointed; flagellum F4–11 slightly longer than wide. S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on dorsal subcentral apical ridge; scape short.

Sculpture: scutum smooth openly punctate; metapostnotum dull, alveolate and striate in lateral corners; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate with smooth interspaces; supraclypeal area smooth, shiny; ocellocular area shiny, with open to sparse punctures; frons shiny, densely punctate; scape dull.

Coloration: terga anteriorly orange, posterior margins transparent orange; mandibles black with brown tip; flagellum black; scape black.

Pubescence: scutum: medium length, open; scutellum: medium length, open; metanotum: medium length, open; scape with long pubescence.

Flower records. *Agrostocrinum* sp. (Hemerocallidaceae), *Baeckea* sp. (Myrtacea), *Leptospermum erubescens* (Myrtacea), *Stylidium bulbiferum*, *Stylidium* sp. (Stylidiaceae), *Thryptomene australis* (Myrtacea), *Thysanotus* sp. (Asparagaceae), *Verticordia acerosa* (Myrtacea).

Distribution. Figure 13J.

Etymology. The specific epithet refers to the two teeth on the ventral margin of the clypeus.

***Leioproctus* (*Colletellus*) *centralis* Leijs, n. sp.**
http://zoobank.org/91E9360C-B1A4-4534-A9D4-3597C74BC5FA
Figures 2D, 14A–N

Specimens examined. (5♂, 6♀): Holotype female, 56 km SE of Alice Springs (24.1833S; 134.0167E), 24 Sep. 1978, Cardale, J., ANIC 32-111661.

Allotype male, 37 km W of Glenayle HS (25.2666S; 122.0333E), 08 Aug. 1983, Houston, T.F. & McMillan, R.P., on *Calotis multicaulis*, WAM 12379;

Paratypes 3 females, 1 males, 56 km SE of Alice Springs (24.1833S; 134.0167E), 03 Oct. 1978, Cardale, J., Malaise trap, ANIC 32-111662,64–67; female, 56 km SE of Alice Springs (24.1833S; 134.0167E), 24 Sep. 1978, Cardale, J., on *Podolepis canescens*, ANIC 32-111663; 3 males, 37 km W of Glenayle HS (25.2666S; 122.0333E), 08 Aug. 1983, Houston, T.F. & McMillan, R.P., on *Calotis multicaulis*, WAM 12375–78.

Diagnosis. Ocellocular area smooth with a few dispersed punctures, metapostnotum dull fine transverse reticulate, terga with transparent posterior margins and depressed pregradular areas. Male S7 lateral lobes with very long branched setae.

Description. Female holotype: body length: 6.5 mm; head width: 2.2 mm. *Relative head measurements*: HW 50, ASD 3.4, AOD 9.2, HL 39, IAD 9.1, LFW 30, OAD 16, OOD 10.0, OW 16, UFW 35, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.14, FSR 0.97, SFR 0.86.

Structure: terga anteriorly little depressed; BTP rounded, elongated; BTP/tibial length ratio 0.26; inner hind tibial spur pectinate with 6 strong teeth.

Sculpture: scutum smooth, closely punctate; metapostnotum dullish, fine transverse reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate; supraclypeal area smooth, openly to closely punctate; labrum dull, brown-orange; ocellocular area smooth without punctures; frons smooth closely punctate; scape brown, smooth and sparsely punctate ventrally.

Coloration: F3–10 orange below, anterior orange, posterior margins transparent orange, T3–4 white entire hair bands; scopa white; mandibles orange with black tip; scape brown.

Pubescence: scutum: short, close, orange-brown; scutellum: short, close, orange-brown; hair bands on T2 laterally; S1–4 with fringe of long straight branched hairs; scape dorsally with open pubescence of white branched hairs.

Description. Male allotype: body length: 6.3 mm; head width: 1.95 mm. *Relative head measurements*: HW 50, ASD 2.7, AOD 8.3, HL 38, IAD 7.8, LFW 27, OAD 13, OOD 9.4, OW 18, UFW 35, HW/HL 1.3, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.07, FSR 1.00, SFR 0.79.

Structure: terga anteriorly moderately depressed; BTP rounded; S7: dorsal apical lobe small, ventral apical lobe large, branched setae present on dorsal subcentral apical ridge and some on ventral apical lobe; scape brown, smooth and sparsely punctate.

Sculpture: scutum smooth, openly to closely punctate; metapostnotum dullish, with transverse irregular reticulation, rougher than female; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, closely punctate; supraclypeal area

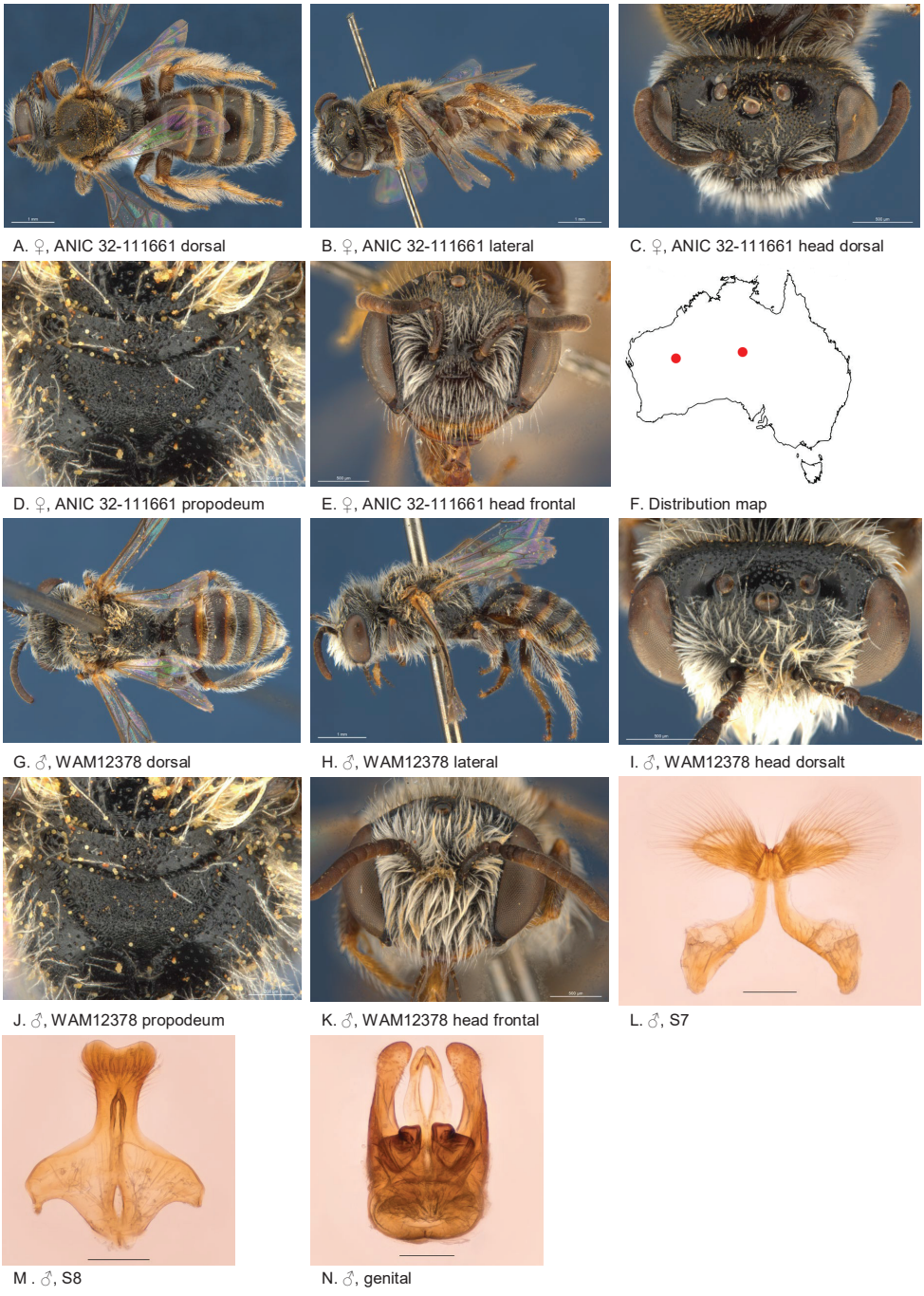


Figure 14. *Leioproctus* (*Colletellus*) *centralis* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**L, M, N**).

smooth, closely punctate; ocellocular area smooth, sparsely punctate; frons smooth closely punctate.

Coloration: labrum orange; terga anteriorly brown-orange, posterior margins transparent orange; mandibles orange with brown tip; F4–11 orange brown below.

Pubescence: scutum: medium length, open, greyish brown; scutellum: medium, length open, greyish brown.

Flower records. *Calotis multicaulis* (Asteraceae), *Podolepis canescens* (Asteraceae).

Distribution. Figure 14F.

Etymology. The specific epithet refers to central Australian distribution of this species.

***Leioproctus* (*Colletellus*) *ciliatus* Leijs, sp. n.**
http://zoobank.org/8E7AAB7B-CBD7-491C-BC33-CD1AFD95FC8B
Figure 15A–F

Specimens examined. (7♀): Holotype: female, East Yuna Nature Reserve (28.4191S; 115.2028E), 23 Sep. 1983, Houston, T.F. & C.A., on *Calandrinia*, WAM 12372;

Paratypes: 3 females, same locality data as holotype, WAM 12369–72; female, Kadji Kadji (29.1833S; 116.458E), 19 Sep. 2009, Leijs, R., blue pan trap, SAMA 32-033479; 2 females, Kadji Kadji (29.1392S; 116.3824E), 16 Sep. 2009, Leijs, R., on *Calandrinia* sp., SAMA 32-033480, BOLD: AUSBS284-13/ RL1503A, SAMA 32-033481 AUSBS285-13/ RL1503B.

Diagnosis. Scutum with short grey pubescence, tergal integument reddish, ocellocular area dull, metapostnotum shiny and lineo-reticulate.

Male unknown.

Description. Female holotype: body length: 5.2 mm; head width: 1.8 mm. *Relative head measurements*: HW 50, ASD 3.2, AOD 8.3, HL 39, IAD 9.4, LFW 31, OAD 14, OOD 8.9, OW 17, UFW 34, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.43, FSR 1.13, SFR 0.96.

Structure: terga anteriorly not depressed; BTP pointed; BTP/tibial length ratio 0.31; inner hind tibial spur ciliate with circa 18 little teeth.

Sculpture: scutum dullish, densely punctate; metapostnotum dullish, lineo-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus dull, finely reticulate with sparse punctures; supraclypeal area dull, finely reticulate with sparse punctures; labrum smooth; ocellocular area dull, minutely reticulate; frons dull, pit-reticulate; scape dull minutely roughened..

Coloration: scape black; flagellum black, last 6 segments light brown below; labrum black; terga anterior brown-orange, posterior margins transparent orange; scopa light brown; mandibles black with brown tip.

Pubescence: scutum: short, close, white-grey; scutellum: short, close, white-grey.

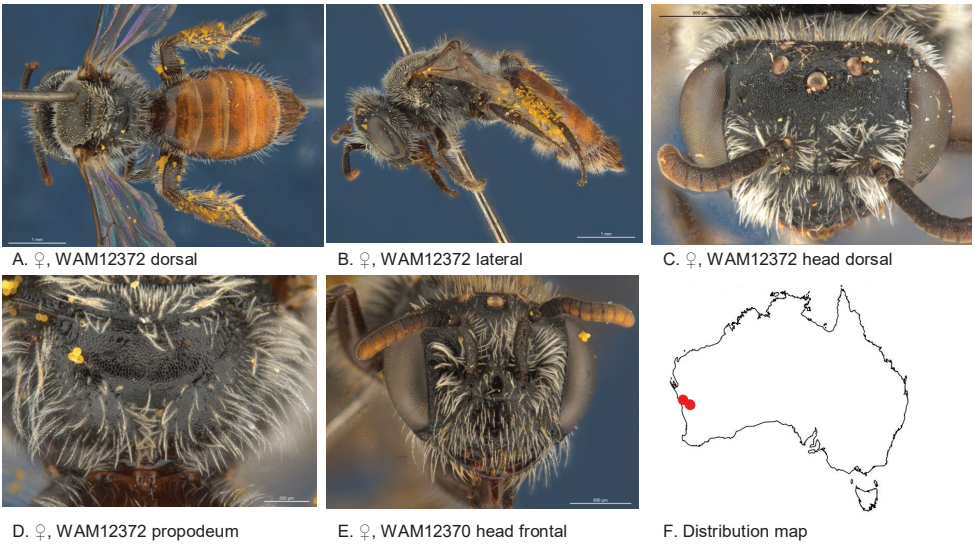


Figure 15. *Leioproctus* (*Colletellus*) *ciliatus* Leijs, sp. n. ♀ holotype.

Remarks. Two specimens have been DNA barcoded, accessible through the following links:

http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS284-13
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS285-13

Flower records. *Calandrinia* sp. (Montiaceae).
Distribution. Figure 15F.
Etymology. The specific epithet refers to the ciliate inner hind tibial spur.

