SYSTEMATICS AND BIOGEOGRAPHY OF HYPTIOGASTRINE WASPS (HYMENOPTERA: GASTERUPTIIDAE)

Pseudofoenus spinitarsis (Westwood) comb. nov.
[Photo: G. Weber]

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To my parents

John and Erica

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Summary

The Hyptiogastrinae are a Gondwanan subfamily of small to medium sized wasps that are predator-inquilines of solitary ground-nesting bees that provision their nests with pollen. Along with the Gasteruptiinae they comprise the family Gasteruptiidae. Whereas *Gasteruption* L. (Gasteruptiinae) is almost cosmopolitan, the Hyptiogastrinae are found mostly in Australia but also in South America, New Zealand, New Guinea and on several south-west Pacific islands. Prior to this study, the latter subfamily comprised some 37 species in five genera; *Aulacofoenus* Kieffer, *Crassifoenus* Crosskey, *Eufoenus* Szépligeti, *Hyptiogaster* Kieffer and *Pseudofoenus* Kieffer. Recent extensive collecting using techniques such as malaise traps has greatly increased the number of specimens available which have provided the basis for the present study. Overall, the project aimed to investigate the phylogenetic relationships among genera and species of Hyptiogastrinae, examine whether the current distribution of taxa can be explained by vicariance events, and revise the taxonomy of species.

A brief literature review is first provided which describes the taxonomic history of the group, and in particular the Hyptiogastrinae. This is followed by an extensive synopsis of the biology of gasteruptiids and a comparison with that of its sister family, the Aulacidae. This latter section is mainly based on a review of the relevant literature but also includes new results based on observations made during this study.

The materials and methods used in the phylogenetic analyses and taxonomic revision are then outlined. This chapter describes the techniques used in the examination of specimens, including field emission scanning electron microscopy, and a detailed discussion of the methods adopted for phylogenetic analyses using PAUP. The fourth chapter details the morphology of the Gasteruptiidae as a prelude to dealing with the phylogenetic analyses and taxonomic revision.

Two series of phylogenetic analyses were conducted; one to test relationships among families and subfamilies and the other to examine relationships within the Hyptiogastrinae. The first set of analyses employed 56 taxa and used *Schlettererius* *cinctipes* (Cresson) (Stephanidae) as the outgroup. Of the included taxa, six exemplar species of Aulacidae were selected, three each from *Aulacus* and *Pristaulacus*, five from *Gasteruption* and 42 hyptiogastrines; nine species of *Aulacofoenus*, three *Crassifoenus*, 23 *Eufoenus*, five *Hyptiogaster* and two *Pseudofoenus*. A data matrix of 58 characters was compiled using MacClade (version 3.7), and was analysed using an heuristic search of 100 random replicates using PAUP with random addition sequence and with all character states unordered. The resultant strict consensus tree showed that the Aulacidae, Gasteruptiidae and Hyptiogastrinae are all monophyletic. Little resolution was achieved within the Hyptiogastrinae, although *Pseudofoenus s. str.* and *Crassifoenus* came out as monophyletic.

The second series of analyses examined relationships within the Hyptiogastrinae in more detail and was based on a separate matrix of 34 informative characters; the characters used in the above analyses were re-examined and redefined where necessary, and a number of additional characters and species were included to better represent the morphological and taxonomic diversity within the subfamily. The most basal *Gasteruption* species in the first analysis was used as the outgroup and 51 taxa included within the ingroup. A number of important outcomes were evident. The genera *Crassifoenus*, *Hyptiogaster* and *Pseudofoenus s. str.* were shown to be monophyletic and are well supported by a number of characters. However, *Crassifoenus* and *Pseudofoenus s. str.* were contained within larger clades which encompass *Aulacofoenus* and *Eufoenus*, the latter genera being polyphyletic.

A new phylogenetically-based classification is proposed for the Hyptiogastrinae reflecting the results of a successively weighting analysis. Two monophyletic groups are recognised: *Hyptiogaster* and *Pseudofoenus s. l.*, the latter genus comprising *Aulacofoenus*, *Crassifoenus* and *Eufoenus* which are synonymised with it. Two monophyletic species groups are designated for *Pseudofoenus s.l.*, with a further 30 species not assigned to any groups.

The results of the phylogenetic analyses are then used to examine the biogeography of the Hyptiogastrinae, in particular whether their current distribution can

be explained by vicariance events alone. The last continental link between Australia and New Zealand occurred by the late Cretaceous (65-70 mya), and the separation of South America from Australia + Antarctica occurred 50 mya in the middle Eocene. If the present hyptiogastrine distribution was determined by geographic barriers (i.e. continental drift), then the New Zealand and South American taxa would be expected to occur basally in the phylogeny. However, this is not the case: they occur separately and in apical positions in the tree generated by successive weighting. Further, the presence of several hyptiogastrine species on oceanic islands in the south-west Pacific shows that the group is capable of dispersal over intermediate distances. Finally, the lack of any significant speciation in South America and New Zealand compared with Australia, together with the results of the phylogenetic analysis, suggests that the Gondwanan distribution of the subfamily is best explained by having an Australian centre of origin and radiation, and that the group has reached New Zealand and South America by dispersal more recently than the break-up of the Australian-Antarctic-South American connection. As far is known, this is the first time a vicariance hypothesis has been rejected convincingly for any group of animals that show such a restricted Gondwanan distribution.

In the penultimate chapter, the taxonomy of the Hyptiogastrinae is revised with a total of 66 species included, 10 in *Hyptiogaster* and 56 in *Pseudofoenus s.l.* As well, two species of *Eufoenus* are listed as species *incertae sedis*. Illustrated keys to genera, species-groups and species are presented, as well as notes on their biology and host relationships where available.

The final chapter represents a broad discussion of the major findings of the study and provides recommendations for future work. The limits of morphological data to fully resolve phylogenetic relationships are discussed, along with the suggestion that molecular systematics may have to be employed in future.

Declaration

This thesis contains no material that has been accepted for the award of any other degree or diploma in any university and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

I consent to this thesis being made available for photocopying and loan if accepted for the award of the degree, providing that acknowledgement is made of any reference to work therein.

Several published papers are included as part of this thesis. Those for which I was the senior author are papers where I carried out the research and provided most of the intellectual input. The papers for which I am the second author are related to the work contained within my thesis and for which I had significant but not majority input.

John T. Jennings
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I dedicate this thesis to my parents, John and the late Erica Jennings who encouraged me from an early age to pursue science.

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Chapter 1.

Introduction

The Evanioidea are one of the most easily recognised and distinct group of parasitic Hymenoptera. All members of the superfamily have the metasoma inserted high on the propodeum, and although this character state is found in some other Hymenoptera, it easily distinguishes the group from virtually all other parasitic wasps. The Gasteruptiidae are readily identified from other groups within the superfamily, the Aulacidae and Evaniidae; gasteruptiids lack fore wing vein 2m-cu, the antennae are inserted at about the mid level of the eyes, and the metasoma is elongate and subclavate (Gauld and Bolton 1996).

The Gasteruptiidae is traditionally divided into two subfamilies; Gasteruptiinae and Hyptiogastrinae (Crosskey 1953a). *Gasteruption* L. is the only genus included in the Gasteruptiinae and Crosskey (1953a) included only *Hyptiogaster* Kieffer and two new genera, *Crassifoenus* Crosskey and *Carinafoenus* Crosskey, in the Hyptiogastrinae. In the first comprehensive treatment of the subfamily, Crosskey (1962) included five genera within the Hyptiogastrinae; *Aulacofoenus* Kieffer, *Crassifoenus*, *Eufoenus* Szépligeti, *Hyptiogaster*, and *Pseudofoenus* Kieffer. Since Crosskey's revision, there has been no change to the classification at either family or subfamily level, although Jennings and Austin (1994a,b, 1997a,b) revised the hyptiogastrine genera except for *Eufoenus*.

Crosskey's classification was not phylogenetically based and pre-dates the use of parsimony-based phylogenetic programs such as PAUP (Swofford 1993, 1997). Also, Crosskey made a number of assertions about the relationships of the two subfamilies, such as Hyptiogastrinae being "the more primitive subfamily", and, he recognised genera on the basis of morphological characters which now appear, in at least some cases, to be variable.

Since Crosskey's work, extensive collecting using techniques such as malaise traps has greatly increased the number of specimens available for study. In addition, it is apparent that there are more than 50 undescribed species existing in various museum collections. Museum records also indicate that there are several undescribed hyptiogastrine species from New Guinea where they were previously unknown. Within the approximately 500 described species of Gasteruptiidae, the Gasteruptiinae (*Gasteruption* spp.) are cosmopolitan (Crosskey 1962). The Hyptiogastrinae on the other hand have a more or less amphinotic distribution (*sensu* Illes 1965), being found Australia, New Zealand, and in a broad band across Argentina, Paraguay and Brazil (Jennings and Austin 1994a,b, 1997b). Two species are also found in New Caledonia, Vanuatu and Fiji (Jennings and Austin 1994a,b, 1997a).

With the inclusion of additional taxa, a re-examination of the characters used by Crosskey (1962), and the inclusion of additional characters, the generic boundaries of Crosskey may no longer be appropriate. Indeed, the existing genera may not be monophyletic.

The economic significance of bees and other insects in pollinating crops such as lucerne and almonds is well known (Jennings and Austin 1996). What is less clear is that native bees are the primary pollinators of flowering plants in many areas - about 40% of all flowering plants are pollinated by Hymenoptera. Habitat destruction is, however, reducing the diversity of forage plants and nest sites for native bees. This can lead to a decline in the abundance and diversity of the bees which then leads to reduced pollination of both agricultural and native plants, and ultimately a further reduction in plant diversity. A taxonomic framework is necessary to support ecological work on native bees and their major regulating agents.

Early records indicated that twig-nesting species of solitary bees (e.g. *Ceratina*, *Heriades* and *Hylaeus*) were the hosts of *Gasteruption* (Höppner 1904; Rau 1928). More recent and extensive records indicate a much wider range of solitary bees and wasps act as hosts for this genus including the families Anthophoridae, Colletidae and Megachilidae. While there is only limited information on the host relationships of the Hyptiogastrinae, it seems likely that they are all predator-inquilines of solitary bees or wasps. *Crassifoenus* is known from the nests of stenotritid bees (Houston 1984b, 1987; Jennings and Austin 1994a), *Eufoenus* from colletid and halictid bees, *Hyptiogaster* from masarine wasps (Houston 1984a; Naumann and Cardale 1987; Jennings and Austin 1997b) and stenotritid bees (Houston 1984b, 1987; Jennings and Austin 1997b), and *Pseudofoenus* from colletids (Jennings and Austin 1994b).

The main aim of this study was to elucidate the systematics and biogeography of hyptiogastrine wasps. Specifically, the study generated a character matrix used to determine the phylogenetic relationships among genera, species groups and species. These relationships were then used to test hypotheses that account for the current distribution of taxa, the most likely being that the genera are found in regions according to the break-up of the southern hemisphere continents, given that the subfamily displays a Gondwanan distribution. Finally, a number of taxa were revised taxonomically and new species described which are associated with native bees.

The present study is organised so that Chapter 2 deals with the literature pertinent to systematics and distribution, Chapter 3 reviews biology and host relationships, Chapter 4 details the methods employed, Chapter 5 discusses the general morphology of the groups, Chapter 6 details the results of the phylogenetic analyses, Chapter 7 presents a discussion of the biogeography of the Hyptiogastrinae, and Chapter 8 revises the Hyptiogastrinae and provides descriptions and keys. Finally, Chapter 9 represents a broad discussion of the major findings and also provides recommendations for future work.