Leioproctus (*Colletellus*) *claviger* Leijs, sp. n.

http://zoobank.org/43E63ECF-0947-4BBA-A296-F2B51569EB1A
Figure 16A–N

Specimens examined. (6♂, 11♀): Holotype female, Dryandra (32.7802S; 116.9675E), 03 Oct. 1982, Howard, C.A. & Houston, T.F., on *Orthrosanthus*, WAM 12384;

Allotype male, Yanchep National Park (31.5350S; 115.6786E), 13 Sep. 1998, Houston, T.F., on *Stypandra glauca*, WAM 21486;

Paratypes: 7 females, Dryandra (32.7802S; 116.9675E), 03 Oct. 1982, Howard, C.A. & Houston, T.F., on *Orthrosanthus*, WAM 12383–90; 2 males, Dryandra (32.7802S; 116.9675E), Sep. 1977, McMillan, R.P., WAM 12391–2; male, Kings Park (31.9580S; 115.8331E), 25 Aug. 1998, Houston, T.F. et al., on *Thryptomene saxicola*, WAM 18634; 2 females , Green Head (30.0650S; 114.9664E), 02 Sep. 1981, McMillan, R.P., WAM 18635, 19113; male, Dawesville (32.6494S; 115.6392E), 15

May 1980, Creagh, S., WAM 21487; female, Bindoo Hill (28.9161S; 115.1833E), 02 Sep. 1995, Cane, J. & Kervin, L., on *Keraudrenia*, WAM 32088; Durokoppin Nature Reserve (31.4102S; 117.7675E), 26 Aug. 1988, Hall, G.P., on *Baeckea*, WAM 12393.

Diagnosis. Ocellocular area pit-reticulate, frons coarsely pit-reticulate, metapostnotum lineo-reticulate, female BTP pointy, hind tibial spur ciliate, male S7 with narrow club shaped ventral apical lobes.

Description. Female holotype: body length: 6.3 mm; head width: 2.35 mm. *Relative head measurements*: HW 50, ASD 2.8, AOD 8.3, HL 37, IAD 11.0, LFW 30, OAD 12, OOD 10.5, OW 15, UFW 35, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.60, FSR 1.23, SFR 0.95.

Structure: terga anteriorly little depressed; BTP pointed; BTP/tibial length ratio 0.29; inner hind tibial spur ciliate, circa 20 teeth.

Sculpture: scutum smooth, closely punctate; metapostnotum horizontal part pit-reticulate, vertical part transverse lineo-reticulate, lateral parts lineo-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth with shallow microsculpture, openly punctate, ventral margin drawn into plate as wide as diameter of ocelli; supraclypeal area smooth with shallow microsculpture, medially without punctures; labrum smooth, black; ocellocular area pit -reticulate, shallower and more shine towards eye; frons pit-reticulate; scape closely punctate.

Coloration: terga anteriorly black-brown, posterior margins narrow, transparent orange; scopa brown; labrum black mandibles; black with brown tip; scape black; flagellum black.

Pubescence: scutum: very short, open and sparse, long, brown; scutellum: very short, open and sparse, long, brown.

Description. Male allotype: body length: 5.8 mm; head width: 1.95 mm. *Relative head measurements*: HW 50, ASD 3.0, AOD 6.0, HL 40, IAD 11.9, LFW 27, OAD 13, OOD 10.9, OW 17, UFW 37, HW/HL 1.2, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.67, FSR 1.10, SFR 1.03.

Structure: terga anteriorly depressed; BTP pointed; flagellum long, F3–11 longer than wide. S7: dorsal apical lobe absent, ventral apical lobe very narrow, setae absent; scape short.

Sculpture: scutum smooth, irregularly closely punctate; metapostnotum horizontal part pit-reticulate, vertical part transverse lineo-reticulate, lateral parts lineo-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus dull, large close punctures; supraclypeal area dull, irregular roughend; ocellocular area pit -reticulate, shallower and more shine towards eye; frons pit-reticulate; scape closely punctate.

Coloration: terga anteriorly black-brown, posterior margins transparent orange; mandibles black with brown tip; flagellum black.

Pubescence: scutum: medium length, open and sparse, light brown; scutellum: medium length, open and sparse, light brown; scape with long pubescence.

Flower records. *Baeckea* sp. (Myrtacea), *Keraudrenia* sp. (Malvaceae), *Orthrosanthus* sp. (Iridaceae), *Stypandra glauca* (Hemerocallidaceae), *Thryptomene saxicola* (Myrtacea).

Distribution. Figure 16F.

Etymology. The specific epithet refers to the club-shaped apical lobe of the male seventh sterna.

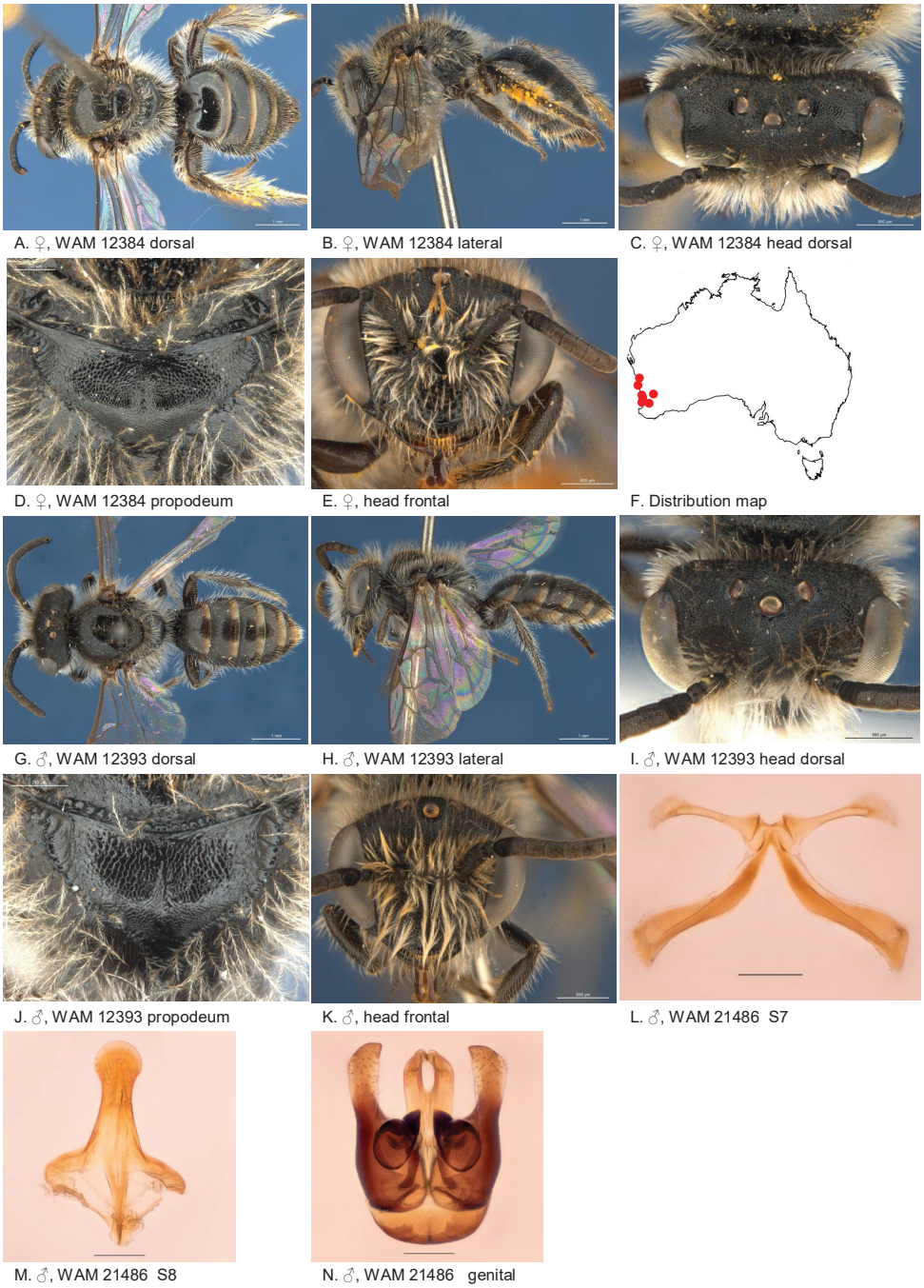


Figure 16. *Leioproctus* (*Colletellus*) *claviger* Leijs, sp. n. ♀ holotype and ♂ allotype and partaype. Scale bar: 0.1 mm (**L, M, N**).

***Leioproctus* (*Colletellus*) *consobrinus* Leijs, sp. n.**
http://zoobank.org/EA941251-C89E-4173-AF0A-366B5BDC1E31
Figure 17A–F

Specimens examined. (3♀): Holotype female, 115 km N of Wiluna (26.5961S; 121.3806E), 29 July 1983, Houston, T.F. & McMillan, R.P., on *Schoenia cassiniana*, WAM 19110; Paratypes: 2 females, 26 mi WNW of Wiluna (26.9438S; 120.3847E), 01 Sep. 1971, Houston, T.F., on *Pimelea*, WAM 19111–2.

Diagnosis. Ocellocular area dull with minute dense punctures, BTP pointed, inner hind tibial spur ciliate, terga dark with narrow transparent posterior margins.

Male unknown.

Description. Female holotype: body length: 6 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 2.8, AOD 8.1, HL 37, IAD 10.9, LFW 32, OAD 12, OOD 9.5, OW 17, UFW 34, HW/HL 1.4, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.84, FSR 1.03, SFR 1.13.

Structure: Terga anteriorly little depressed; BTP pointed; BTP/tibial length ratio 0.28; inner hind tibial spur ciliate with circa 18 small teeth.

Sculpture: scutum smooth, openly to closely punctate; metapostnotum lineo-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate, ventral margin broad; supraclypeal area smooth, sparsely punctate laterally; ocellocular area dull, dense minute punctures; frons densely small punctate; scape dull.

Coloration: terga anteriorly black-brown, posterior margins narrow, transparent orange; scopa light brown; labrum black; scape brown-black; flagellum black, apical 7 segments dark brown; mandibles black, medially brown, with black tip.

Pubescence: scutum very short, open and sparse, long, brown; scutellum very short, open and sparse, long, brown.

Flower records. *Pimelea* sp. (Thymelaeaceae), *Schoenia cassiniana* (Asteraceae).

Distribution. Figure 17F.

Etymology. The specific epithet refers to the average *L.* (*Colletellus*) habitus of this species.

***Leioproctus* (*Colletellus*) *constrictus* Leijs, sp. n.**
http://zoobank.org/BFC7FD24-06E5-45DB-BB15-552C8AE08AEA
Figure 18A–M

Specimens examined. (12♂, 29♀): Holotype female, 16 km WNW of Merredin (31.6169S; 118.3486E), 29 Oct. 1978, Houston, T.F., on *Grevillea paradoxa*, WAM 12343;

Allotype male, WAM 12345, same locality data as holotype;

Paratypes: 6 females, 3 males, 16 km WNW of Merredin (31.6169S; 118.3486E), 29 Oct. 1978, Houston, T.F., on *Grevillea paradoxa*, WAM 12339–42,44,46–49; 5 fe-

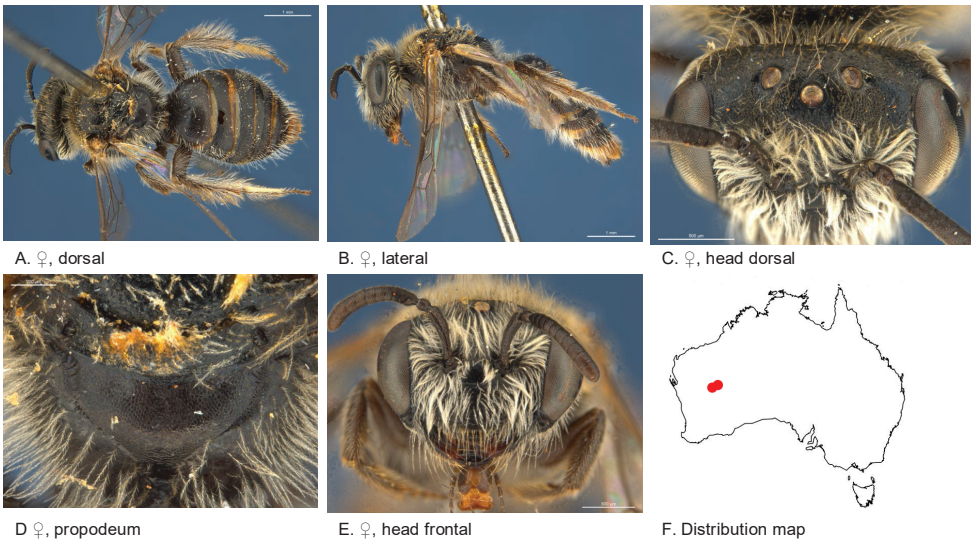


Figure 17. *Leioproctus* (*Colletellus*) *consobrinus* Leijs, sp. n. ♀ holotype WAM19110.

males, 3.5 km W of Yellowdine (31.3286S; 119.6503E), 27 Oct. 1978, Houston, T.F., on *Grevillea paradoxa*, WAM 12350–4; female, 18 km SSW of Mulline (29.8686S; 120.3506E), 23 Sep. 1982, Houston, T.F. & Hanich, B.P., on *Eremophila pantoni*, WAM 12355; male, 1 km S of Evanston (29.7477S; 119.4814E), 23 Sep. 1982, Houston, T.F. & Hanich, B.P., on *Grevillea paradoxa*, WAM 19116; 2 females, 3 males, Dowerin (31.1925S; 117.0367E), 21 Oct. 1984, McMillan, R.P., on *Grevillea*, WAM 19828–32; 14 females, 3 males, 29 km NE of Eneabba (29.5911S; 115.4397E), 26 Oct. 2000, Houston, T.F. & Mueller, O., on *Grevillea petrophiloides*, WAM 31884-900; 1 male, Lochada, Omega track 1.5 km N of Mungada Rd, WA, (29.18332S; 116.45798E), 18 Sep. 2009, R. Leijs, on *Ecdeiocolea monostachya*. SAMA 32-033499.

Diagnosis. Ocellocular area, clypeus, scutum, metapostnotum and terga shiny with open to sparse punctures, post-gradular areas depressed, female BTP rounded, inner hind tibial spur ciliate, male S7 ventral apical lobes with long branched setae.

Description. Female holotype: body length: 5.9 mm; head width: 1.9 mm. *Relative head measurements*: HW 50, ASD 2.6, AOD 7.9, HL 38, IAD 9.4, LFW 28, OAD 16, OOD 8.4, OW 17, UFW 32, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.52, FSR 1.08, SFR 0.93.

Structure: terga anteriorly strongly depressed; BTP rounded; BTP/tibial length ratio 0.18; inner hind tibial spur ciliate with 5–10 slender teeth.

Sculpture: scutum smooth with sparse punctures; metapostnotum smooth, shiny, shallow pit-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth with open to sparse punctures; supraclypeal area smooth, sparsely punctate; ocellocular area smooth, shiny, sparsely punctate; frons smooth openly punctate; vertex roughened with punctures.

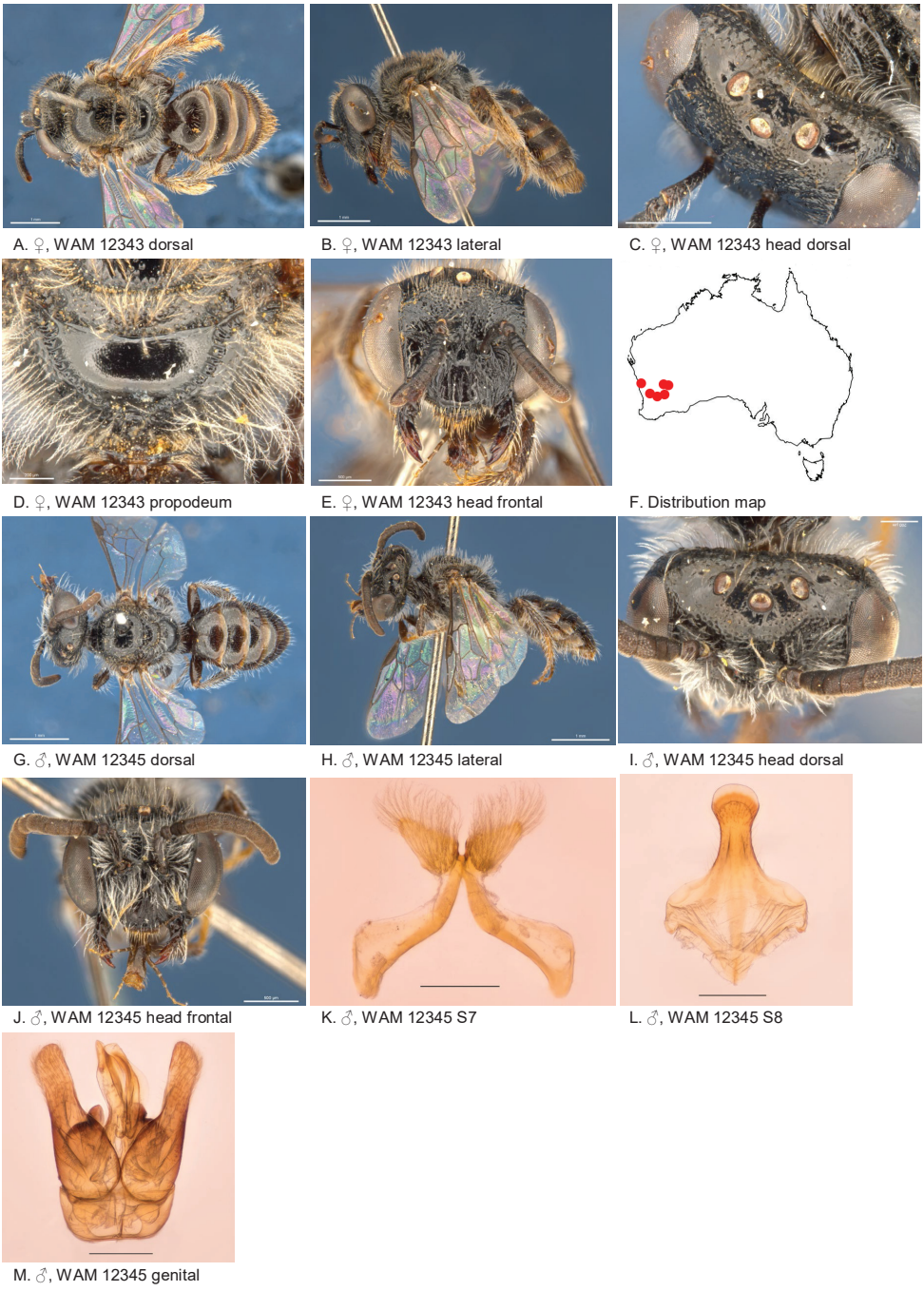


Figure 18. *Leioproctus* (*Colletellus*) *constrictus* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**K, L, M**).

Coloration: terga anteriorly brown-black, posterior margins transparent orange; scopa light brown; labrum brown; mandibles brown with darker tip; flagellum F9–11 orange/brown below.

Pubescence: scutum: dispersed, medium length, branched; scutellum: long, sparse, light brown; metanotum: medium length, branched, dense on posterior margin; sterna 1–4 with fringes of long simple hairs, S5 with fringe of dense branched white hairs; scape smooth, few punctures and a few short hairs.

Description. Male allotype: body length: 4.2 mm; head width: 1.52 mm. *Relative head measurements*: HW 50, ASD 3.4, AOD 6.6, HL 38, IAD 10.3, LFW 26, OAD 16, OOD 8.9, OW 18, UFW 33, HW/HL 1.3, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.61, FSR 1.00, SFR 1.00.

Structure: terga anteriorly strongly depressed; BTP rounded, slightly elongated. S7: dorsal apical lobe absent, ventral apical lobe medium large, branched setae present on entire ventral apical lobe.

Sculpture: scutum smooth, sparsely punctate; metapostnotum smooth with shallow microsculpture; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate , ventral margin width about 1/3 ocellar diameter; supraclypeal area smooth with open to sparse punctures; ocellocular area smooth, almost no punctures; frons smooth openly to closely punctate; scape minutely roughened.

Coloration: terga anteriorly brown, posterior margins transparent orange; labrum black; mandibles brown with red-brown tip; flagellum brown, lighter towards the tip; scape black.

Pubescence: scutum: long sparse whitish; scutellum: long sparse whitish; metanotum medium length branched dense on posterior margin.

Flower records. *Eremophila pantone* (Scrophulariaceae), *Grevillea paradoxa* (Proteaceae), *Grevillea petrophiloides* (Proteaceae), *Grevillea* sp. (Proteaceae), *Ecdeiocolea monostachya* (Ecdeiocoleaceae).

Distribution. Figure 18F.

Etymology. The specific epithet refers to strongly depressed post gradular areas of T2–3 in both sexes.

Leioproctus (*Colletellus*) *laciniosus* Leijs, sp. n.

http://zoobank.org/6F55542F-8CED-4F4F-8C58-12E37AA81079

Figures 2B, 19A–M

Specimens examined. (5♂, 3♀): Holotype female, Bon Bon Stn (30.7789S; 135.3841E), 26 Oct. 2010, Leijs, R., on *Angianthus brachypappus*, SAMA 32-033484, BOLD: AUSBS140-12/RL1673A.

Allotype male, same locality data as holotype, SAMA 32-033486; BOLD: AUSBS143-12/RL1673B.

Paratypes: female, SAMA 32-033483, BOLD: AUSBS141-12/RL1673C, male, SAMA 32-033485, BOLD: AUSBS142-12/RL1673D, same locality data as holo-

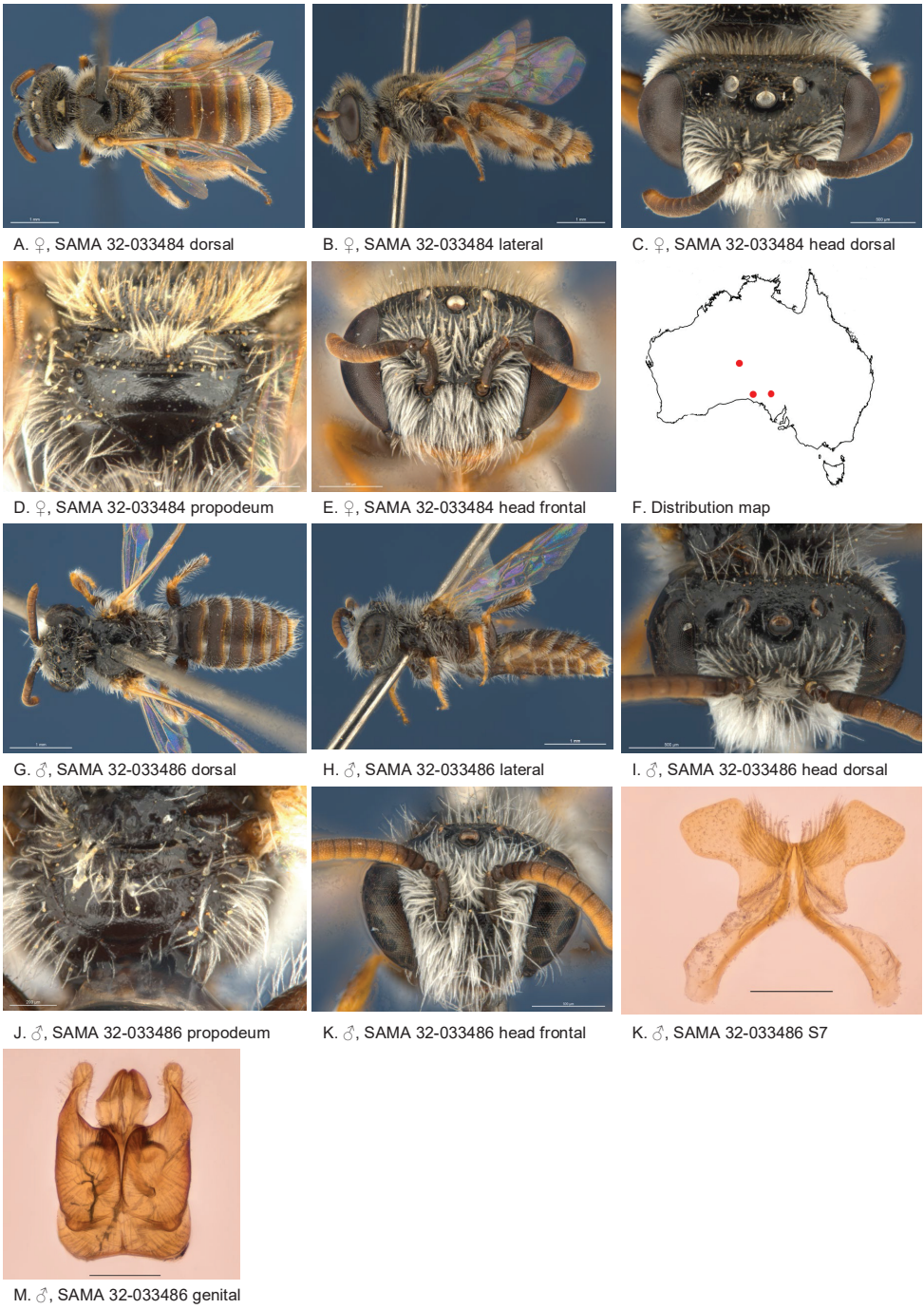


Figure 19. *Leioproctus* (*Colletellus*) *laciniosus* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**K, M**).

type; female, Lake Wilson, 11 Sept 2015, SA, 26.0285S; 129.6159E, P. Hudson; 3 males, Ooldea (30.8915S; 132.0925E), 03 Oct. 1968, Key, Upton, Balderson, ANIC 32-111874–6;

Diagnosis. First recurrent vein meeting to the first submarginal cross vein, T2–4 with adpressed hair bands on posterior margins, female BTB rounded, inner hind tibial spur pectinate.

Description. Female holotype: body length: 5.6 mm; head width: 1.9 mm. *Relative head measurements*: HW 50, ASD 2.6, AOD 8.3, HL 35, IAD 9.4, LFW 28, OAD 15, OOD 9.1, OW 17, UFW 33, HW/HL 1.4, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.39, FSR 1.71, SFR 0.79.

Structure: terga anteriorly not depressed; BTP rounded; BTP/tibial length ratio 0.22; inner hind tibial spur pectinate with 10 teeth.

Sculpture: scutum smooth with sparse punctures; metapostnotum smooth, shiny, horizontal part shorter than vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; scape dull with microsculpture; clypeus shiny, openly punctate; supraclypeal area shiny, some punctures; labrum smooth; ocellocular area smooth, shiny; frons smooth openly punctate.

Coloration: terga anteriorly brown-orange, posterior margins transparent white, T2–4 with white adpressed hair bands; scopa white; labrum orange clypeus with orange anterior rim; mandibles orange with black tip; scape brown; flagellum F1–3 black, F4–10 orange/brown below.