Chapter 2.

Systematics and distribution of the Evanioidea

2.1. Introduction

All members of the Evanioidea have the metasoma inserted high on the propodeum, although this character state is found in a few Ichneumonoidea, Cynipoidea and Chalcidoidea (Naumann 1991). Since Hedicke (1939) divided the Evanioidea into three families, the Aulacidae, Gasteruptiidae and Evaniidae, this classification has remained unchanged. However, the grouping of the Evaniidae with the Aulacidae and Gasteruptiidae has been questioned by numerous authors (e.g. Townes 1950; Crosskey 1951; Crosskey 1962; Carlson 1979; Naumann 1991; Gauld and Bolton 1996), the high insertion of the metasoma possibly having been acquired independently by the Evaniidae, as it has within other groups of Hymenoptera, albeit less obviously. A close relationship between the Aulacidae and Gasteruptiidae is less problematic and is at least putatively supported by several morphological characters. Gasteruptiidae and Aulacidae have a similar, rigid abutment of the pronotum and mesepisternum and a similar fusion or partial fusion of the first and second metasomal segments (Naumann 1991). Quicke *et al.* (1994) found some similarities between the ovipositor in the Aulacidae and Gasteruptiidae, but not Evaniidae. Both aulacids and gasteruptiids have a medial thickening of the ventral wall of the upper valve, but the latter has a mid-dorsal longitudinal ridge which is absent in aulacids. Evaniidae, however, differ in that their ovipositor is dorso-ventrally compressed rather than diverging as in aulacids and gasteruptiids. Apart from the high point of insertion of the metasoma, the only other putative synapomorphy for the three families is the loss of functional spiracles from all segments of the metasoma except the eighth (Gauld and Bolton 1996). In contrast, Dowton and Austin (1994), in a phylogenetic analysis of the mitochondrial 16S rRNA gene, have shown some tentative support for the Evaniidae being closely related to the Gasteruptiidae, but this finding was based on results for three exemplar species and did not include representatives of the Aulacidae.

2.1. Systematics

The Evaniidae were first recognised by Latrielle (1802) as the Evaniales. Leach (1830) recognised the Evanides, Shuckard (1841) the Evaniadae and Provancher (1883) the Evaniidae.

These early authors included all evaniid, aulacid and gasteruptiid wasps within these groupings, however, it should be noted that evaniid wasps (Evaniidae *sensu* Hedicke 1939) have been largely excluded from the following review as they are clearly different in appearance (e.g. shape of the metasoma) and in biology from the aulacids and gasteruptiids, in that they are highly specialised parasitoids of cockroach oothecae (e.g. Gauld and Bolton 1996).

During the past 150 years, there have been numerous changes to both the status and boundaries of the family Gasteruptiidae. Crosskey (1962) has detailed the many early changes and provided a bibliography.

The oldest name for the present family comprising the Gasteruptiidae is Foenidae (Kirby in Richardson 1837), based on the type-genus *Foenus* Fabricius, 1798. *Foenus* is, however, a junior synonym of *Gasteruption* Latreille (Schletterer 1885). Ashmead (1900) was the first to introduce the name Gasteruptioninae when he recognised three subfamilies within the family Evaniidae; Evaniinae, Gasteruptioninae, and Aulacinae. Up to this time, the Evaniidae was usually divided into two subfamilies, Evaniinae and Aulacinae. Ashmead separated the Gasteruptioninae from the Aulacinae by a combination of characters including the point of insertion of the antennae, fore wing venation, and the point of attachment of the metasoma. Ashmead also separated the Gasteruptioninae from the Evaniinae by a range of characters including head and metasoma shape, and the habits (behaviour) of the included species. Various names have been used for the family including Gasteruptionini, Gasteruptionidae, Gasteruptiinae and Gasteruptiidae (detailed in Crosskey 1962).

Hedicke (1939) was the first to recognise the Aulacidae, Evaniidae, and Gasteruptiidae as separate families. Although a few later authors such as Townes (1950) and Krombein *et al.* (1958) continued to include the aulacids within the Gasteruptiidae, they have usually been treated as a separate family (e.g. Richards 1956; Crosskey 1962; Naumann 1991; Mason 1993; Gauld and Bolton 1996).

In 1953, Crosskey divided the Gasteruptiidae into two subfamilies; Gasteruptiinae and Hyptiogastrinae. He included only the genus *Gasteruption* in the Gasteruptiinae and *Hyptiogaster* and two new genera, *Crassifoenus* and *Carinafoenus*, in the Hyptiogastrinae, with *Hyptiogaster* Kieffer designated as the type genus.

In a later revision of the subfamily, Crosskey (1962) included five genera within the Hyptiogastrinae; *Aulacofoenus*, *Crassifoenus*, *Eufoenus*, *Hyptiogaster*, and *Pseudofoenus*. He synonymised *Carinafoenus* within *Hyptiogaster*. Crosskey indicated that the two subfamilies were easily distinguished by the structure of the mandibles, which are long and broadly overlapping in the resting position in Hyptiogastrinae (see Fig. 8.13), but short and abutting each other in Gasteruptiinae. He also indicated differences in, *inter alia*, fore wing venation and presence/absence of a prefemur (Figs 8.5, 9).

Aulacofoenus was erected without description by Kieffer (1911) as a monotypic genus to accommodate *Hyptiogaster szépligetii* Kieffer, and Hedicke (1939) continued to recognise *Aulacofoenus* as monotypic. In his 1962 revision, Crosskey transferred four species from *Hyptiogaster* to *Aulacofoenus*: *A. asymmetricus* (Turner) and *A. fallax* (Schletterer) from Australia, and *A. deletangi* (Schletterer) and *A. infumatus* (Schletterer) from South America. He distinguished *Aulacofoenus* from *Hyptiogaster* by the latter having a long, exserted ovipositor, and the first flagellomere being about equal to or shorter than the second. Further, he distinguished *Aulacofoenus* from both *Eufoenus* and *Pseudofoenus* by the presence of a trochanteral groove, this groove appearing to be the only distinguishing character state between *Aulacofoenus* and *Eufoenus*. *Aulacofoenus* can be further separated from *Pseudofoenus* by the number of discal cells in the fore wing (Jennings and Austin 1994b), and from *Crassifoenus* by the form of the hind tarsi in females and the length of first flagellomere compared with the second (Jennings and Austin 1994a). *Aulacofoenus* was revised by Jennings and Austin (1997a), who recognised fourteen species, ten of which were described as new. They also transferred *Hyptiogaster thoracicus* (Guérin Menéville) to *Aulacofoenus*, and placed two species into synonymy (see Appendix A5).

Crassifoenus was erected by Crosskey (1953) to include two species, *C. grossitarsis* (Kieffer) and *C. macronyx* (Schletterer), both of which have a long malar space, the first four hind tarsal segments strongly contracted and deeply bilobed, and hind femur and tibia incrassate. Not obvious from the original description of the genus is that it is only the females that possess modified hind tarsi; in males they are normally elongate and not strongly bilobed.

Jennings and Austin (1994a) revised the genus and described one new species (see Appendix A3).

Eufoenus was erected by Szépligeti (1903) without description, although in a key to genera, he distinguished *Eufoenus* from both *Pseudofoenus* and *Gasteruption* by the fore wing in *Eufoenus* having two discoidal cells whereas the other genera have only one. He included four species in *Eufoenus*; *G. antennale* Schletterer, *G. plicatum* Schletterer, *G. humerale* Schletterer and *G. crassiceps* Schletterer, but did not specify the type, although under Article 69 of the International Code of Zoological Nomenclature (1985), *G. antennale* is recognised as the type species of *Eufoenus* as it was the first species listed. *Eufoenus humerale* was later transferred to *Hyptiogaster* (Kieffer 1903), and *E. crassiceps* has been placed in several genera until being synonymised with *H. rufus* (Westwood) (Jennings and Austin 1997a).

Crosskey (1962) indicated that Bradley (1909) designated *G. antennale* as the type species for *Eufoenus*. In fact, Bradley (1908 and 1909) erroneously designated *G. antennale* as the type for *Hyptiogaster*. *Hyptiogaster* was erected without description by Kieffer (1903), with *G. crassiceps* Kieffer being designated as the type species. Bradley (1909) erroneously synonymised *Eufoenus* with *Hyptiogaster* on two grounds; a) that *G. antennale* was included in *Hyptiogaster*, and b) that Szépligeti's paper erecting *Eufoenus* was published after that of Kieffer.

Two additional genera were later erected. Kieffer (1911a) described *Hemifoenus* to accommodate *H. brevithorax* Kieffer, which he defined on a range of characters including the position of the cubitus on the fore wing, the shape of the thorax and the form of the hind tarsi in the female. *Trigonofoenus* was erected without description by Kieffer (1911a) to accommodate *G. trianguliferum* Kieffer. In a key to genera, he defined the genus on the basis of the cubitus being formed by the extension of the median vein, the hind wing lacking a second cubital cell, and the mesonotum with two parapsidal grooves.

However, Crosskey (1962) synonymised both *Hemifoenus* and *Trigonofoenus* with *Eufoenus*. He did so on the basis that the type of *Hemifoenus*, *H. brevithorax*, was synonymous with *E. spinitarsis* Westwood, and the type of *Trigonofoenus*, *G. trianguliferum* Kieffer, was synonymous with *E. australis* (Westwood). Crosskey (1962) included 19 species in *Eufoenus* and also indicated that two other species, *H. flavinervis* Kieffer and *H. crassitarsis* Kieffer, probably also belonged to *Eufoenus.*

Hyptiogaster was erected without description by Kieffer (1903), with *Gasteruption crassiceps* Kieffer designated as the type species. He included 11 species, none of which is currently included in *Hyptiogaster* (Crosskey 1962). *Hyptiogaster* is readily distinguished from all other Hyptiogastrinae by its elongate exserted ovipositor, and from *Gasteruption* by its wing venation (see Chapter 8). Jennings and Austin (1997b) revised the genus, and in doing so, recognised ten species, seven of which were described as new (see Appendix A6).

Crosskey (1953) erected 8 species-groups for *Hyptiogaster.* These species groups, their main characteristics and their included species were:

1. *asymmetrica*-group. Frontal carina very strong, horn-like; hind tarsi strongly asymmetrical; hind trochanter with a transverse groove. One included species, *asymmetrica* (Turner). Crosskey (1962) transferred this species to *Aulacofoenus* (see also Jennings and Austin 1997a).

2. *fallax*-group. Frontal carina present; hind trochanter with a transverse groove. One included species, *fallax* (Schletterer). Crosskey (1962) transferred this species to *Aulacofoenus* (see also Jennings and Austin 1997a).

3. *australis*-group. Frontal carina present; hind tarsi symmetrical; hind trochanter without a groove; propodeum with a short median longitudinal carina; terminal flagellar segments elongate. Three included species, *patellata* (Westwood), *australis* (Westwood) and *ferruginea* Crosskey. Crosskey (1962) transferred all three species to *Eufoenus.*

4. *inaequalis*-group. Frontal carina present; hind tarsi symmetrical; hind trochanter without a groove; propodeum without a short median longitudinal carina; terminal flagellar segments quadrate. Two included species, *inaequalis* Turner and

nitidiuscula Turner. Both species were transferred by Crosskey (1962) to *Eufoenus*.

5. *brevithorax*-group. Frontal carina absent; hind tarsi asymmetrical; mesepimera rectangular, coarsely 'shagreened', and not reaching ventral side of thorax. Three included species, *brevithorax* (Kieffer) *interrupta* Crosskey, and *darwini* (Westwood). All three species were transferred to *Eufoenus* by Crosskey (1962). At the same time, Crosskey synonymised *E. brevithorax* with *E. spinitarsis* (Westwood).

6. *szépligetii*-group. Frontal carina absent; hind trochanter with a transverse groove; mesonotum red with an anchor-shaped black mark; neotropical in distribution. Three included species, *szépligetii* (Kieffer), *infumata* (Schletterer) and probably *deletangi* (Schletterer). Crosskey (1962) transferred all three species to *Aulacofoenus* (see also Jennings and Austin 1997a). Jennings and Austin (1997a) synonymised *A. szépligetii* with *A. deletangi.*

7. *extranea*-group. Frontal carina absent; 'prescutum' and lateral parts of scutum strongly raised and with very strong parallel transverse ridges. One included species, *H. extranea* Turner. This species was transferred by Crosskey (1962) to *Eufoenus*.

8. *floricola*-group. Frontal carina absent; 'prescutum' not raised and without regular transverse carinae. Seven included species, *pilosa* Kieffer, *antennalis* (Schletterer), *plicatum* (Schletterer), *microcephala* Crosskey, *ritae* Cheesman, *floricola* Turner and *minima* Turner. All but *H. microcephala* were transferred to *Eufoenus* by Crosskey (1962).

Of these eight species groups of *Hyptiogaster* erected by Crosskey (1953), species in groups 1, 2 and 6 have since been transferred to *Aulacofoenus* with most of the species in the remaining groups (3, 4, 5, 7 and 8) having been transferred to *Eufoenus*. In their revisions of *Aulacofoenus* and *Hyptiogaster*, Jennings and Austin (1997a,b) did not employ species groups.

Pseudofoenus was erected by Kieffer (1902) to accommodate three existing species of *Gasteruption* with only one discal cell in the fore wing. Following a substantial period of instability in the generic placement of gasteruptiid species, which saw *Pseudofoenus* expand to include 24 species, Crosskey (1962) revised the genera and restricted *Pseudofoenus* to five species, viz. *P. crassipes* (Smith), *P. nocticolor* Kieffer, *P. pedunculatus* (Schletterer), *P. unguicularis* (Smith), and *P. unguiculatus* (Westwood). Valentine and Walker (1991) transferred four of these species, including the type species *P. pedunculatus*, to the Australian genus *Hyptiogaster* without justification and thus inadvertantly made *Pseudofoenus* a junior synonym. Jennings and Austin (1994b) reinstated *Pseudofoenus* as a valid genus and redescribed the species (see Appendix A4). Further, the International Commission on Zoological Nomenclature has placed *Pseudofoenus* on the Official List of Generic Names in Zoology and designated *P. unguiculatus* as the type species (ICZN 1998).

2.2. Distribution

The Evaniidae are world-wide in their distribution (Kieffer 1912), although the 400 described species are mainly tropical (Gauld and Bolton 1996). The approximately 150 described species of Aulacidae are found in all biogeographic regions (Gauld and Bolton 1996), although Kieffer (1912) records only one species, *Aulacus thoracicus* Westwood, from the Afro-tropical region. Prinsloo (1985) states that nothing is known about Aulacidae in southern Africa.

Within the approximately 500 described species of Gasteruptiidae, the Gasteruptiinae (*Gasteruption* spp.) are cosmopolitan (Kieffer 1912; Crosskey 1962), although they are unknown from Polynesia and Hawaii (Crosskey 1962).

The Hyptiogastrinae on the other hand have a more or less amphinotic distribution (*sensu* Illes 1965), being found on the Australian mainland and in Tasmania, New Zealand, and in a broad band across Argentina, Paraguay and Brazil (Jennings and Austin 1994a,b, Jennings and Austin 1997b). Several species are also found in New Guinea, New Caledonia, Vanuatu and Fiji (Jennings and Austin 1994a,b, 1997a). The subfamily may have had a more widespread distribution in the past as the fossil genus *Hyptiogastrites* Cockerell from Burmese amber, probably from the late Cretaceous (Ross 1997, 1998), appears to belong in the subfamily (Cockerell 1917; Crosskey 1962). [A preliminary examination of the type specimen of *Hyptiogastrites electrinus* Cockerell, however, places this genus in the Aulacidae.]

Rasnitsyn (1975) erected an additional subfamily, Baissinae, within the Gasteruptiidae and included the fossil gasteruptiid genus *Baissa* Rasnitsyn. Additional fossil taxa have since been placed in this subfamily. They include *Manlaya* spp. (Rasnitsyn 1980, 1986, 1990), *Aulocopsis laiyangensis* (Hong and Wang 1990) and *Humiryssus leucus* (Lin 1980), although the latter two taxa are only tentatively placed here (Rasnitsyn *et al.* 1998). More recently, Rasnitsyn *et al.* (1998) described a number of additional fossil species belonging to the genus *Manlaya* and included a key to 18 described species. In addition, they erected a new genus *Tillywhimia*, which they tentatively placed in the Baissinae, and in which they include two species. They also indicate that there are numerous undescribed species of *Manalaya* from the Lower and Mid Cretaceous from Transbaikalia, Mongolia, southern England and eastern China. Rasnitsyn (1991) also erected another subfamily, Kotujellitinae, within the Gasteruptiidae. Exactly what relationship these subfamilies have with the extant Gasteruptiinae and Hyptiogastrinae is unknown.

Chapter 3.

Synopsis of aulacid and gasteruptiid biology

Compared with many other groups of Hymenoptera, the Aulacidae and Gasteruptiidae have been little studied, probably because they are not used as biocontrol agents. This chapter aims to bring together the very scattered literature on the biology and host relationships of these two families to determine whether any patterns exist. The biology and host relationships of evaniid wasps have not been included given that they are parasitoids of cockroach oothecae (e.g. Naumann 1991; Gauld and Bolton 1996) and thus quite different to that of aulacids and gasteruptiids. It should also be noted that the hyptiogastrine genera referred to in this chapter are those prior to the proposed generic reclassification outlined in Chapter 6.

3.1. Oviposition

During oviposition in aulacids, the metasoma is raised and the ovipositor directed antero-ventrally so that the valves pass between the hind coxae and through a guide formed by apposed grooves or notches on the inner surface of the hind coxae (Townes 1938; Townes 1951; Skinner and Thompson 1960; Naumann 1991). Some *Aulacus*, mostly those with short ovipositors, however, do not have coxal grooves (Townes 1951).

Aulacus have been associated with a wide range of tree species which simply reflects those trees infested by their hosts. In Europe, their xiphydriid wasp hosts (*Xiphydria* spp.) lay their eggs in bark crevices of a range of deciduous angiosperm trees including *Acer* (maple) (Schimitschek 1974), *Alnus* (alder) (Skinner and Thompson 1960; Schimitschek 1974; Evenhuis and Vlug 1975; Carlson 1979; Oehlke 1983a), *Betula* (birch) (Schimitschek 1974; Oehlke 1983a), *Ostrya* (hop hornbeam) (Schimitschek 1974), *Populus* (poplar) (Schimitschek 1974; Oehlke 1983a), *Quercus* (oak) (Schimitschek 1974), *Salix* (willow) (Schimitschek 1974; Evenhuis and Vlug 1975; Oehlke 1983b) and *Ulmus* (elm) (Schimitschek 1974). In North America, host trees include *Acer*, *Alnus*, *Betula*, *Carpinus* (hornbeam), *Fagus* (beech), *Malus* (crab-apple), *Quercus* , *Tilia* (lindens and limes), and *Rhus* (sumac) (Townes 1951; Smith 1979, 1996).

Collecting data shows that *Pristaulacus* species have been reared or collected from a wide range of both gymnosperm and angiosperm trees (Table 3.1 and Appendix A1.1). Again, these associations reflect the plant species infested by their hosts. For example *P. bilobatus*

(Provancher) has the same distribution as *Tsuga canadensis* (L.) Carr. (eastern hemlock) and the distribution of *P. pacificus* (Cresson) parallels that of *Pseudotsuga taxifolia* (Poir.) Britt. (Douglas fir) (Townes 1950).

Table 3.1. Summary of plant families from which *Pristaulacus* has emerged. See Appendix A1.1 for full records.

Distribution	Plant Family	No. of plant species recorded
Australian	Leguminosae	1
	Rutaceae	1
Nearctic	Betulaceae	3
	Cupressaceae	1
	Fagaceae	1
	Juglandaceae	2
	Pinaceae	15
	Rosaceae	1
	Salicaceae	1
Oriental	Dipterocarapaceae	1
Palaearctic	Celestraceae	1
	Fagaceae	1
	Leguminosae	2
	Myrsinaceae	1
	Pinaceae	1

There is no information on oviposition in *Pristaulacus*, but they have guides on the hind coxae similar to *Aulacus* (Crosskey 1951; Naumann 1991), and it is presumed that oviposition would be similar since their hosts are also wood boring larvae.

Gasteruption jaculator (L.) has been observed ovipositing into nests of *Osmia leaiana* Kirby (Megachilidae) that was nesting in a dead willow tree (Morley 1916). The female wasp hovers around the nests, touching the antennae on the entrance. The wasp repeatedly settles and thrusts the full length of the ovipositor into the nest while the valvulae remain at right angles to the trunk. In the case of an already sealed nest, the wasp pierces it by hard pushing without any drilling action. Gasteruptiidae do not have grooves on the hind coxae to guide the ovipositor as do the Aulacidae.

Hyptiogastrine wasps employ a hovering flight similar to that of *Gasteruption* when searching for and inspecting host nests. This has been observed for *Crassifoenus* (Houston 1984a), *Eufoenus* (Houston 1969; Naumann 1983; Jennings and Austin unpublished), and *Hyptiogaster* (Houston 1984a). Because the hosts of hyptiogastrine wasps are mostly ground nesting, often many centimetres below the surface, the wasps must enter the nest tunnel to oviposit. *Eufoenus* has been observed entering host nests abdomen first (Houston 1969). However, oviposition has not been observed for any hyptiogastrine species.

3.2. Mode of development

Aulacid larvae appear to be endoparasitoids, with the female wasp laying its egg in the egg of the host (Skinner and Thompson 1966; Askew 1971), although it has been suggested in one study that they are ectoparasitoids and that the host larvae may be paralysed by the female wasp before oviposition (Sedivy and Capek 1988).

Female *Aulacus striatus* Jurine locate the egg-shaft of xiphydriid wasps, insert the ovipositor and lay single eggs in as many of the batch of host eggs as can be reached (Skinner and Thompson 1960). *Aulacus burquei* (Provancher) also lays its eggs in a similar manner (Deyrup 1984). The ovaries of *A. striatus* contain some 200 eggs which, when mature, are pedunculate and 0.6 mm in length (Bugnion and Popoff 1911; Crosskey 1951). The body of the egg is almost spindle-shaped with an attenuated thread-like stalk.

The larva of *A. striatus* completes its feeding when the host xiphydriid larva has fed for almost a year (Skinner and Thompson 1960). It then proceeds to kill the host larva which by this stage has almost reached the surface of the wood. Having emerged from the host, the *A. striatus* larva spins a cocoon in which it pupates (Skinner and Thompson 1960). Askew (1971) confirms that aulacid larva emerge from fully grown *Xiphydria* larvae.