Pubescence: scutum: dispersed, medium length, branched; scutellum: dispersed, medium length, branched; metanotum: medium length, branched, dense on posterior margin; S2–4 hair bands, long branched.

Description. Male allotype: body length: 4.4 mm; headwidth: 1.6 mm. *Relative head measurements*: HW 50, ASD 2.4, AOD 6.6, HL 37, IAD 9.8, LFW 25, OAD 16, OOD 8.9, OW 17, UFW 33, HW/HL 1.4, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.54, FSR 1.64, SFR 0.87.

Structure: terga anteriorly not depressed; BTP rounded. S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on apico medial area of ventral apical lobe.

Sculpture: scutum smooth with sparse punctures; metapostnotum shiny; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate; supraclypeal area shiny, openly to closely punctate; labrum; ocellocular area smooth, shiny, almost no punctures; frons smooth openly to sparsely punctate; vertex.

coloration: terga anteriorly brown-orange, posterior margins transparent white; mandibles brown at base, orange medially with brown tip; flagellum F1–3 black, F4–11 orange/brown below.

Pubescence: scutum: dispersed, medium length, branched; scutellum: dispersed, medium length, branched; metanotum: dispersed, medium length, branched; S2–4 with fringes of short hairs; scape shiny with medium length branched white hairs.

Remarks. Four examined specimens have been DNA barcoded, accessible through the following links:

http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS140-12
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS141-12
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS142-12
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS143-12

Flower records. *Angianthus brachypappus* (Asteraceae).
Distribution. Figure 19F.
Etymology. The specific epithet refers to fringe of white hairs on the posterior T2–4.

***Leioproctus* (*Colletellus*) *longivultu* Leijs, sp. n.**
http://zoobank.org/317DB039-333A-4E08-88BA-9E69532873D5
Figure 20A–F

Specimens examined. (4♀): Holotype female, 7 km E of Boologooro (24.2733S; 114.0308E), 27 Aug. 1980, Howard, C.A. & Houston, T.F., on *Calandrinia polyandra*, WAM 19841;

Paratypes 3 females, 10 km NNW of Meedo (25.6991S; 114.7175E), 23 Aug. 1980, Howard, C.A. & Houston, T.F., on *Calandrinia polyandra*, WAM 12373–4, 19838.

Diagnosis. Ocellocular area smooth, sparse to openly punctate, metapostnotum dull, pit-reticulate, face longer that wide.

Male unknown.

Description. Female: body length: 6.3 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 3.1, AOD 8.5, HL 45, IAD 8.7, LFW 31, OAD 16, OOD 9.7, OW 17, UFW 34, HW/HL 1.1, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.49, FSR 0.88, SFR 1.04.

Structure: terga anteriorly not depressed; BTP pointed; BTP/tibial length ratio 0.34; inner hind tibial spur pectinate with 3 large teeth; Clypeus ventral margin narrow, 1/4 of ocellar diameter.

Sculpture: scutum smooth, closely punctate; metapostnotum triangular shaped, dull, pit-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, closely punctate, supraclypeal area smooth, closely punctate; ocellocular area smooth openly punctate; frons smooth closely punctate; scape somewhat shiny.

Coloration: terga anteriorly brown-orange, posterior margins transparent orange; scopa light brown; labrum dark brown; mandibles orange with brown tip; brown; flagellum F4–10 orange brown.

Pubescence: scutum: very short, close, light brown; scutellum: very short, close, light brown; sterna 1–4 with fringes of long branched hairs, S5 with dense fringe of hairs.

Flower records. *Calandrinia polyandra* (Montiaceae).
Distribution. Figure 20F.
Etymology. The specific epithet refers to the elongated face of this species.

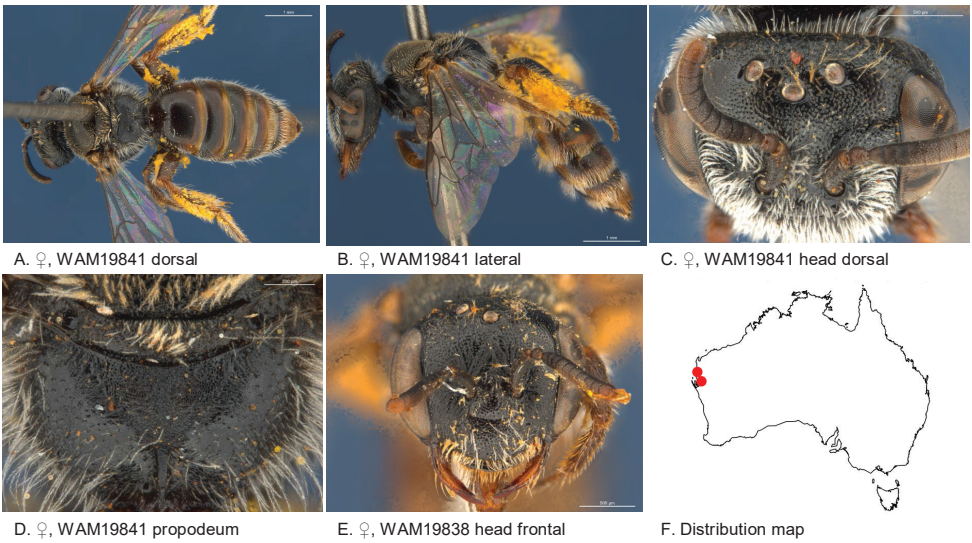


Figure 20. *Leioproctus* (*Colletellus*) *longivultu* Leijs, sp. n ♀ holotype.

***Leioproctus* (*Colletellus*) *lucidus* Leijs sp. n.**
http://zoobank.org/30B4E9A5-1DBC-4C6E-8DFA-7B72AD068E8F
Figure 21A–F

Specimens examined. (1♀): Holotype female, 12 km ENE of Bungalbin Hill (30.29S; 119.69E), 11 Sep. 1979, Houston, T.F. et al., WAM 19833.

Diagnosis. Integument of most body parts smooth and shiny, terga with narrow transparent posterior margins and open fringes of white hairs.

Male unknown.

Description. Female: body length: 6 mm; head width: 1.9 mm. *Relative head measurements*: HW 50, ASD 3.2, AOD 8.0, HL 37, IAD 9.8, LFW 31, OAD 13, OOD 9.7, OW 17, UFW 34, HW/HL 1.4, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.57, FSR 0.97, SFR 1.04.

Structure: terga anteriorly not depressed; BTP rounded; BTP/tibial length ratio 0.26; inner hind tibial spur pectinate with 5 strong teeth; clypeus ventral margin width about half ocellar diameter.

Sculpture: scutum smooth, openly punctate; metapostnotum smooth with shallow microsculpture; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate; supraclypeal area smooth, openly to closely punctate; ocellocular area smooth, almost no punctures; frons smooth openly to closely punctate; scape below shiny with sparse punctures.

Coloration: terga anteriorly brown, posterior margins transparent orange; scopa light brown hairs; labrum dark-brown; mandibles red-brown darker at basis; scape dark-brown; flagellum dark brown, apical 7 segments brown.

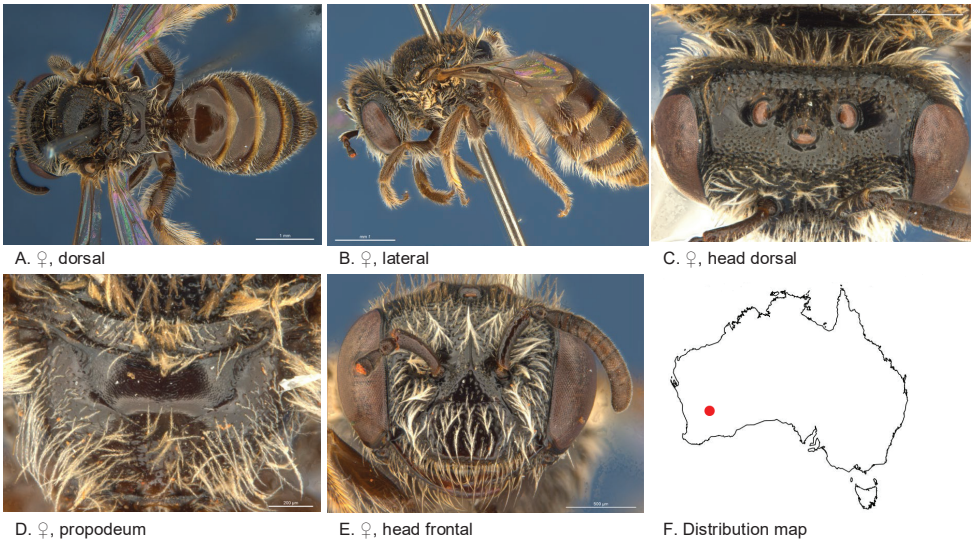


Figure 21. *Leioproctus* (*Colletellus*) *lucidus* Leijs, sp. n. ♀ holotype WAM19833.

Pubescence: scutum: medium to short, sparse brown; scutellum: medium to short, sparse brown; sterna S5 with fringe of dense white hairs.

Flower records. No data.

Distribution. Figure 21F.

Etymology. The specific epithet refers to the smooth and shiny integument on head, scutum and terga of this species.

***Leioproctus* (*Colletellus*) *nitidifuscus* Leijs, sp. n.**
http://zoobank.org/1344DABE-B302-4945-8E61-B8C2B8553644
Figure 22A–F

Specimens examined. (6♀): Holotype female, Kalbarri NP (27.8333S; 114.4667E), 14 Aug. 2003, Bickel, D., yellow pan trap, AM, K4473004.

Paratypes 5 females, same locality data as holotype, AM, K447300–03, 05.

Diagnosis. Entire body smooth and shiny, abdomen brown, terga with transparent posterior margins.

Male unknown.

Description. female holotype: body length: 4.8 mm; head width: 1.5 mm. *Relative head measurements*: HW 50, ASD 3.8, AOD 9.5, HL 43, IAD 9.9, LFW 34, OAD 15, OOD 10.5, OW 18, UFW 36, HW/HL 1.2, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.92, FSR 1.16, SFR 1.09.

Structure: terga anteriorly not depressed; BTP rounded, elongated; BTP/tibial length ratio 0.28; inner hind tibial spur ciliate with circa 20 fine teeth.

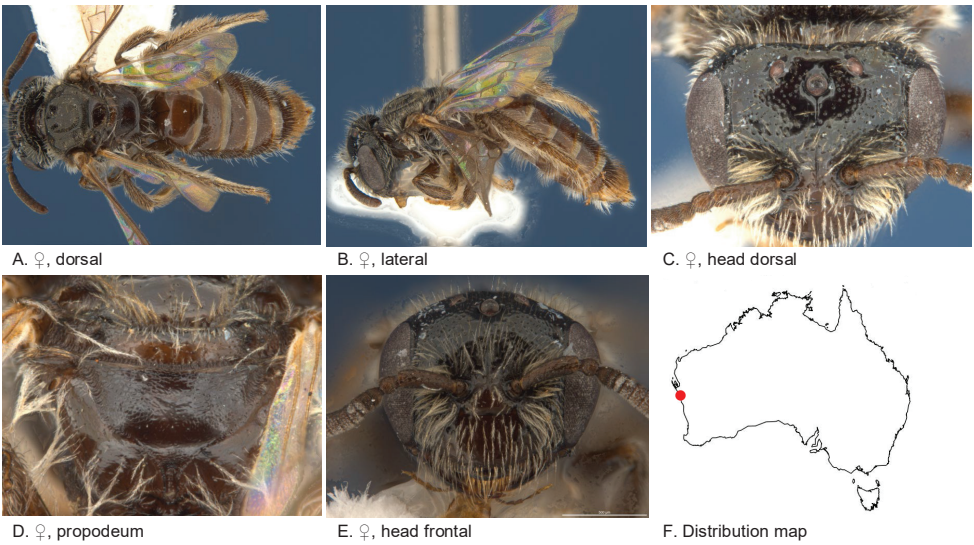


Figure 22. *Leioproctus* (*Colletellus*) *nitidifuscus* Leijs, sp. n. ♀ holotype AM K447304.

Sculpture: scutum smooth, openly punctate without punctures on scutellum; metapostnotum almost entirely smooth, some transverse shallow reticulation medio-anteriorly, horizontal part 3 times as long as vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, sparse punctures; supraclypeal area smooth without punctures; labrum with row of orange setae; ocellocular area smooth, shiny, some scattered punctures near eye; frons smooth openly to sparsely punctate; scape dull, roughly sculptured with punctures and reticulation.

Coloration: terga anteriorly brown-orange, posterior margins transparent white; scopa white; mandibles brown, orange tip; flagellum dark, apical two segments with orange tint below.

Pubescence: scutum: open, short and some scattered, long; scutellum: almost bare; S2–4 with open medium length branched hairs, S5 with dense fringe of branched hairs.

Flower records. No data.

Distribution. Figure 22F.

Etymology. The specific epithet refers to very smooth and brown integument of large parts of the body of this species.