Different species of *Gasteruption* deposit their eggs in proximity to the host egg, with the exact positioning depending on the species (Malyshev 1964, 1966). *Gasteruption caudatum* Szépligeti is ectoparasitic in that it lays its eggs on the egg of *Osmia leucomelena* Kirby. *Gasteruption pyrenaicus* (Guérin-Méneville) lays its eggs on the store of honey just in front of the egg of *Ceratina* (Anthophoridae); *G. jaculator* (L.) lays its eggs on the wall of the cell in front of the food store of *Colletes daviesanus* Smith (Colletidae); and *G. freyi* (Tournier) lays its eggs outside the cell of *Hylaeus (*Colletidae) on the outside of its lining membrane. Höppner (1904) however, reported that *G. assectator* F. is ectoparasitic on *Hylaeus* where it oviposits onto the mature host larva.

The larvae of Gasteruptiidae are reported to be predators or predator-inquilines of various solitary bees and wasps (e.g. Höppner 1904; Malyshev 1966; Carlson 1979). Other authors have used the term secondary cleptoparasitoid (synonymous with predator-inquiline) (e.g. Valentine and Walker 1991) or ectoparasitoid (synonymous with predator) (e.g. Prinsloo 1985) when referring to gasteruptiids. In the past it was suggested that *Gasteruption* do not behave as parasitoids but as true carnivores, since nothing remains of the immature stages of the host bee except the remnants of the cuticle and an empty cranial capsule (Malyshev 1966). However, this concept is now well out of date with current knowledge of parasitoid biology (e.g. see Gauld and Bolton 1996).

In *Gasteruption*, there are considerable differences among species in the exact method of parasitism, with the larvae of some species consuming the host egg and others consuming the host larvae. For example, shortly after hatching, the larvae of *G. caudatum* and *G. pyrenaicus* consume the host egg (Malyshev 1966). The second instar larvae of these two species feed on the food store of the host bee. In some cases the larva completes its development by consuming the food store in more than one cell: if the partitions are weak or brittle partitions, the larva may invade surrounding cells where it consumes both bee larvae and food stores. In comparison, upon eclosion, the larva of *G. assectator* consumes the mature *Hylaeus* larva (Höppner 1904). The larva then invades the cell of a second larva and consumes that also.

Several *Gasteruption* from southern Africa are known to be ectoparasitic. *Gasteruption robustum* Kieffer is ectoparasitic upon the larvae of *Xylocopa* spp. (Anthophoridae) (Whatmough 1974; Prinsloo 1985). The gasteruptiid larva kills the host egg and then feeds on the pollen paste provided for the bee larva. *Gasteruption caffrarium* Schletterer is ectoparasitic on *Hylaeus* (Skaife 1953). The egg hatches after three days and the parasitoid larva consumes the bee egg before feeding on the honey and pollen store. The larva may also move to the adjoining cell where it feeds on the food store before devouring the bee larva. *Gasteruption punctulatum* Schletterer is also ectoparasitic, in this case on the larvae of *Hylaeus (Notohylaeus) heraldicus* (Smith) (Skaife 1979).

3.3. Larvae

The larva of only one aulacid, *A. striatus*, has been described in any detail. It has an incomplete, sclerotised epistoma with two dorso-lateral projections that extend to the frontal area; large, unsclerotised tridentate mandibles with a short sclerotised blade; disc-shaped maxillary and labial palps and antennae; labral, stipital and labial sclerites are present (Short 1952, 1959; Finlayson and Hagen 1977).

The only larva of the Gasteruptiidae described is for *G. assectator*, although Malyshev (1964) depicts a number of species. When compared with the head of *A. striatus*, the larva of *G. assectator* is similar in that it possesses large tridentate mandibles but differs in that the labral, stipital and labial sclerites are absent (Short 1952). The body of the fully mature larva is clothed with bands of stout, brown, backwardly-directed setae, most evident on the dorsal surface (Crosskey 1951). The larva is elongate and measures 7-7.5 mm in length and 2-2.25 mm in width.

3.4. Pupation and emergence

The only aulacid species studied is *A. striatus*. Having emerged from its xiphydriid host, the larva spins a cocoon in which it pupates (Crosskey 1951; Skinner and Thompson 1960). The cocoon is reddish pink (Ratzeburg 1852) and is fine, translucent and testaceous, and has the remains of the host larvae attached (Sedivy and Capek 1988). The adult emerges about two weeks later, escaping by gnawing a hole through the thin cap of wood left by the host. *Aulacus burquei* also spins a cocoon (Deyrup 1984). No information is available for any *Pristaulacus* spp.

Information on *Gasteruption* is also very scarce. The larva of *G. robustum* pupates at the end of the host bee's tunnel where it seals itself off with a tough partition made from an excretion from the anus (Whatmough 1974). *Gasteruption caffrarium* pupates inside two cells of *Hylaeus* (Skaife 1953), while *G. assectator* pupates in a cocoon within the cell of its host (Crosskey 1951).

The pupal stages and emergence of the Hyptiogastrinae are very poorly known. Houston (1984a) has observed a cocoon of *Hyptiogaster* sp. in a cell of *Paragia tricolor* Smith (Vespidae), and Jennings and Austin (1997b) have described the pupa of *Aulacofoenus thoracicus* (Guérin Menéville).

3.5. Adults

Virtually no information is available on the mating behaviour of aulacid or gasteruptiid wasps, although Skinner and Thompson (1960) describe the courtship and mating of *Aulacus striatus*. Similarly, little is known of the internal anatomy of aulacids, although the digestive system and ovaries of *A. striatus* have been described (Bugnion and Popoff 1911). The oesophagus is long and straight, the crop dilated and the proventriculus short, striated and without a valve, while no caecae are apparent. The ventriculus is ovoid, measures 2-3 mm in length and about 1.3 mm in diameter, and is composed of small yellowish polygonal cells. There are 16 malphigian tubules. The ileum is short and without any apparent demarcation from the rectum. Four rectal plates are arranged in pairs, one anteriorly and the other posteriorly.

Haack and Wilkinson (1987) reported an interesting case of the pseudoscorpion, *Dendrochernes* cf. *morosus* (Banks), which was phoretic on adult *Pristaulacus niger* (Shuckard), that had emerged from trunk sections of *Pinus elliottii* var. *elliottii* (slash pine) in Florida. Up to three pseudoscorpions were attached to the legs and pedicel of the abdomen of a single aulacid.

Although some information has been provided on feeding behaviour of adult aulacids and gasteruptiids for British species (Crosskey 1951), there is a lack of information for most species and regions. *Aulacus* and *Gasteruption* are known to visit flowers (Crosskey 1951), but whether they are feeding on pollen and/or nectar is not stated. There is nothing published on adult feeding of *Pristaulacus* or for any members of the Hyptiogastrinae.

Aulacus striatus have been recorded on the flowers of Umbelliferae in the Palaearctic region (Crosskey 1951; Hedqvist 1973). Umbelliferae produce pollen and also have nectariferous disks (the stylopodium) (Jessop and Toelken 1986). Aulacid mouthparts do not appear to be adapted to nectar feeding as they have a very short glossa (*sensu* Crosskey 1951), although they may not need a very long glossa to reach the stylopodium. During this study, the mouth parts of a number of *Aulacus* spp. from various museum collections in Australia and the United States were examined and found to have no pollen in or around them suggesting that they are not pollen feeders.

There are no records of *Pristaulacus* visiting flowers. Australian species have an elongate glossa, although somewhat shorter than in Gasteruptiidae, and typical of other nectar feeding species. However, the North American species examined do not have an elongate glossa. No pollen was found on the mouthparts of a range of museum specimens of *Pristaulacus* spp. from either North America or Australia, suggesting that they are also nectar feeders.

Gasteruption have an elongate glossa, suggesting that they too are nectar feeders. The galea are flattened and foliaceous with a fringe of stout comb-like setae on the inner margin (the galeal pecten), the fused glossae (the glossa *sensu* Crosskey) are well developed, and paraglossae reduced (Crosskey 1951). Examination of the mouthparts during this study of a range of *Gasteruption* spp., revealed pollen on approximately one-third of individuals, although the load varied considerably with species. Given the range of plants visited which produce both pollen and nectar, it is likely that at least some *Gasteruption* feed on both nectar and pollen.

Although data for most regions are either scarce or non-existent, adult *Gasteruption* have been recorded as visiting a wide range of flowers from many species and families (Table 3.2 and Appendix A1.2). Umbelliferae appear to be favoured by *Gasteruption* in the Palaearctic region and Myrtaceae in the Australian region. Myrtaceae are dominant in the Australian flora with over 1500 species (Chippendale 1988) and it is therefore not surprising that *Gasteruption* have been widely recorded as visiting this plant group. Myrtaceae visited by *Gasteruption* include *Angophora, Eucalyptus, Leptospermum, Lophostemon,* and *Melaleuca*

(Appendix A1.2). These genera produce both pollen and nectar (Blake and Roff 1972; Clemson 1985) in large quantities, and are visited by many groups of insects. Other plants visited such as *Schinus* (Anacardiaceae), *Banksia* and *Grevillea* (Proteaceae) and *Atalya* (Sapindaceae) also produce both pollen and nectar (Clemson 1985).

The Hyptiogastrinae have an elongate labio-maxillary complex making them ideal nectar feeders (Appendix A5, Figs 2-3). The galea are flattened and foliaceous with a distinct galeal pecten, as in *Gasteruption*. The function of the galeal pecten, which is perhaps most developed in *Aulacofoenus* (Appendix A5, Figs 2-3), is at present not clear. The fused glossae are well developed in all hyptiogastrine wasps and are often "sieve like" (Appendix A3, Figs 23-24)). This presumably increases their surface area and thus assists in the uptake of nectar. The labio-maxillary complex of gasteruptiids are articulated (Crosskey 1951), although in museum specimens, the glossa are often retracted behind the mandibles.

Records of plant visitations/associations for the Hyptiogastrinae are more widespread than for other biological information (Table 3.2 and Appendix A1.2). There is no apparent pattern to the range of plants visited, although the wasps visit similar plants to *Gasteruption*. The plants recorded mostly produce both pollen and nectar, although *Eufoenus* and *Hyptiogaster* have been recorded from *Acacia* spp. (Appendix A1.2), which do not have floral nectaries although some species have extra-floral nectaries, often located at the base of the phyllodes (Clemson 1985). Museum data labels do not indicate whether any species were collected feeding on the extra-floral nectaries or were at flowers. Most museum specimens of hyptiogastrines inspected in this study had pollen in and around the mouthparts, ranging from just one or two grains in some *Crassifoenus* to very heavy pollen loads in some *Pseudofoenus*, often more than 50 grains per specimen (Appendix A4, Fig. 20 - note pollen grains). These observations suggest that hyptiogastrine wasps may feed on both nectar and pollen. Alternatively, it is also possible that pollen may simply have been picked up during the process of feeding on nectar, and the results reflect more the type of flower visited rather than direct feeding on pollen. Additional field observations are necessary to confirm this.

Table 3.2. Summary of aulacid and gasteruptiid plant associations by region and family indicated by recorded visits to flowers and/or collection from flowers. See Appendix A1.2 for full records. (n/a = not available)

Genus	Distribution	Plant Family	No. plant species recorded
Aulacidae			
Aulacus	Palaearctic	Umbelliferae	n/a
Pristaulacus	No records	-	-
Gasteruptiidae			
Gasteruptiinae			
Gasteruption	Australian	Anacardiaceae	1
		Frankeniaceae	1
		Myrtaceae	21
		Pittosporaceae	1
		Proteaceae	2
		Rhamnaceae	1
		Sapindaceae	2
		Umbelliferae	1
	Nearctic	Compositae	1
		Umbelliferae	1
	Palaearctic	Alliaceae	1
		Anacardiaceae	1
		Caryophyllaceae	1
		Celestraceae	1
		Compositae	4
		Ericaceae	1
		Euphorbiaceae	3
		Fabaceae	1
		Labiatae	1
		Proteaceae	1
		Rhamnaceae	1
		Rutaceae	1
		Saxifragaceae	1
		Umbelliferae	15
Hyptiogastrinae			
Aulacofoenus	Australian	Chloanthaceae	1
		Fabaceae	2
		Goodeniaceae	1
		Myrtaceae	1
		Rutaceae	1
Crassifoenus	Australian	Myrtaceae	2
Eufoenus	Australian	Amaranthaceae	1
		Compositae	1
		Fabaceae	1
		Labiatae	1
		Myrtaceae	5
		Pittosporaceae	1
		Proteaceae	2
		Verbenaceae	1
Hyptiogaster	Australian	Fabaceae	2
		Goodeniaceae	1
		Labiatae	1
		Myrtaceae	3
Pseudofoenus	New Zealand	Myrtaceae	3
		Scrophulariaceae	1

Nectar feeding has been observed for one species of *Eufoenus*, where the elongate glossae are used to probe the nectaries of *Calytrix tetragona* (Myrtaceae) (Fig. 3.1).

Until further field observations are made, the exact mode of feeding of aulacids and gasteruptiids remains unclear, although pollen analysis, together with observations on the structure of the mouthparts and recorded plant visitations, suggest that aulacids are nectar feeders and gasteruptiids feed on both pollen and nectar, although for the latter group this may differ among species.

3.6. Phenology

Aulacus striatus would appear to be univoltine (Skinner and Thompson 1960). Although there is no direct evidence to support this for other aulacids, collecting data indicate that adults for most species fly for a relatively short period each year, thus suggesting they have an annual life-cycle. For example, *A. pallipes* Cresson has been collected in the U.S.A. mostly in July (Townes 1950), and the seasonal flight activity of *A. burquei* is in the period early May to late July and for *A. lovei* Ashmead late May to mid July (Smith 1996).

Pristaulacus may be either univoltine or multivoltine depending on the species, although again there are very few studies other than dates of collection. *Pristaulacus beesoni* (Turner) apparently has an annual life cycle in northern India with emergence from May to September (Beeson 1941). Smith (1996) indicates that for *P. flavicrurus* (Bradley), the flight activity takes place in June and July in North America, and for both *P. strangaliae* (Rohwer) and *P. stigmaterus* (Cresson) the flights occur in May to the end of July. However, *P. rufitarsis* (Cresson) may have a life cycle that extends for more than three years. The cerambycid host, *Saperda calcarata* Say, has a life cycle from three to five years, depending on temperature (Anon. 1979). If *P. rufitarsis* emerges from the host larva only when it is fully grown and has chewed its way close to the surface of the wood, as is the case with *A. striatus* (Skinner and Thompson 1960; Askew 1971), then it too may take three to five years to complete its life cycle.

Gasteruption caffrarium is multivoltine with two or three generations occurring each year (Skaife 1953). Collection data for other *Gasteruption* indicate that in North America, *G.*

assectator are collected between late June and late August, whereas *G. pattersonae* Melander & Brues are collected from late April to mid September (Townes 1950).

An analysis of collecting data in Australia indicates that for *Aulacofoenus fallax* (Schletterer) and *A. thoracicus*, adults are not collected in the colder and wetter Autumn and Winter months (Fig. 3.2), being mostly collected in the warmer months. Similar data are evident for *Crassifoenus macronyx* (Schletterer) and *Hyptiogaster* spp. The bee hosts are also not collected in these time periods (Houston pers. comm. 1996), and also this reflects the absence of flowering of many of the plants visited by adult wasps (Table 3.2).

For the two South American species, *A. deletangi* (Schletterer) and *A. infumatus* (Schletterer), the collecting period is more restricted, the former being collected in October and November and the latter from November to February (Fig. 3.2). Among *Eufoenus* species, the range of collecting dates is more variable; some species are similar to the pattern for *Aulacofoenus*, whereas *E. floricolus* (Turner),which is very widespread in its distribution (Fig. 8.191), has been collected from September to May (Fig. 3.2). On the other hand, *E. extraneus* (Turner) which is endemic to Fiji, is not collected in the drier months of November to January (Fig. 3.2). Data for *P. unguiculatus* (Westwood) indicates a shorter collecting period in the South Island of New Zealand than is found in the North Island (Fig. 3.2), possibly reflecting the colder conditions encountered on the South Island.

The above collecting data for Hyptiogastrinae suggests that they are for the most part univoltine. Whether or not this is the case for *E. floricolus* and *E. extraneus* is less obvious given the wide range of collecting dates.

3.7. Host relationships

3.7.1. Aulacidae

Members of this family are thought to be endoparasitoids of wood boring Hymenoptera or Coleoptera (e.g. Carlson 1979; Gauld and Bolton 1996), and the summary of available host data (Table 3.3) indicates that this is indeed the case, but there are apparent differences between regions and genera.

For *Aulacus*, host data indicates they mostly parasitise xiphydriid wasps in the northern hemisphere and cerambycids in the southern hemisphere (Table 3.3 and Appendix A1.3). There are three documented exceptions to this pattern; *A. striatus* Jurine has been bred from *Xylotrechus capricornis* (Gebler) (Cerambycidae) in Europe (Sedivy and Capek 1988), while there are doubtful records of *A. striatus* from *Purpuricenus koehleri* L. (Cerambycidae) (Giraud 1877; Gaulle 1908) and *A. aneurus* Walkley from *Dendroctonus* (Scolytidae) in New Mexico (Walkley 1952; Krombein *et al.* 1958; Carlson 1979). Since there are no specimens of the latter species in the USNM collection reared from *Dendroctonus,* Carlson (1979) considered the latter record to be doubtful. Smith (1996) suggests that both *A. schiffi* Smith and *A. impolitus* Smith probably parasitise wood-boring Coleoptera, but no host records are available.

Table 3.3. Known regional distribution and host groups of aulacids showing numbers of recorded aulacid species and host species. (? = uncertain record)

Genus	Distribution	No. aulacid species recorded as parasitic on each host group	Host Groups	No. host species recorded
Aulacus	Australian	8	Cerambycidae (Col.)	8
	Nearctic	1	Buprestidae (Col.)	1
		1	?Scolytidae (Col.)	1
		1	Xiphydridae (Hym.)	5
	Palaearctic	1	Cerambycidae	2
		3	Xiphydriidae	5
Pristaulacus	Australian	8	Cerambycidae	7
	Nearctic	6	Buprestidae	7
		9	Cerambycidae	18
	Oriental	1	Buprestidae	1
		3	Cerambycidae	3
	Palaearctic	1	?Bostrychidae (Col.)	1
		1	Buprestidae	2
		5	Cerambycidae	7
		1	?Cleridae (Col.)	1
		1	Xiphydriidae	2

When parasitising Xiphydriidae, aulacids are recorded only from the genus *Xiphydria* (Appendix A1.3). This host family is a small group of wood boring wasps that are found in most temperate and tropical forest regions, except in Africa (Benson 1954; Riek 1955; Smith 1976). The larvae bore into dead or dying branches and small limbs of deciduous broad-leaved trees. Many tropical species are rarely encountered (Smith 1976), as is the case for the

Australian species (Riek 1955). Because of the scarcity of xiphydriid hosts, in the southern hemisphere *Aulacus* appears to parasitise alternative hosts (Cerambycidae) that have a similar biology to the xiphydriids, i.e. boring into wood (Table 3.3 and Appendix A1.3).

Pristaulacus, with the exception of one species, are recorded as parasitoids of various wood boring beetles (Table 3.3 and Appendix A1.3). Both Oriental and Nearctic species parasitise buprestid and/or cerambycid larvae. For example, *P. editus* (Cresson) and *P. minor* (Cresson) parasitise buprestid and cerambycid larvae which are often found in pine cones (Townes 1950). Cerambycids are the only wood boring beetles recorded as hosts of *Pristaulacus* in the Australian region (Table 3.3 and Appendix A1.3).

In the Palaearctic region, apart from cerambycids and buprestids, *Pristaulacus* has been recorded as possibly parasitic on bostrychids and clerids. *Pristaulacus bimaculatus* Kieffer has been reared from the timber of *Ceratonia siliqua* (carob) infested with *Scobicia pustulata* F. (Bostrychidae) and *Denops albofasciata* Charpentier (Cleridae) (Oehlke, 1983b). However, whether they are the real hosts has yet to be demonstrated. *Pristaulacus patrati* Serville is recorded as a parasitoid of *Xiphydria annulata* Jurine (Lichtenstein and Picard 1918; Györfi 1964; Oehlke 1983b) and *X. longicollis* Geoffroy (Schimitschek 1974).

3.7.2. Gasteruptiidae

Early records indicated that twig-nesting species of solitary bees (e.g. *Ceratina*, *Heriades* and *Hylaeus*) were the hosts of *Gasteruption* (Höppner 1904; Rau 1928). More recent and extensive records indicate a much wider range of solitary bees and wasps act as hosts for this genus including the families Anthophoridae, Colletidae, Megachilidae, and Vespidae (Masarinae) (Table 3.4 and Appendix A1.4).

The available data also suggest that individual *Gasteruption* species vary from being polyphagous to having a more restricted host range. For example, *G. assectator* and *G. jaculator* (L.), have a wide host range (Colletidae, Megachilidae, Sphecidae and Vespidae), while others such as *G. caudatum* and *G. freyi* (Tournier) are recorded as parasitising only Megachilidae and Colletidae, respectively (see Appendix A1.4). However, these data are based on a restricted number of records and should therefore be treated with caution.

While there is only limited information on the host relationships of the Hyptiogastrinae, it seems likely that they are predator-inquilines of solitary bees. There are museum records of *Aulacofoenus asymmetricus* (Turner) "at the nests" of the halictid bee *Nomia australica* Smith on Kangaroo Island, South Australia (Table 3.4 and Appendix A1.4). There are no observations available for the Neotropical species.

Adults of *Crassifoenus houstoni* Jennings and Austin have been observed hovering over and entering the burrows of *Ctenocolletes* (Stenotritidae) bees (Houston 1984b). Females spent several minutes within the host burrow but parasitism was not confirmed on excavation of the nests. There is also one record of *Crassifoenus macronyx* leaving the nest of *Stenotritus* sp. (Stenotritidae) near Maree, South Australia (Appendix A1.4).

Little is known about the host relationships of *Eufoenus* species and yet this is by far the largest hyptiogastrine genus, with 22 described species (Crosskey 1962) prior to the proposed revision of the subfamily (see Chapter 8). *Eufoenus* adults have been observed in South Australia circling nests of the colletid *Xanthesma furcifera* (Cockerell) and entering the nest shafts by wriggling their bodies as they pushed, abdomen first, into the sand (Houston 1969). *Eufoenus* have also been observed engaging in a "bouncing, hovering" flight near the nesting sites of *Hylaeus* (Colletidae) in the Northern Territory (Naumann 1983). This behaviour has also been observed during this study for several other species of *Eufoenus* that occur near Adelaide, South Australia.