Leioproctus (*Colletellus*) *pectinatus* Leijs, sp. n.

http://zoobank.org/F3DBB807-A671-4C61-BE15-9878922ED85C

Figure 23A–F

Specimens examined. (4♀): Holotype female, 25 km SW of Tangadee (24.5688S; 118.7636E), 22 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Calandrinia*, WAM 12333;

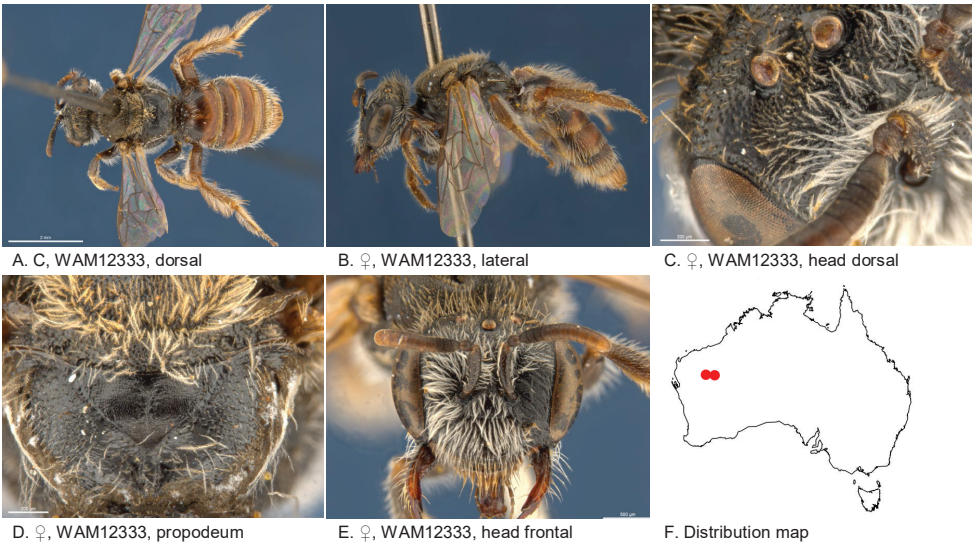


Figure 23. *Leioproctus* (*Colletellus*) *pectinatus* Leijs, sp. n. ♀ holotype.

Paratypes female, 24 km NNE of Beyondie (24.7055S; 120.2558E), 17 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Calandrinia*, WAM 12329; 2 females, 25 km SW of Tangadee (24.5688S; 118.7636E), 22 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Calandrinia*, WAM 12331–2.

Diagnosis. Ocellocular area openly punctate, propodeal triangle small, shiny and micro alveolate, inner hind tibial spur strongly pectinate.

Male unknown.

Description. Female: body length: 6.7 mm; head width: 1.9 mm. *Relative head measurements*: HW 50, ASD 2.8, AOD 9.0, HL 44, IAD 10.0, LFW 32, OAD 17, OOD 9.3, OW 17, UFW 34, HW/HL 1.1, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.38, FSR 1.00, SFR 0.93.

Structure: terga anteriorly little depressed; BTP rounded; BTP/tibial length ratio 0.18; inner hind tibial spur pectinate with 2–5 strong teeth; flagellum F1>F2, F1–9 wider than long.

Sculpture: scutum smooth, with close to dense punctation; metapostnotum shiny, finely microalveolate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate, smooth between, anterior margin not drawn in thin plate; supraclypeal area shiny, openly punctate, smooth between; scape shiny; labrum medially slightly raised; ocellocular area punctate; frons punctate; vertex punctate.

Coloration: terga anteriorly black, posterior margins transparent orange, fovea on T2 black; scopa white; mandibles orange brown with darker tip; scape with white pubescence F1–9 black, orange towards the tip.

Pubescence: scutum: medium length, open; scutellum: medium long, open; metanotum medium length, open; sterna 1–4 with fringes of long branched hairs, S5 with dense fringe of hairs; scape with white pubescence.

Flower records. *Calandrinia* sp. (Montiaceae).
Distribution. Figure 23F.
Etymology. The specific epithet refers to the strongly pectinate inner hind tibial spur.

***Leioproctus* (*Colletellus*) *pilotapilus* Leijs, sp. n.**
http://zoobank.org/CA4D2A0A-FD06-4220-A93B-22EAE0F4951F
Figure 24A–N

Specimens examined. (3♂, 6♀): Holotype female, 41km E of Charlies Knob (24.6808S; 124.9858E), 01 Aug. 1983, Houston, T.F. & McMillan, R.P., on *Schoenia cassiniana*, WAM 12401;

Allotype male, WAM 12402 same data as holotype;

Paratypes 1 male , 41km E of Charlies Knob (24.6808S; 124.9858E), 01 Aug. 1983, Houston, T.F. & McMillan, R.P., on *Schoenia cassiniana*, WAM 12402-3; 1 female, 1 male, 11 km SW of Leake, Mount (25.8486S; 119.0769E), 16 Aug. 1984, Houston, T.F. & Hanich, B.P., on *Podolepis canescens*, WAM 12404–5; male, Cohen, Lake (24.4508S; 125.0308E), 01 Aug. 1983, Houston, T.F. & McMillan, R.P., on *Schoenia cassiniana*, WAM 12406; female, Throssell, Lake (27.6230S; 124.1144E), 13 Sep. 1982, Houston, T.F. & Hanich, B.P., on *Helichrysum*?, WAM 12407; 2 females, 11 km NNE of Anketell (27.9872S; 118.9508E), 04 Sep. 1981, Houston, T.F., WAM 19836–7; female, 10 km NNW of Meedo (25.6991S; 114.7175E), 23 Aug. 1980, Howard, C.A. & Houston, T.F., on *Helipterum craspedioides*, WAM 19840.

Diagnosis. Ocellocular area smooth with dispersed punctures, metapostnotum with minute shallow pit-reticulation, female scutum covered with dense short brown pubescence, BTP rounded, inner hind tibial spur strongly pectinate, terga with transparent posterior margins.

Description. Female holotype: body length: 6.6 mm; head width: 1.8 mm. *Relative head measurements*: HW 50, ASD 2.3, AOD 9.2, HL 39, IAD 9.4, LFW 31, OAD 16, OOD 9.9, OW 17, UFW 35, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.22, FSR 1.00, SFR 0.86.

Structure: terga anteriorly little depressed; BTP rounded; BTP/tibial length ratio 0.16; inner hind tibial spur pectinate with 4 large spines.

Sculpture: scutum smooth, closely punctate; metapostnotum minute shallow pit-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate , ventral margin narrow brown; supraclypeal area smooth, openly to closely punctate; ocellocular area dull, finely pit-reticulate; frons smooth openly to closely punctate; scape shiny but not smooth.

Coloration: terga anteriorly brown, posterior margins wide, transparent orange; white lateral hair bands on T2–3, T4 entire; scopa white; mandibles brown with dark tip; labrum brown; scape black; flagellum brown-black.

Pubescence: scutum: short, close, brown; scutellum: short, close, brown; S2–4 with rows of long openly spaced branched hairs, S5 with fringe of closely spaced branched hairs.

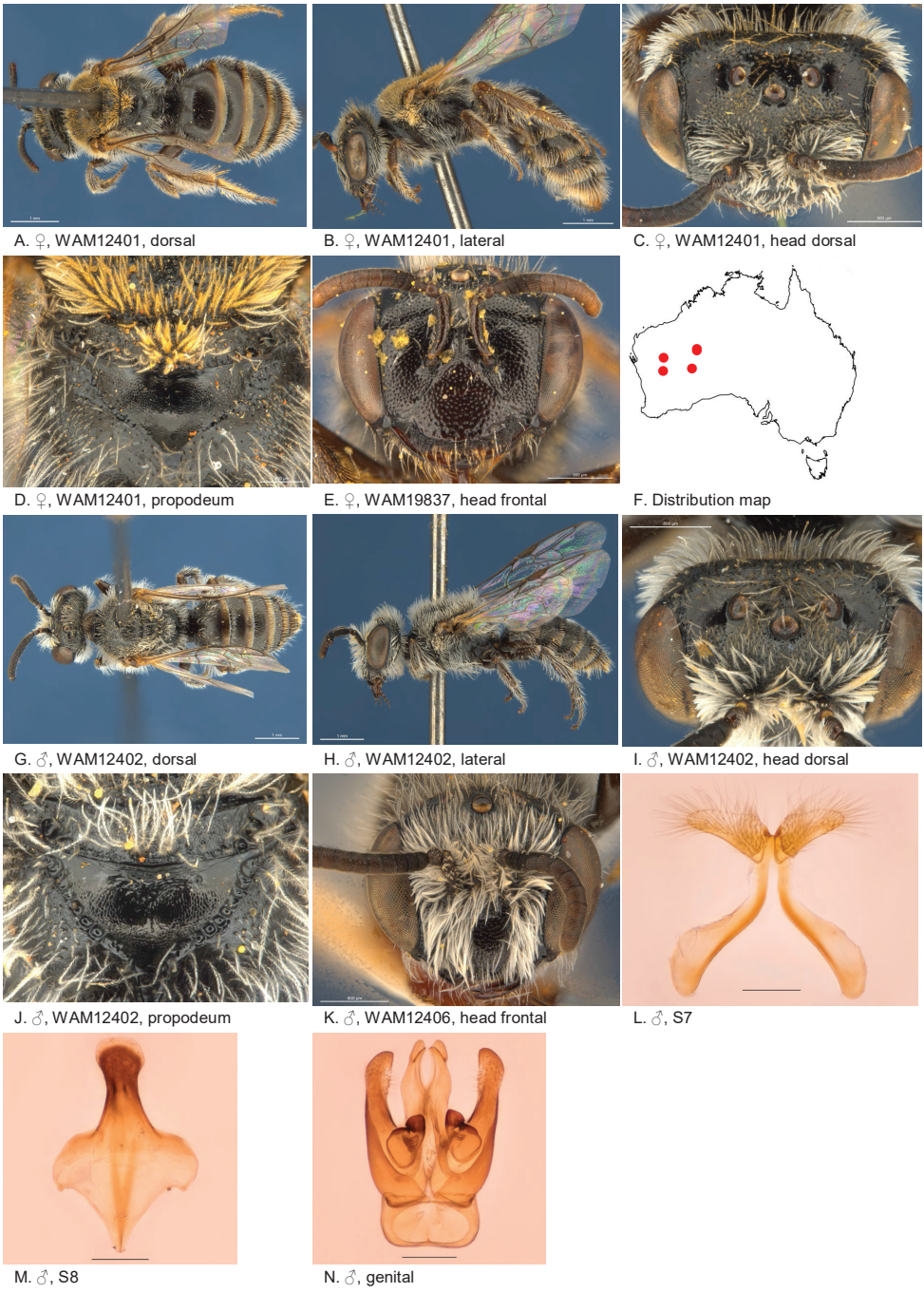


Figure 24. *Leioproctus* (*Colletellus*) *pilotapilus* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**L, M, N**).

Description. Male: measurements: body length: 5.9 mm; head width: 1.85 mm. *Relative head measurements*: HW 50, ASD 2.8, AOD 7.3, HL 41, IAD 8.7, LFW 28, OAD 15, OOD 10.3, OW 18, UFW 36, HW/HL 1.2, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.24, FSR 0.93, SFR 1.00.

Structure: terga anteriorly little depressed; BTP rounded; F4–11 about as wide as long. S7: dorsal apical lobe absent, ventral apical lobe large, with robust simple setae on ventral apical lobe.

Sculpture: scutum smooth with microsculpture, sparsely punctate; metapostnotum dullish, minute shallow pit-reticulate, some transverse striation medio-anteriorly; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth, openly to closely punctate ; supraclypeal area smooth, openly to closely punctate ; ocellocular area shiny, micro-reticulate; frons smooth openly to closely punctate; scape dull.

Coloration: terga anteriorly brown-black, posterior margins wide, transparent orange; mandibles brown with reddish tip; labrum black; scape brown-black; flagellum brown.

Pubescence: scutum: long, open, whitish; scutellum: long, open, whitish; scape with white, plumose pubescence.

Flower records. *Helipterum craspedioides* (Asteraceae), *Helichrysum*? sp. (Asteraceae), *Podolepis canescens* (Asteraceae), *Schoenia cassiniana* (Asteraceae).

Distribution. Figure 24F.

Etymology. The specific epithet refers to the dense and short pubescence on the scutum.

Leioproctus (*Colletellus*) *quadripinnatus* Leijs, sp. n.

http://zoobank.org/6FC7C6B3-9D13-4123-8750-ACEFC0B557D7

Figure 25A–I

Specimens examined. (1♂): Holotype male, Eagle Bay (33.5591S; 115.0692E), 27 Sep. 1975, Spencer, K., WAM 19115.

Diagnosis. Ocellocular area smooth with a few sparse fine punctures, metapostnotum entirely smooth, S7 slender dorsal and ventral apical lobes bearing robust simple setae.

Female unknown.

Description. Male holotype: body length: 4.5 mm; head width: 1.5 mm. *Relative head measurements*: HW 50, ASD 3.3, AOD 5.9, HL 45, IAD 11.1, LFW 27, OAD 15, OOD 12.2, OW 18, UFW 37, HW/HL 1.1, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.43, FSR 0.91, SFR 1.19.

Structure: terga anteriorly little depressed; BTP rounded, very short; flagellum short, F1–9 wider than long. S7: dorsal apical lobe slender, ventral apical lobe slender, robust simple setae present on dorsal subcentral apical ridge and ventral apical lobe; scape short.

Sculpture: scutum smooth sparsely punctate; metapostnotum smooth, without or very shallow microsculpture, almost wholly vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate; supraclypeal area shiny, openly punctate; labrum orange; ocellocular area smooth with sparse fine punctures; scape dull.