Eufoenus has been captured entering the burrow of the colletid *Euryglossula chalcosoma* (Cockerell) in Queensland (Houston 1969). In another study, many hundreds of *Eufoenus inaequalis* (Turner) have been observed congregating around the nest shafts of the colletid *Cladocerapsis persooniae* Rayment (Parrott 1955). Apart from these observations and several new records of *Eufoenus* associated with colletids compiled during this study (Appendix A1.4), there is one new record of parasitism on the stenotritid *Nomia australica* Smith (Table 3.4 and Appendix A1.4).

Table 3.4. Summary of the known distribution, species numbers and host groups of the gasteruptiid genera (Note: generic names are those used prior to this study) See Appendix A1.4 for full listing of host records. (? = uncertain record)

Subfamily/Genus	Approx. no. described species	Distribution	Host Groups	References
Gasteruptiinae				
Gasteruption	85	Palaearctic	Colletidae Megachilidae Sphecidae ?Trigonalyidae ?Vespidae	Hedicke 1939; Oehlke 1983a
	16	Nearctic	Colletidae Megachilidae Sphecidae ?Vespidae	Carlson 1979
	35	Neotropical	?	Hedicke 1939
	34	Oriental	?	Hedicke 1939; Mani & Muzaffer 1943; Pasteels 1958b
	74	Afrotropical	Anthophoridae Colletidae Megachilidae	Pasteels 1956a, 1958a, 1962
	137	Australian	Colletidae Sphecidae Megachilidae ?Vespidae	Pasteels 1956a, 1957a, 1957b
Hyptiogastrinae				
Aulacofoenus	14	Australian	?Halictidae	Crosskey 1962; Naumann 1991
			Colletidae	Jennings & Austin 1997a
	2	Neotropical	?	Crosskey 1962
Crassifoenus	3	Australian	Stenotritidae	Houston 1984b, 1987; Jennings & Austin 1994a
Eufoenus	21	Australian	Colletidae Halictidae	Crosskey 1962; Naumann 1991
Hyptiogaster	10	Australian	Stenotritidae	Houston 1975, 1984b
			Vespidae	Houston 1984a
Pseudofoenus	2	New Zealand	Colletidae	Crosskey 1962; Naumann 1991; Jennings & Austin 1994b

It appears that *Hyptiogaster* is parasitic in the nests of Masarinae (Vespidae) and Stenotritidae (Table 3.4). This genus has been observed hovering over the nesting area of the masarine *Paragia tricolor* Smith in Western Australia (Houston 1984a). Although none of the wasps were seen to enter the vespid's tunnels, *Hyptiogaster* larvae were found in three cells. Houston suggested that the larvae develop on the pollen stores, probably after destruction of the *Paragia* eggs. *Hyptiogaster* has been observed entering nests of *P. decipiens* Shuckard (Naumann and Cardale 1987). *Hyptiogaster* has also been seen entering and leaving the nest shafts of *Stenotritus pubescens* (Smith) (Stenotritidae), presumably to lay eggs (Houston 1975), and *Ctenocolletes ordensis* Michener (Stenotritidae) has been recorded as a host for *Hyptiogaster* (Houston 1984b).

Records for *Pseudofoenus* in New Zealand suggest they are parasitoids of colletid bees (Table 3.4 and Appendix A1.4). *Pseudofoenus pedunculatus* (Schletterer) has been recorded as a predator-inquiline of *Leioproctus metallicus* (Smith) (Gourlay 1930; Valentine and Walker 1991), and *P. crassipes* (Smith) and *P. unguicularis* (Smith) are associated with *Paracolletes* spp. (Jennings and Austin 1994b).

Figure 3.1. *Eufoenus* sp. feeding on flower of *Calytrix tetragona* (Myrtaceae) [Photo: G. Weber]

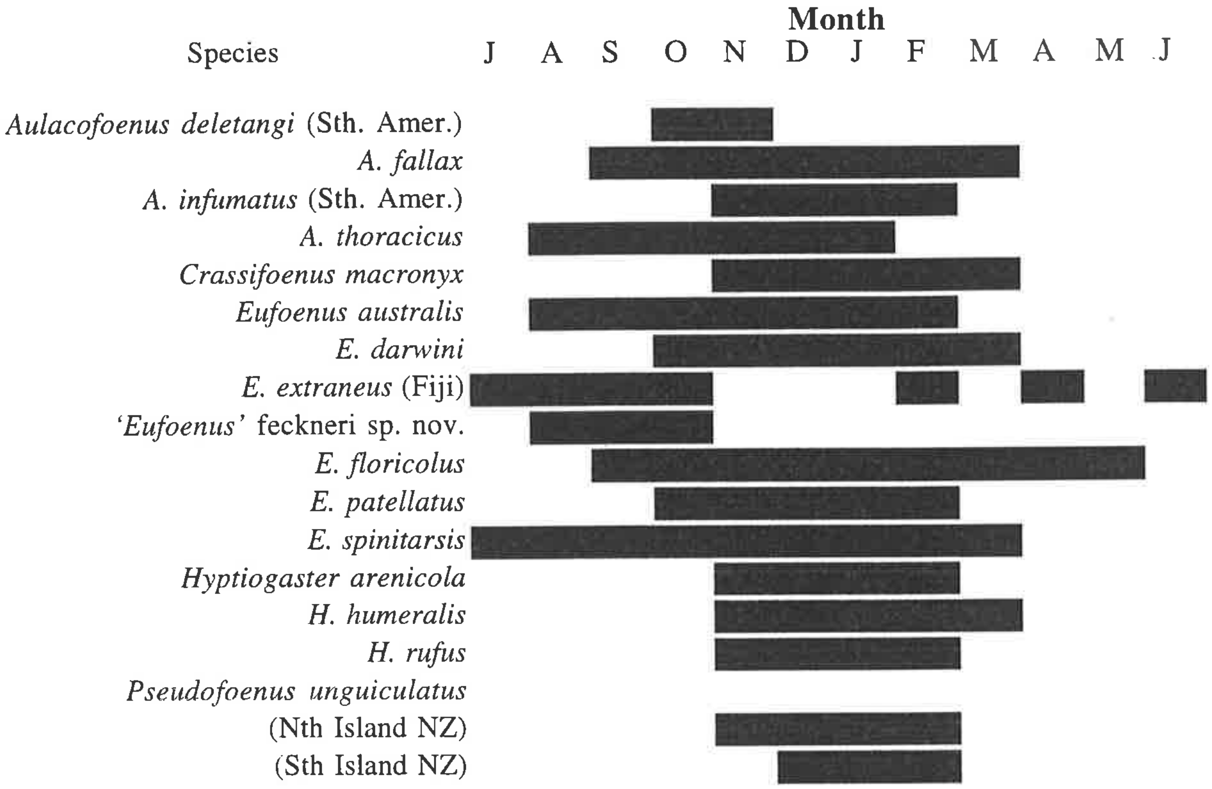


Figure 3.2. Diagram showing an analysis of collecting dates for selected hyptiogastrine species derived from museum data labels. Note: specific names used here are those prior to the proposed revision of taxa (see Chapter 8).

Chapter 4.

Materials and Methods

4. 1. Microscopy

Specimens were examined under a Zeiss dissecting microscope. Those for scanning electron microscopy were examined under either a Cambridge Stereoscan 250 (Mk 3B) SEM, a Phillips XL20 SEM or Phillips XL30 field emission SEM (FESEM). They were first cleaned by removing obvious dirt and other debris, and then either sputter-coated with gold or examined uncoated. The majority of taxa under study contained few specimens (sometimes only the holotype), and in these cases they were examined uncoated under the Phillips XL30 FESEM at 1kv and a spot size of four. This led some of the images being of lower contrast and hence poorer quality.

Specimens used for genitalic examination were partly dissected prior to the removal of the metasoma, hydrated in distilled water for up to 24 h, and the genitalia teased out with a fine needle.

4. 2. Terminology

Terminology for general morphology follows Jennings and Austin (1994a; see Appendix A3), and that for wing venation follows the modified Comstock-Needham system after Sharkey (1988), but with some modifications, and using the nomenclature of van Achterberg (1979) for cells (see Jennings and Austin 1994a). Terminology for surface sculpturing follows Harris (1979), and for male genitalia Crosskey (1951). The number of hamuli on the hind wings is given separately for each wing because of variation within many specimens, e.g. 3/4 indicating three hamuli on the left hind wing and four on the right. Measurements referring to the scape exclude the length of the radicle, which is clearly defined by a constriction (Appendix A5, Fig. 5). Where measurements are based on more than one specimen, data are presented in the form of a mean followed by the range.

4. 3. Abbreviations

Abbreviations of institutions are those used by Arnett *et al.* (1997) as follows:

AEIC	American Entomological Institute, Gainesville, Florida
AMSA	Australian Museum, Sydney

ANIC	Australian National Insect Collection, Canberra
BPBM	Bernice P. Bishop Museum, Hawaii
BMNH	The Natural History Museum, London
CASC	California Academy of Sciences, San Francisco
CNCI	Canadian National Collection of Insects, Ottawa
FIJI	University of South Pacific, Suva, Fiji
IMLA	Instituto Miguel Lillo, Tucuman, Argentina
LCNZ	Lincoln University Entomology Research Museum, Canterbury
MACN	Museo Argentina de Ciencias Naturales, Buenos Aires
MAMU	Macleay Museum, Sydney
MCSN	Museo Civico de Storia Naturale "Giacomi Doria", Genoa
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts
MHNG	Museum d'Histoire Naturelle, Geneva
MVMA	Museum of Victoria, Melbourne
NHMW	Naturhistorisches Museum Wien, Vienna
NMNZ	National Museum of New Zealand, Wellington
NSWA	New South Wales Department of Agriculture, Sydney
NZAC	New Zealand Arthropod Collection, Auckland
OMNZ	Otago Museum, Dunedin
OXUM	Hope Entomological Collections, Oxford
QPIM	Queensland Department of Primary Industries, Brisbane
QMBA	Queensland Museum, Brisbane
RMNH	Rijksmuseum van Naturlijke Historie, Leiden
SAMA	South Australian Museum, Adelaide
TAMU	Texas A & M University, College Station
UQBA	University of Queensland, Brisbane
USNM	Smithsonian Institute, Washington, D.C.
WADA	Western Australian Department of Agriculture, Perth
WAMA	Western Australian Museum, Perth

WARI	Waite Campus Collection, The University of Adelaide, Adelaide
ZMHB	Museum fur Naturkunde der Humboldt Universitat, Berlin
ZMUH	Zoologisches Institut und Zoologisches Museum, Universitat von Hamburg, Hamburg
ZSMC	Zoologische Staatssammlung, Munich.

4. 4. Localities

Distributions for species were plotted only for material with precise locality data. New Zealand locality codes used are those given in Crosby *et al.* (1976).

4. 5. Phylogenetic analyses

4.5.1. Software and computing

Microsoft Word 5.1a and 6.0 were used for word processing and for creating some tables and figures. Microsoft Excel 4.0 was used to manipulate morphometric data and to create more complex tables and figures.

PAUP for UNIX 4.0.0d (various versions), PAUP for Power Macintosh 4.0b2a (Swofford 1997), and PAUP 3.1.1 (Swofford 1993) were used for parsimony-based phylogenetic analyses. Maclade 3.07 (Maddison and Maddison 1997) was employed to input the data matrix in a NEXUS spreadsheet format and to trace character distributions on trees. AutoDecay 2.9.8 (Eriksson 1997) was used to calculate Bremer support or decay values (Bremer 1994).

Various computers including a Digital AlphaServer 2100/275 running UNIX 4.0d, a Mac LC III, and a Power Macintosh 7300/180 were used to run the phylogenetic analyses. In the analyses, 100 random replicates were run using PAUP (various versions) with random addition sequence, tree-bisection-reconnection (TBR) branch swapping, steepest descent and MULPARS options, and with all character states unordered, i.e. there was no *a priori* assumption made regarding character evolution. This approach has been taken by many workers including Ponder and Lindberg (1997).

4.5.2. Treatment of characters

Characters used in phylogenetic analyses are generally assumed to represent independent variables and may be viewed as random (Pleijel 1995). The assumption of randomness will be violated if a number of characters are linked. In this study, potential characters were divided, where possible, into binary states to minimise hierachical linkage and the problem of scoring non-applicable states (Wilkinson 1995; Pleijel 1995).

Quantitative or morphometric characters comprise continuous measurements, and as such, are difficult to divide into discrete states. At least 10 specimens were measured for the particular character, or if there were fewer than 10, all specimens were measured. Quantitative characters were coded using the segment coding technique of Chappill (1989). The means of the individual measurements were arranged in ascending order and then one standard deviation (SD) was added to the minimum mean in the table. All taxa equal to or less than the mean plus one SD were coded with one state. The standard deviation was then added to this value, and the values below this were assigned to the next state, and so on until all mean measurements were assigned a state (see Appendix A2.3 for an example of the procedure).

4.5.3. Options in parsimony analysis

PAUP can be used to search for the most parsimonious tree(s) in a number of ways: a) 'Exhaustive' or exact searching, b) 'Branch and Bound', or c) 'Heuristic'. The 'Exhaustive' option searches for all possible tree topologies and evaluates each one to find the optimal tree(s) for a given data matrix. For large matricies this method is not feasible because the search time becomes impossible (Swofford 1993). For example, there are over 2 million trees for 10 taxa and 34 million trees for 11 taxa. 'Branch and Bound' also provides an exact method for searching a large data matrix, but is still very time consuming, especially if the data are homoplasious, or the characters unordered. For large data sets, as is the case in this study, the 'Heuristic' option was the only realistic method. Whilst computing time is greatly diminished using this option, it is not possible to determine whether the analysis is hindered by a local optimum (Swofford 1993). 'Heuristic' methods find an initial tree(s) by stepwise addition and then this tree is subjected to trial rearrangements that attempt to find shorter trees (Swofford 1993). This process is referred to as 'branch swapping'.

Stepwise addition can be conducted in a number of ways, each option starting at a different point. The 'as is' option simply adds taxa in the same order as in the matrix and is not usually considered very effective (Swofford 1993). The 'closest' option adds branches that require the smallest increase in tree length, the 'simple' option is similar to the 'as is' option but branches are added on the basis of the distance between each taxon and a reference taxon, while the 'random' option uses a pseudorandom number to generate a permutation of the taxa to be used in the addition sequence (Swofford 1993). Iqbal (1998) evaluated these four options available in PAUP along with two branch swapping algorithms, SPR (subtree pruning and grafting) and TBR (tree bisection and reconnection). He concluded that the random addition sequence with TBR branch swapping was the most appropriate as this option produced the maximum number of shortest trees.

Bryant (1995) indicated that uninformative characters play no role in tree formation in which the identity and distinctiveness of the terminal taxa are assumed, i. e. tree topology is unaffected. Yeates (1992) argues that their removal is unwarranted. However, tree length and CI values are increased with their inclusion. CI measures the number of extra transformations per character required to explain the character-state pattern among taxa on a cladogram (see Chapter 4.5.4). Given that autapomorphies are unique to one taxon and entail a single transformation they cannot contribute to homoplasy and hence CI. Uninformative characters were therefore included in preliminary analyses (see section 6.4.), but in following analyses they were excluded.

The strict consensus tree was used to summarise information when more than one most parsimonious tree was obtained from the analysis (Anderberg and Tehler 1990). The strict consensus tree contains only those monophyletic groups that are in common to all competing trees, whilst nodes that disagree are collapsed into polytomies.

Data matrices were further analysed using a variety of weighting procedures:

1). Characters were weighted to determine the influence of multi-state characters on the analysis. Swofford and Begle (1993) indicate that multi-state characters have a greater influence on an analysis than binary characters. 'Scaling' of weights is achieved by choosing the smallest common multiple in order to avoid roundoff error. For example, if the data set contains a mixture of two- and three-state characters, then 2 is used as the base weight so that three-state characters have a base weight of 1 and two-state characters a weight of 2. If there are two- to five-state characters, then five-state characters have a weight of 3, four-state 4, three-state 6 and two-state 12. One drawback is that tree length is proportionally increased (i.e. twice as long in the former example and 12 times in the latter), which makes direct comparison of consensus tree length difficult.

2). Successive weighting was undertaken using both integer coding and additive binary coding. Carpenter (1988) recommends that when using multistate characters, additive binary rather than integer coding be used. The rationale behind this is that integer coding may result in greater weight being given to a particular character simply as a function of its score, whereas in additive binary coding each state of each character is individually evaluated. For example, in additive binary, if an integer coded character with three states is coded as 0, then it is divided into two 'characters', both coded 0. If it is integer coded as 1, then the two additive binary 'characters' are coded 1 and 0. If the integer code is 2, then it is coded as 1 and 1.

3). The characters were reweighted using the maximum rescaled consistency index (CI) after Farris (1989). In this procedure, characters with complete homoplasy have a weight of 0 and those with no homoplasy 1000. An heuristic search is conducted and a strict consensus tree generated. The characters are then successively reweighted until at least two successive searches yield strict consensus trees with the same topology (Swofford and Begle 1993).

4.5.4. Measures of tree fitness

PAUP can calculate and display a number of indices that measure the 'fit' of characters to a particular tree. They can also be used to interpret the results of an analysis. The consistency index (CI) (Kluge and Farris 1969) is a direct measure of homoplasy in a tree. CI is a measure of *m/s*, where *m* is the minimum amount of change that a character may show on any conceivable tree, and *s* is the length or number of steps required by that character on the tree being evaluated (Farris 1989; Swofford and Begle 1993). CI thus measures the number of extra transformations per character required to explain the character-state pattern among taxa on a cladogram. Transformation series with little or no homoplasy will have higher CI values (1 being the highest value), whereas those that show considerable homoplasy will have low values (0 being the lowest) (Wiley *et al.* 1991). Goloboff (1991) indicates that CI is the best measure of homoplasy associated with character distribution.

The retention index (RI), proposed by Farris (1989), is a measure of the maximum possible amount of change that a character can aquire on any conceivable tree. Farris also proposed the rescaled consistency index (RC) as the product of CI and RI. Rholf's CI (Rholf 1982) is a measure of the overall agreement of all trees included in the strict consensus tree, and is automatically calculated by PAUP.

The bootstrap procedure is a non-parametric statistical test used to assess confidence limits on phylogenies and is expressed as a percentage (Felsenstein 1985; Sanderson 1989). It approximates the distribution of taxonomic characters by resampling from the original data to form a new data set. Original characters may be sampled more than once or may even be omitted. This procedure is repeated a large number of times to construct an approximate sampling distribution. The resultant tree is then scored for the attribute of the phylogeny that is of interest (Sanderson 1989).

Decay indices or Bremer support values define how many extra steps are needed to collapse or lose a branch in the consensus tree (Bremer 1988, 1994). Decay indices were determined by searching for the most parsimonious tree constrained so as not to include the node in question in the topology. AutoDecay 2.9.8 (Eriksson 1997) was used to create constraint trees for the nodes in the strict consensus tree. The program does this by using the reverse constraint option in PAUP, and at the same time extracts the Bremer support values.

Chapter 5.

Morphology of Gasteruptiidae

This chapter describes the general morphology of gasteruptiid wasps to support the selection of characters used in the phylogenetic analyses (Sections 6.3 & 6.5.1), and those used in the taxonomic revision of the Hyptiogastrinae (Chapter 8). The morphology of the adults only is described here and illustrated in Figs 5.1 to 5.11 and elsewhere as indicated in the text.

5.1. Head

The head of gasteruptiid wasps is about equal in width to or slightly wider than mesosoma and elongate ventrally. The length of the malar space plus mandibles is about as long or longer than the height of the eye (Figs 5.1-3). A lateral epistomal suture may be present (Fig. 5.2) or absent so that the clypeus is continuous with the gena. The clypeal margin is generally sinuate (Fig. 5.2), but may have a truncate medial lobe (Appendix A6, Fig. 50). The mandibles are either elongate, strongly curved distally (Fig. 5.2) and broadly overlap when closed, as in hyptiogastrines or they are short and do not broadly overlap when closed as in *Gasteruption*. They are about as long as the clypeus or much shorter, generally have two medial teeth, although sometimes there may be one tooth or three teeth, and have a large inwardly directed basal tooth (Fig. 5.2). The labio-maxillary complex is elongate and protrudes well below the mandibles (Figs 5.1-3), but at rest may be folded up behind the mandibles. Maxillary palps are 6-segmented and labial palps 4-segmented (Fig. 5.3). A frontal carina may be present (Fig. 5.2-3) or absent (Fig. 5.1). Sub-antennal sutures are present, indistinct to clearly visible, defining a small triangular subantennal area on the medial face (Fig. 5.2). The antennae are inserted on the face about level with the middle of the eyes (Fig. 5.2). In the female, the antenna is 14-segmented, whereas in the male, it is 13- or rarely 14-segmented. The first flagellomere is variable in length among species when compared with the second segment, the radicle is well defined (Fig. 5.4), and the terminal flagellomere is generally much longer than wide. The eyes are large and elliptical (Figs 5.1-3). The ocelli form a small to large triangle on the vertex (Fig. 5.2). The distance from the lateral ocellus to eye margin is generally less than the distance between the lateral ocellus and occipital carina. The occipital carina may be either smooth or sculptured (Fig. 8.17).

5.2. Mesosoma

The propleuron is elongate, forming a 'neck' (Figs. 5.1), and sometimes has a prominent ventro-lateral carina (Appendix A5, Fig. 25). The pronotum rarely has antero-dorsal and antero-lateral tooth-like processes (Appendix A6, Figs 31, 47-48,), but generally they are absent (Fig. 5.10). The mesoscutum is almost as broad as long, and may be rounded (Fig. 5.10) or distinctly truncate anteriorly. It may have distinct or indistinct admedial lines, and sometimes may have medial lines (Fig. 5.10). The notauli are percurrent and either punctate or scrobiculate (Fig. 5.10). The parapsidal lines are indistinct (Fig. 5.10) and the pit of the metapleural apophysis is deep. The mesepisternum is usually divided into two by a lateral carinate depression. The propodeal spiracle is elongate (Fig. 5.11), and generally has a fringe of setae. The propodeum is separated from the metapleuron by a carinate furrow, and there is generally a medial longitudinal carina (Appendix A6, Fig. 27), although this varies from being short to percurrent.