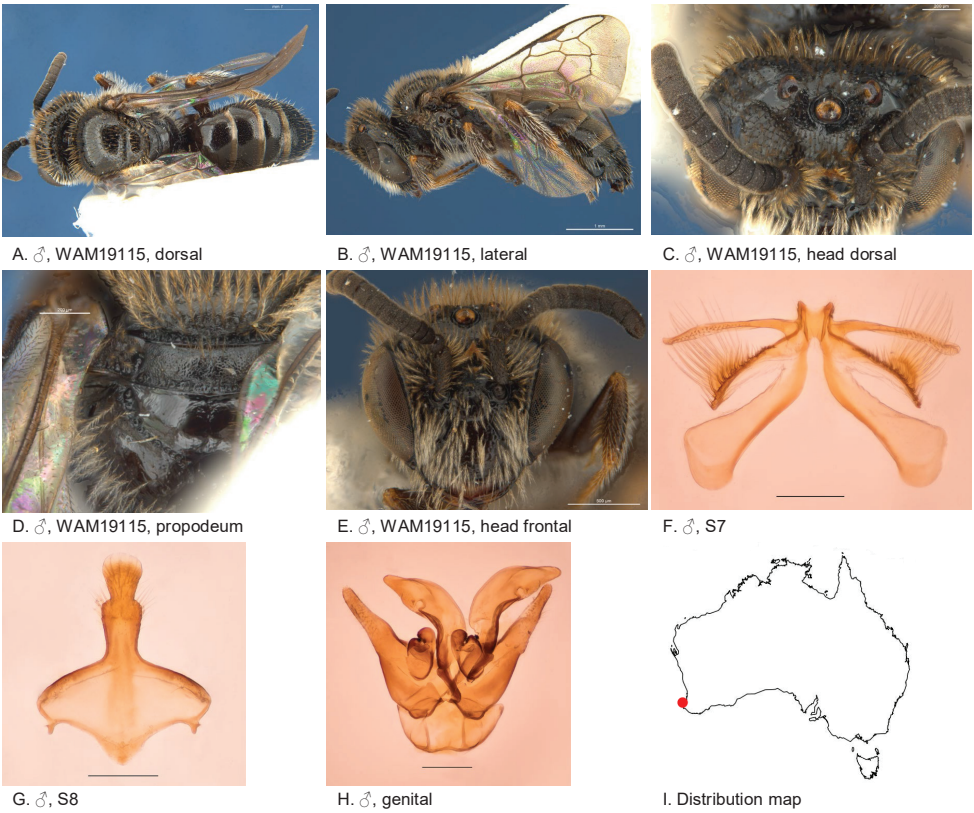


Figure 25. *Leioproctus* (*Colletellus*) *quadripinnatus* Leijs, sp. n. ♂ holotype. Scale bar: 0.1 mm (**F, G, H**).

Coloration: terga anteriorly brown, posterior margins transparent pale orange; mandibles brown with lighter tip.

Pubescence: scutum: medium length sparse, light brown; scutellum: medium length, sparse, light brown.

Flower records. No data.

Distribution. Figure 25I.

Etymology. The specific epithet refers to thin feathery like apical lobes of the male sterna 7.

***Leioproctus* (*Colletellus*) *rubicundus* Leijs, sp. n.**
http://zoobank.org/A33ADBE8-8CF0-487B-9D54-F79F69DA6F42
Figures 2A, 26A–N

Specimens examined. (2♂, 5♀): Holotype female, Bon Bon Stn (30.7789S; 135.3841E), 26 Oct. 2010, Leijs, R., on *Angianthus brachypappus*, SAMA 32-033488 AUSBS145-12/RL1630A;

Allotype male, Pernatty Stn, North Tiffin Hill (31.4826S; 137.7454E), 05 Sep. 2016, Leijs, R., on *Gunniopsis*, SAMA 32-033492, KR4734;

Paratypes 2 females, SAMA 32-033487, 89; BOLD: AUSBS139-12/RL1631; AUSBS144-12/RL1631B same locality data as holotype; 2 females, 1 male, Pernatty Stn, North Tiffin Hill (31.4826S; 137.7454E), 05 Sep. 2016, Leijs, R., on *Gunniopsis*, SAMA 32-033490,91,93 KR4732,33,35; 1 female, from salt lake, SA, (30.8161S; 134.3042E), P. Hudson.

Diagnosis. First recurrent vein meeting to the first submarginal cross vein, ocellocular area smooth, without punctures, metapostnotum smooth, shiny, horizontal part shorter than vertical, T2–4 with semi erect hairs on posterior margins, female BTB rounded, inner hind tibial spur pectinate.

Description. Female holotype: body length: 6.1 mm; head width: 2.1 mm. *Relative head measurements*: HW 50, ASD 3.0, AOD 8.9, HL 34, IAD 8.6, LFW 33, OAD 15, OOD 9.0, OW 18, UFW 35, HW/HL 1.5, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.63, FSR 1.72, SFR 0.84.

Structure: terga anteriorly not depressed; BTP rounded; BTP/tibial length ratio 0.21; inner hind tibial spur pectinate with 10 teeth.

Sculpture: scutum smooth with sparse punctures; metapostnotum smooth, shiny, horizontal part shorter than vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, closely punctate, orange anterior rim; supraclypeal area shiny, closely punctate; ocellocular area smooth, shiny; frons smooth openly to sparsely punctate; scape shiny, sparsely punctate.

Coloration: terga anteriorly orange, laterally brown medially, posteriorly orange, transparent posterior margins, no adpressed hair bands; scopa white; mandibles orange with brown tip; flagellum F1–3 black, F4–10 orange/brown below; scape black.

Pubescence: scutum: dispersed, medium length, branched; scutellum: dispersed, medium length, branched; metanotum: dispersed, medium length, branched; S2–4 hair bands, long, branched.

Description. Male allotype: body length: 5.5 mm; head width: 1.7 mm. *Relative head measurements:* HW 50, ASD 2.5, AOD 7.9, HL 38, IAD 9.4, LFW 27, OAD 15, OOD 8.6, OW 17, UFW 33, HW/HL 1.3, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.72, FSR 1.39, SFR 1.00.

Structure: terga anteriorly not depressed; BTP rounded; flagellum F1–3 black, F 4–11 brown below, shorter than wide.

Sculpture: scutum smooth with almost no punctures; metapostnotum shiny with microsculpture, horizontal part shorter than vertical; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, closely punctate; supraclypeal area shiny, closely punctate; ocellocular area smooth, shiny, almost no punctures; frons smooth, openly to closely punctate; scape shiny, sparsely punctate.

Coloration: terga anteriorly black, posterior margins transparent orange; mandibles black with brown tip; scape black.

Pubescence: scutum: white, dispersed, medium length, branched; scutellum: white, dispersed, medium length, branched; S2–4 short dense apical hair bands.

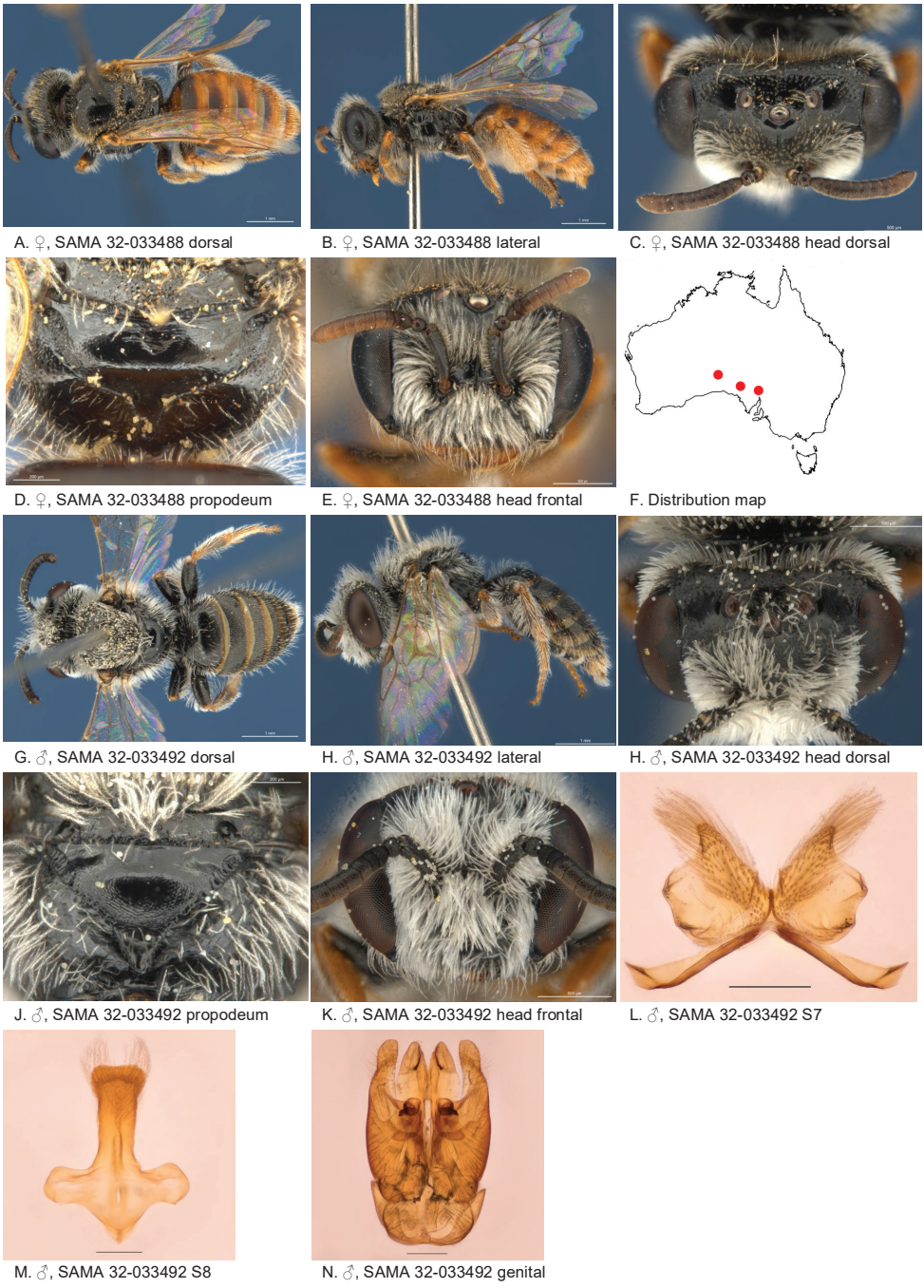


Figure 26. *Leioproctus* (*Colletellus*) *rubicundus* Leijs, sp. n. ♀ holotype and ♂ allotype. Scale bar: 0.1 mm (**L, M, N**).

S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on apico-medial area of ventral apical lobe.

Remarks. Three specimens have been DNA barcoded, accessible through the following links:

http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS139-12
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS144-12
http://www.boldsystems.org/index.php/Public_RecordView?processid=AUSBS145-12

Flower records. *Angianthus brachypappus* (Asteraceae), *Gunniopsis* sp. (Aizoaceae).
Distribution. Figure 26F.
Etymology. The specific epithet refers to the colour of the female metasoma.

***Leioproctus* (*Colletellus*) *rubricinctus* Leijs, sp. n.**
http://zoobank.org/A754B7A1-FEC3-4602-98A4-1A03EC0FC877
Figure 27A–H

Specimens examined. (10♂): Holotype male, Bullfinch (30.5797S; 119.1144E), 07 Sep. 1979, Houston, T.F. et al., WAM 12357;

Paratypes 5 males, WAM 12356,58–61 same locality data as holotype; 3 males, Bullfinch (30.7147S; 119.1144E), 07 Sep. 1979, Houston, T.F. et al., on *Thryptomene tuberculata*, WAM 12362–4; 1 male, Kadji Kadji (29.1833S; 116.458E), 19 Sep. 2009, Charles Darwin Bush Blitz, Leijs, R., blue pan trap, SAMA 32-033499/RL1526.

Diagnosis. Ocellocular area dull, densely punctate and irregular roughened, frons irregular pit-reticulate, terga with pregradular depressions, posterior margins broadly orange transparent, F3–9 longer than wide.

Female unknown.

Description. Male holotype: body length: 4.9 mm; head width: 1.7 mm. *Relative head measurements:* HW 50, ASD 3.2, AOD 6.0, HL 37, IAD 11.5, LFW 26, OAD 14, OOD 10.9, OW 16, UFW 36, HW/HL 1.3, LFW/UFW 0.7. *Relative wing measurements*: MSR 1.56, FSR 1.00, SFR 1.04.

Structure: terga anteriorly depressed; BTP rounded; flagellum F1=F2, long, F3–9 longer than wide. S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on posterior area of dorsal subcentral ridge.

Sculpture: scutum dull, transverse lineo-reticulate and openly punctate; metapostnotum pit-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus dull, finely irregularly roughened; supraclypeal area somewhat shiny, finely irregularly roughened; scape short, dull; ocellocular area dull, densely punctate and irregularly roughened; frons irregular pit-reticulate.

Coloration: terga anteriorly orange, posterior margins transparent orange; labrum orange; mandibles black with red-brown tip.

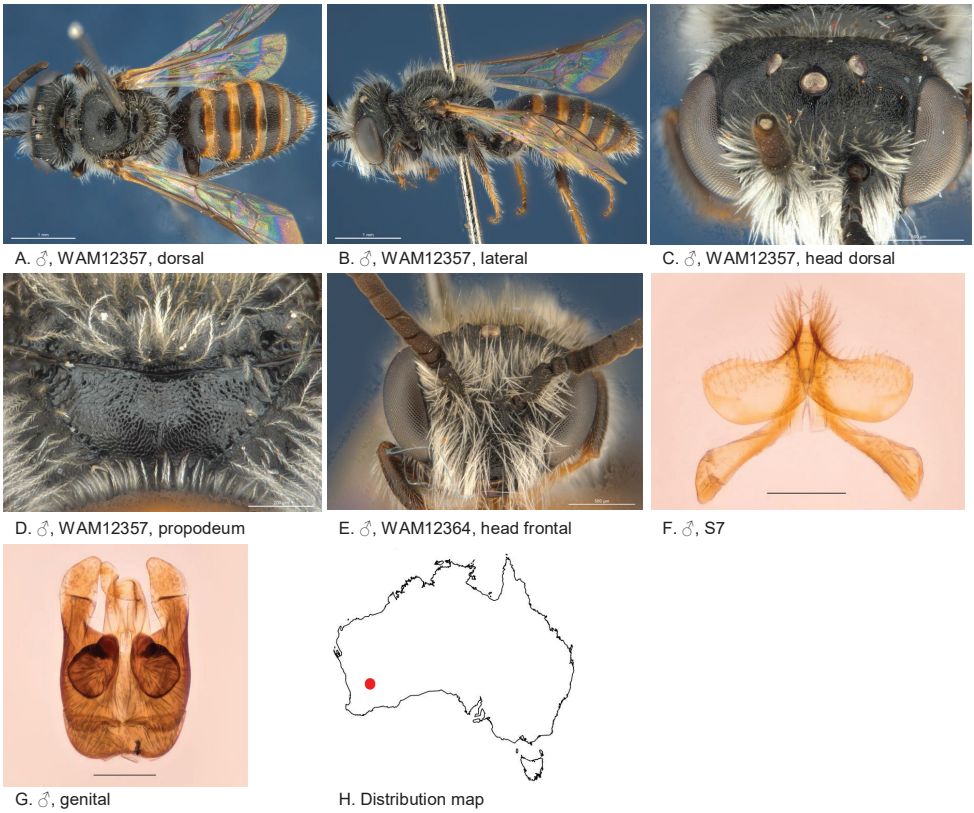


Figure 27. *Leioproctus* (*Colletellus*) *rubricinctus* Leijs, sp. n. ♂ holotype. Scale bar: 0.1 mm (**F, G**).

Pubescence: scutum: short, fine and dispersed, long, off-white; scutellum: short, fine, with dispersed, long off-white; scape with long white pubescence.

Flower records. *Thryptomene tuberculate* (Myrtacea).

Distribution. Figure 27H.

Etymology. The specific epithet refers to the red colouration of the anterior parts of the T2–4.

***Leioproctus* (*Colletellus*) *similis* Leijs, sp. n.**
http://zoobank.org/A801B9A1-9DF9-4CE7-A2E8-E4227C8358FF
Figure 28A–F

Specimens examined. (4♀): Holotype female, Mt Gibson Stn (29.8014S; 117.4028E), 28 Aug. 2001, Leijs, R., on *Borya*, SAMA 32-033482;

Paratypes 2 females, Paynes Find (29.2636S; 117.6831E), 01 Aug. 1982, Main, B.Y., WAM 12366–7; female, 22 km E of Bullfinch (30.7866S; 119.1144E), 18 Sep. 1979, Houston, T.F. et al., WAM 12380.

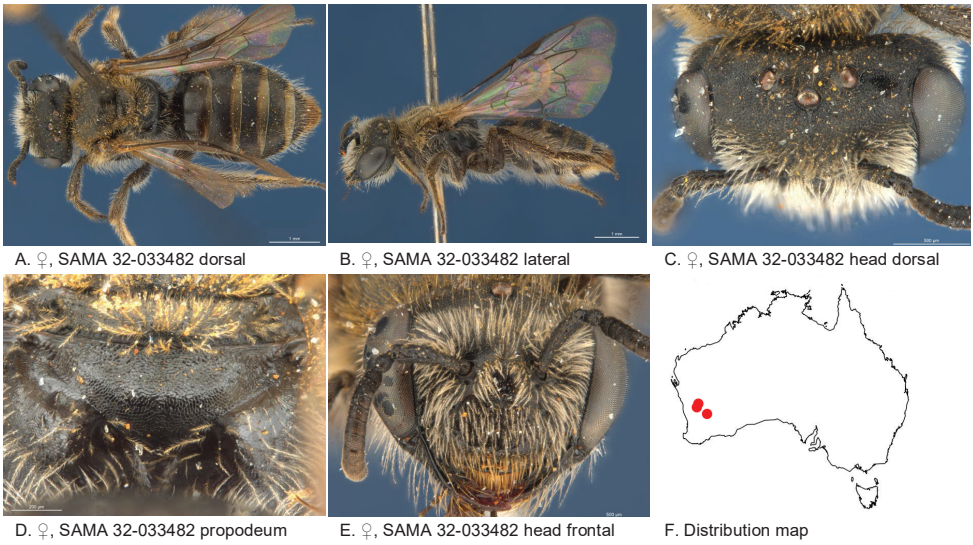


Figure 28. *Leioproctus* (*Colletellus*) *similis* Leijs, sp. n. ♀ holotype.

Diagnosis. Ocellocular area dull, finely roughened, frons dull roughly pit-reticulate, scutum medium length dense brown pubescence, terga dark with brown transparent posterior margins.

Male unknown.

Description. Female holotype: body length: 5.8 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 2.8, AOD 8.4, HL 37, IAD 11.7, LFW 31, OAD 12, OOD 9.5, OW 17, UFW 35, HW/HL 1.4, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.68, FSR 1.00, SFR 1.10.

Structure: terga anteriorly; BTP pointed; BTP/tibial length ratio 0.3; inner hind tibial spur ciliate.

Sculpture: scutum anteriorly transverse lineo-reticulate, densely punctate; metapostnotum fine pit-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus dull, microroughened, with open large punctures; supraclypeal area somewhat shiny, with microsculpture without punctures; ocellocular area dull, finely roughened; frons dull roughly pit-reticulate.

Coloration: terga anteriorly brown-orange, posterior margins transparent orange; scopa brown; labrum black; mandibles black; scape black; flagellum black.

Pubescence: scutum: medium length, brown; scutellum: medium length, brown; S2–4 medially on posterior margin with long simple hairs.

Flower records. *Borya* sp. (Boryaceae).

Distribution. Figure 28F.

Etymology. The specific epithet refers to the common habitus of this species within this subgenus.

***Leioproctus* (*Colletellus*) *splendens* Leijs, sp. n.**
http://zoobank.org/9995F3B5-0D0E-407D-BD8E-89C2EC665356
Figure 29A–F

Specimens examined. (2♀): Holotype female, 14 km SE of Tamala (26.3666S; 113.9817E), 28 Aug. 1997, Houston, T.F. & Mathiasen, P., on *Calandrinia*, WAM 21484;

Paratype female, same locality data as holotype, WAM 21485.

Diagnosis. Integument of metapostnotum and terga smooth and shiny without punctures, ocellocular area smooth, closely punctured.

Male unknown.

Description. Female holotype: body length: 4.5 mm; head width: 1.5 mm. *Relative head measurements*: HW 50, ASD 2.7, AOD 7.7, HL 40, IAD 11.5, LFW 31, OAD 16, OOD 9.3, OW 17, UFW 34, HW/HL 1.3, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.68, FSR 1.21, SFR 1.13.

Structure: terga anteriorly little depressed; BTP pointed; BTP/tibial length ratio 0.23; inner hind tibial spur ciliate with circa 18 small teeth.

Sculpture: scutum smooth, closely punctate; metapostnotum minute shallow pit-reticulate; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus smooth with microsctructure, openly punctate, ventral margin broad; supraclypeal area smooth with microsculpture, sparsely punctate; ocellocular area smooth, closely punctured; frons densely punctate; scape dull.

Coloration: terga anteriorly brown-orange, posterior margins wide, transparent orange; scopa light brown; labrum black; mandibles black with brown tip; scape brown-black; flagellum dark brown, last 5 segments light brown below.

Pubescence: scutum: short, close, brown; scutellum: short, close, brown.

Flower records. *Calandrinia* sp. (Montiaceae).

Distribution. Figure 29F.

Etymology. The specific epithet refers to the smooth and shiny integument on metapostnotum and terga of this species.

***Leioproctus* (*Colletellus*) *submetallicus* Leijs, sp. n.**
http://zoobank.org/0E3D2719-C8C5-4D19-9145-5D10E8A03A6E
Figure 30A–N

Specimens examined. (2♀, 1♂): Holotype female, Mt Gibson Stn (29.6870S; 117.3723E), 23 Aug. 2001, Leijs, R., on *Grevillea*, SAMA 32-033496;

Allotype male, Northampton (28.08S; 114.67E), 11 July 1959, ANIC 32-111877;

Paratype female, Mt Gibson Homestead (29.6075S; 117.4108E), 29 Aug. 2001, Leijs, R., SAMA 32-033497.

Diagnosis. The only species with faint metallic integument of head and thorax.

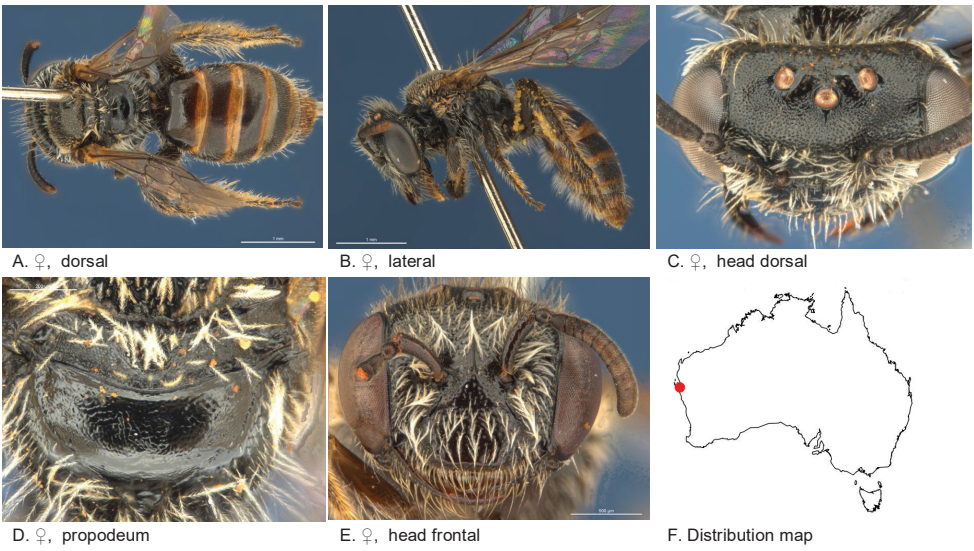


Figure 29. *Leioproctus* (*Colletellus*) *splendens* Leijs, sp. n. ♀ holotype WAM21484.

Description. Female holotype: body length: 6 mm; head width: 1.9 mm. *Relative head measurements*: HW 50, ASD 3.3, AOD 8.4, HL 38, IAD 10.0, LFW 29, OAD 13, OOD 11.3, OW 16, UFW 36, HW/HL 1.3, LFW/UFW 0.8. *Relative wing measurements*: MSR 1.61, FSR 1.18, SFR 1.00.

Structure: terga anteriorly not depressed; BTP pointy; BTP/tibial length ratio 0.26; inner hind tibial spur ciliate; flagellum short, F1–9 wider than long.

Sculpture: scutum dull, transverse lineo-reticulate and openly punctate, with faint metallic shine; metapostnotum transverse lineo-reticulate to finely irregular roughened; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus large openly punctate, microsculpture between punctures; supraclypeal area small densely punctate; scape relatively slender about 5 times as long as wide proximally; ocellocular area minutely roughened; frons irregularly pit-reticulate with faint metallic shine.

Coloration: terga anteriorly brown, posterior margins almost not transparent; scopa light brown, lighter ventrally; labrum black; mandibles black with brown tip.

Pubescence: scutum: short, orange-brown, with sparse long hairs; scutellum: short, orange-brown, with sparse long hairs; S5 with dense fringe of white hairs.

Description. Male: body length: 5.9 mm; head width: 1.85 mm. *Relative head measurements*: HW 50, ASD 3.4, AOD 6.3, HL 40, IAD 9.2, LFW 24, OAD 13.8, OOD 10.9, OW 16.7, UFW 36.2, HW/HL 1.3, LFW/UFW 0.67. *Relative wing measurement*: MSR 1.26, FSR 1.24, SFR 1.0.

Structure: terga anteriorly almost not depressed; BTP short, almost not pointy; flagellum F1 < F2, F1–10 wider than long, F11 longer than wide. S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on dorsal subcentral apical ridge.

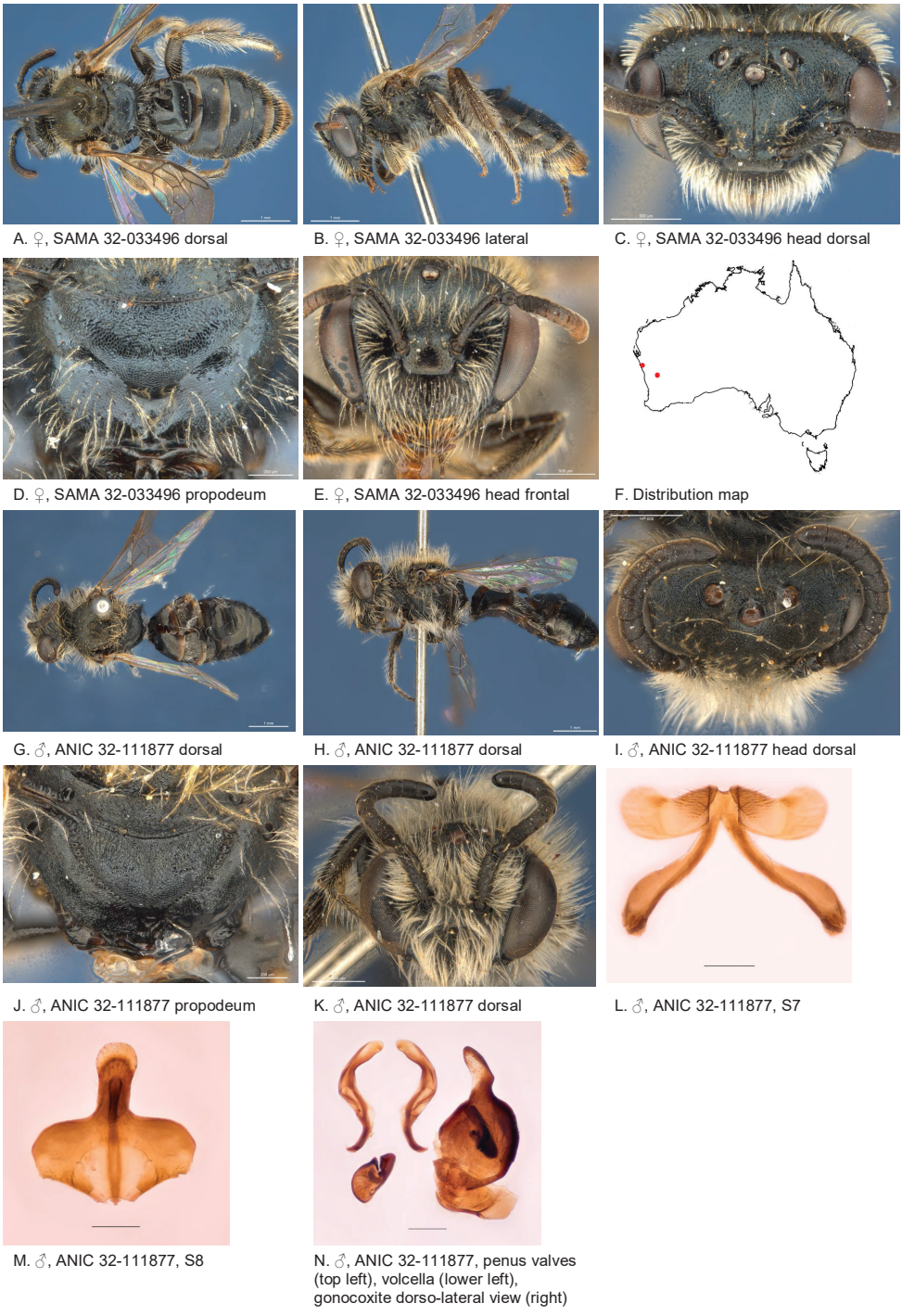


Figure 30. *Leioproctus* (*Colletellus*) *submetallicus* Leijs, sp. n. ♀ holotype and ♂ allotype.

Sculpture: scutum dull, transverse lineo-reticulate and openly punctate, with faint metallic shine; metapostnotum transverse lineo-reticulate to finely irregular roughened; T1–3 lineo-reticulate; clypeus large openly to closely punctate, rough microsculpture between punctures; supraclypeal area small densely punctate; scape almost 4 times longer than wide, roughly sculptured; ocellocular area minutely roughened; frons irregularly pit-reticulate.

Coloration terga anteriorly black, posterior margins almost not transparent, brown; mandibles black with brown tip.

Pubescence: scutum and scutellum: open, long, branched, light brown; face with long white branched pubescence.

Flower records. *Grevillea* sp. (Proteaceae).

Distribution. Figure 30F.

Etymology. The specific epithet refers to the faint metallic shine on the head and thorax.

Leioproctus (*Colletellus*) *velutinellus* Michener, 1965

Figure 31A–N

Specimens examined. (24♂, 7♀): Holotype female, Kojarena nr. Geraldton, West Australia, 6 Sep. 1926, Nicholdson, K95546, AM;

Allotype male, Gooseberry Hill (31.9541S; 116.0469E), 07 Oct. 1994, Houston, T.F., on *Stylidium*, WAM 14417;

Other specimens: 5 males, Gooseberry Hill (31.9541S; 116.0469E), 09 Oct. 1986, Houston, T.F., on *Stylidium bulbiferum*, WAM 12412–6; 3 males, 1 female, Gooseberry Hill (31.9541S; 116.0469E), 07 Oct. 1994, Houston, T.F., on *Stylidium*, WAM 14411,14–16; male, Gooseberry Hill (31.9541S; 116.0469E), 07 Oct. 1994, Houston, T.F., WAM 14418; female, Gooseberry Hill (31.9550S; 116.0489E), 15 Oct. 2009, Batley, M., on *Stylidium bulbiferum*, AM 359774; 3 females, 63 km NW of Perth (32.3536S; 116.3306E), 21 Nov. 1981, Howard, C.A. & Houston, T.F., on *Stylidium* near *divaricatum* & *bulbiferum*, WAM 12417–9; male, Glen Forrest (31.9111S; 116.0992E), 19 Sep. 1976, Postmus, S.M., WAM 12420; male, Garden Island (32.205S; 115.6733E), 12 Nov. 1975, Postmus, S.M., WAM 14419; female, Walyunga National Park (31.7213S; 116.0708E), 17 Oct. 1993, Houston, T.F., on *Boronia* , WAM 14420; male, Burma Road Nature Reserve (29.0000S; 115.0831E), 15 Sep. 1986, McMillan, R.P., WAM 22322; 11 males, Lesmurdie (32.0125S; 116.0328E), 14 Oct. 2009, Batley, M., on *Stylidium bulbiferum*, AM 359756–63,66–67, 361121.

Diagnosis. Ocellocular area dull, minutely and very densely roughened, frons dull, minutely roughened, vertex dull, minutely roughened, metapostnotum slightly striate in lateral corners, terga with post gradular depressions, scutum covered with dense short brown pubescence.

Description. Female WAM14415: body length: 5.9 mm; head width: 2 mm. *Relative head measurements*: HW 50, ASD 2.9, AOD 8.0, HL 35, IAD 10.0, LFW 29,

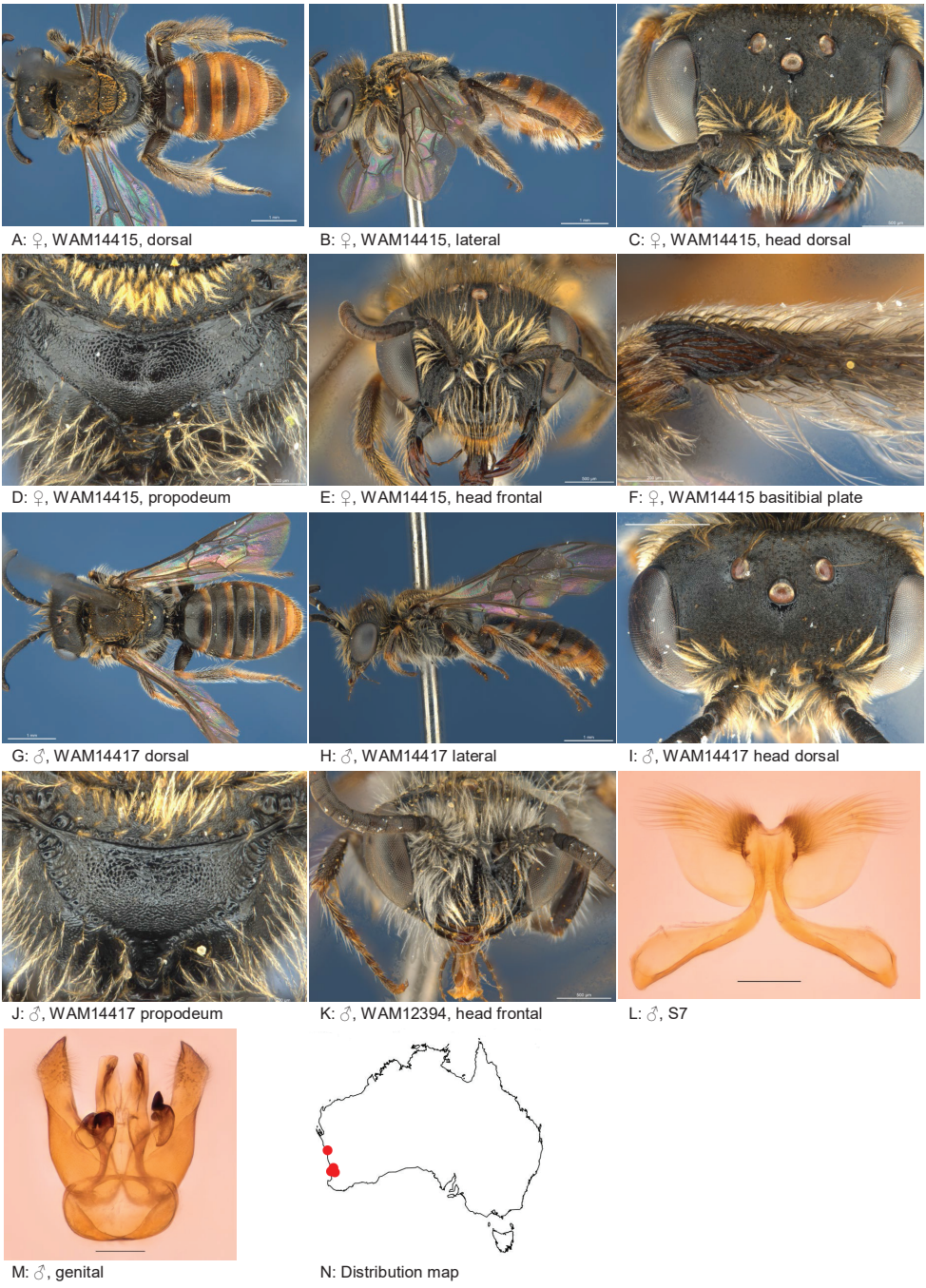


Figure 31. *Leioproctus* (*Colletellus*) *velutinellus* Michener, ♀ WAM14415, ♂ allotype. Scale bar: 0.1 mm (**L, M, N**).

OAD 13, OOD 10.6, OW 15, UFW 34, HW/HL 1.4, LFW/UFW 0.9. *Relative wing measurements*: MSR 1.33, FSR 1.08, SFR 0.93.

Structure: terga anteriorly depressed; BTP pointed, long; BTP/tibial length ratio 0.35; inner hind tibial spur ciliate with circa 22 little teeth.

Sculpture: scutum dull, densely punctate; metapostnotum shiny, with dense contiguous depressions, minutely striate in lateral corners; scape dull; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus shiny, openly punctate, with micro depressions between punctures, ventral margin drawn into thin plate; supraclypeal area without punctures, only micro depressions; labrum smooth; ocellocular area dull, very dense micro roughened; frons dull, micro roughened; vertex dull, micro-roughened.

Coloration: terga anteriorly orange, posterior margins transparent orange; scopa white; labrum black; mandibles black with brown tip; flagellum F1–3 black, F4–10 little lighter below.

Pubescence: scutum: light brown, dense, short, branched; scutellum: dense, short, branched; metanotum: dense, short, branched; S1–4 with fringes of long branched hairs, S5 with dense fringe of hairs; scape with open medium length blond pubescence.

Description. Male: body length: 5.4 mm; head width: 1.9 mm. *Relative head measurements*: HW 50, ASD 2.6, AOD 6.9, HL 36, IAD 11.4, LFW 26, OAD 12, OOD 10.0, OW 18, UFW 36, HW/HL 1.4, LFW/UFW 0.7. *Relative wing measurement*: MSR 1.39.

Structure: terga anteriorly depressed; BTP pointed; flagellum F1 > F2, F1–3 wider than long, F4–11 slightly longer than wide. S7: dorsal apical lobe absent, ventral apical lobe large, branched setae present on dorsal subcentral apical ridge.

Sculpture: scutum dull, densely punctate; metapostnotum shiny, with dense contiguous depressions, slightly striate in lateral corners; scape short, dull; T1 lineo-reticulate, T2–3 transverse lineo-reticulate; clypeus dense fine punctate, large punctures only at margins; supraclypeal area openly to sparsely punctate with underlying dense fine punctures; ocellocular area dull, very dense micro-roughened; frons dull, micro-roughened.

Coloration: terga anteriorly black-brown; terga posterior margins transparent orange; mandibles black with brown tip.

Pubescence: scutum: dense, short, branched; scutellum: dense, short, branched; metanotum: dense, short, branched; scape with long pubescence.

Remarks. The female of this species is redescribed based on specimen WAM 14415, however comparison with the holotype did not reveal differences. The male of the species is described here for the first time. While Michener (2007) mentioned that the male genitalia and hidden sterna were illustrated by Michener (1965), these images could not be found in the referred publication, which explicitly states that the subgenus is only known in the female.

Flower records. *Boronia* (Rutaceae), *Stylidium bulbiferum* (Stylidiaceae), *Stylidium* nr *divaricatum* (Stylidiaceae), *Stylidium* sp. (Stylidiaceae).

Distribution. Figure 31N.

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Supplementary material 1

Supplementary table – specimen info

Authors: Remko Leijs, James Dorey, Katja Hogendoorn

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: species data

Link: https://doi.org/10.3897/zookeys.811.28924.suppl1