5.3. Wings

The fore wings of gasteruptiid wasps are capable of plication (Fig. 3.1). The pterostigma and venation is well developed (Figs 5.7, 5.9). There are three distinct forms of fore wing venation. In the first form, typical of most hyptiogastrines, the fore wing vein 1-Rs+M intersects the basal cell about one-quarter to one-third distance from M+Cu, forming a discal cell bounded by 1-Rs+M, m-cu, 1-Cu(b) and 1-M (Fig. 5.9). In the second form, typical of most *Gasteruption*, 1-Rs+M intersects the basal cell at M+Cu, such that a small discal cell is formed bounded by 1-Rs+M, 1m-cu, 1-Cu and 2-Cu (Appendix A4, Fig. 8). Crosskey (1962) and Jennings and Austin (1994b) indicate that various degrees of occlusion of the discal cell may occur (Appendix A4, Figs 9-13) In the third form (found in only two hyptiogastrine species), the first discal cell is absent and veins 1-Rs+M and 1-Cu(b) are fused to form Rs+M+Cu(b) (Fig. 5.8). Veins 1-M and m-cu may be either present or absent. Hind wing vein 1-Cu (and 1-M) may be present but is absent in most species (Fig. 5.8). There may be 2-8 hamuli, but this number is generally variable within a species.

5.4. Legs

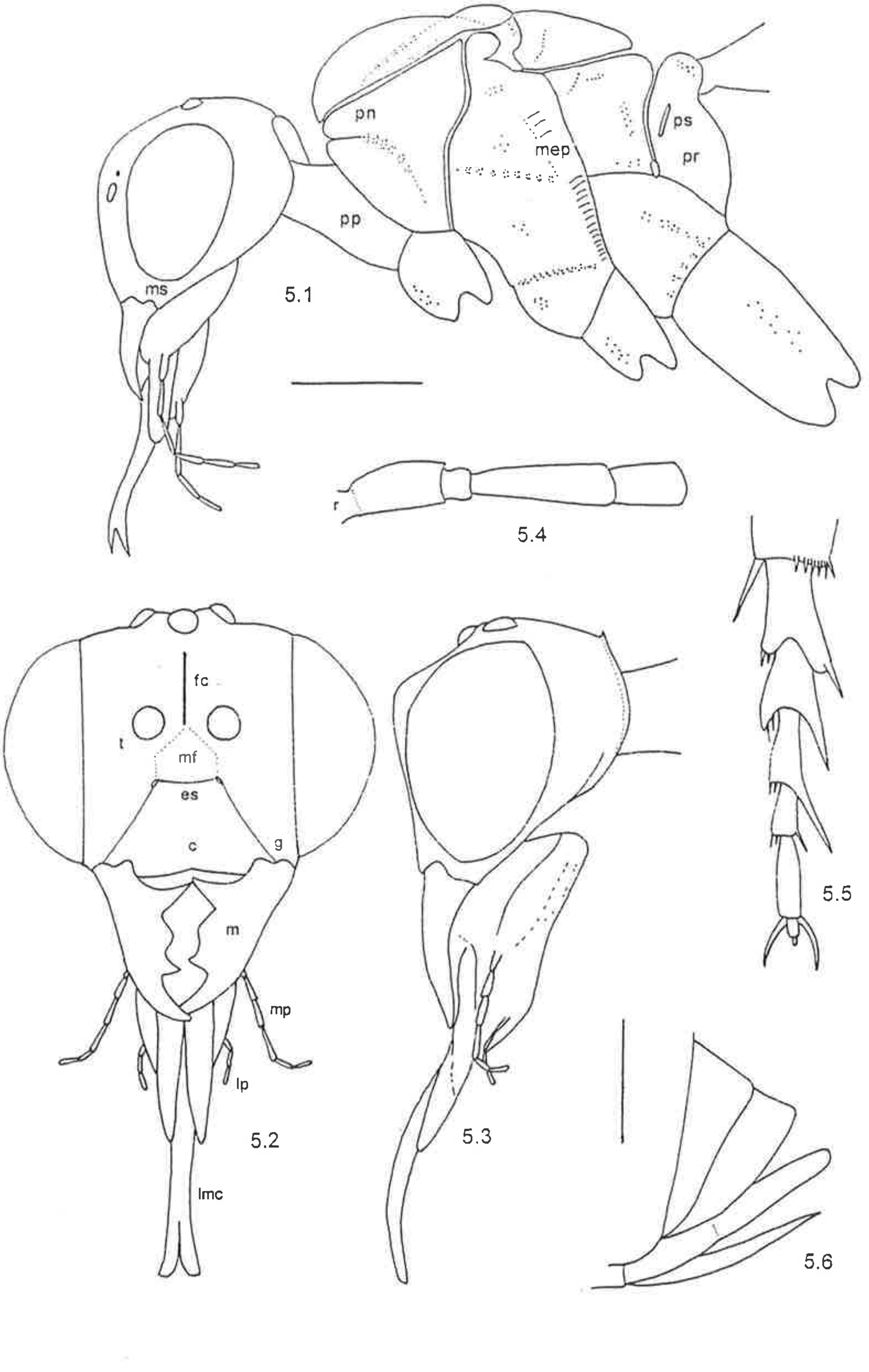
The inner surface of the mid tibia of females rarely has a subapical notch, and this is absent in males. The mid coxa has a transverse basal groove. A prefemur is either present (Fig. 8.5) or absent (Fig. 8.9) on the hind leg. The hind trochanter may have a transverse groove (Fig. 8.5, 8.21) or it may lack a groove (Fig. 8.53), however this character is sometimes variable within a species. The hind femur and tibia are incrassate and about equal in length. The mid and hind tibia each have two spurs, with the outer hind tibial spur being shorter and more robust than the inner spur (Fig. 8.154). The fore and mid tarsi are generally pubescent. The hind tarsal segments are variable in length, with segments 1-4 generally having a ventro-apical pecten of short spines (Fig. 5.5). The hind tarsal claws are simple, variable in size, but generally shorter than hind tarsal segment 5 (Fig. 5.5). Hind tarsal segments usually symmetrical, rarely segments 1-3, and rarely 4 are sometimes asymmetrical (Fig. 5.5).

5.5. Metasoma

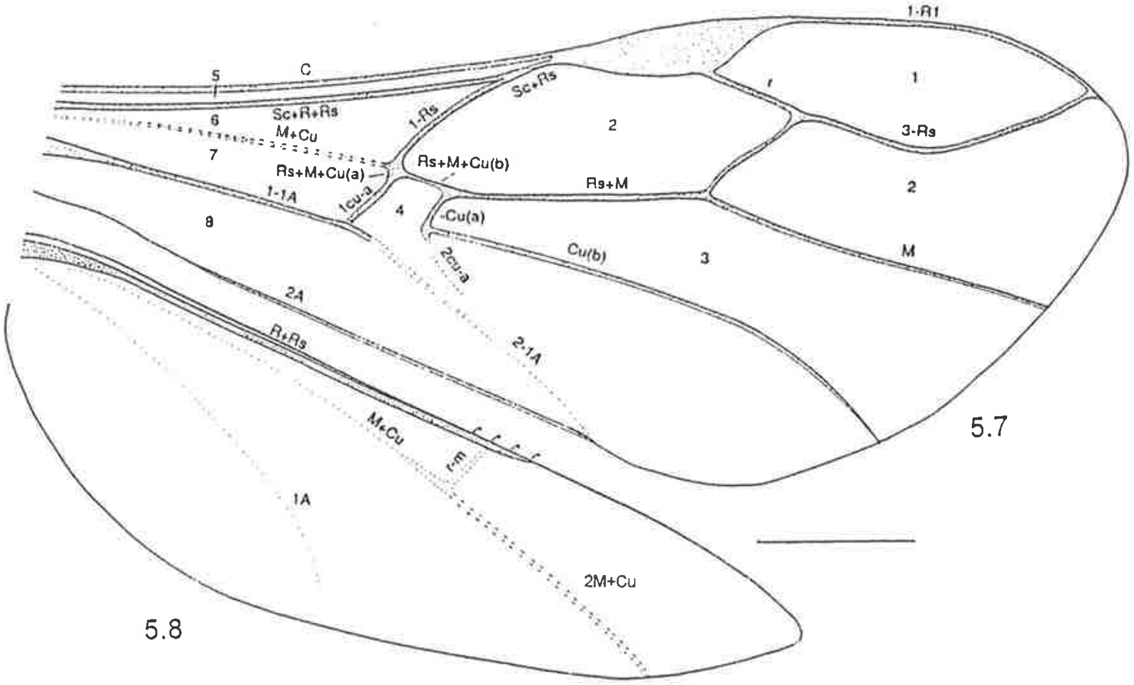
The metasoma is elongate and much longer than the mesosoma. Metasoma attached high on propodeum (Fig. 5.11). T1 and T2 are fused, and sometimes have a longitudinal median ridge (Appendix A5, Fig. 46). The subgenital sternite of females is simple, and may (Fig. 8.6), or may not (Fig. 8.7), have a slit or notch.

5.6. Genitalia

The ovipositor is either short, robust, upwardly curved (Fig. 5.6), and normally hidden by ovipositor sheaths (Appendix A3, Figs 26-27), or exserted and protruding well beyond apex of the metasoma. The digitus in males is broad and spathulate, and about the same length as the length of the basiparameres (Fig. 8.11).

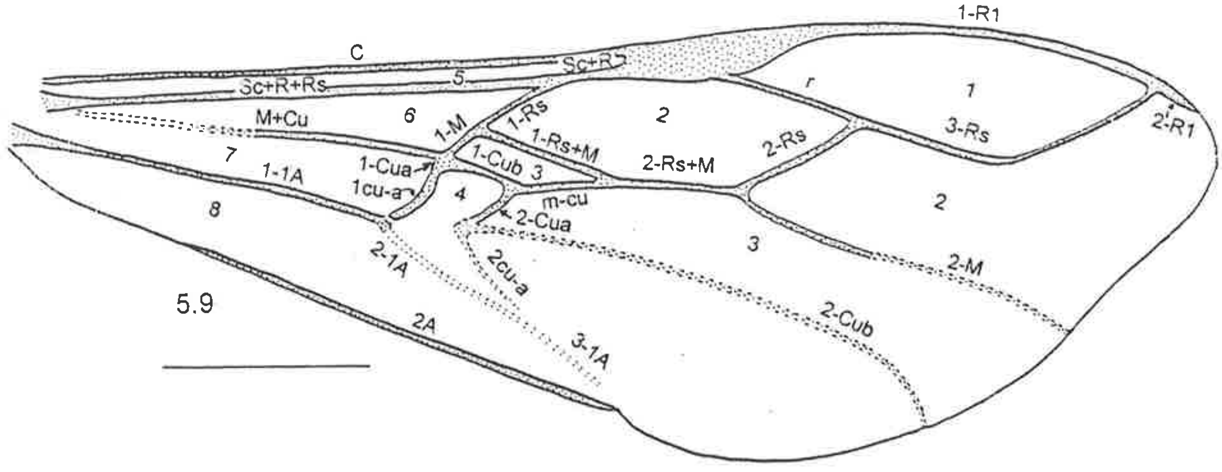


Figures 5.1-5.6. *Pseudofoenus unguiculatus* (Westwood), ♀, **5.1.** lateral view of head and mesosoma, (Jennings and Austin 1994b). *Aulacofoenus thoracicus* (Guérin Menéville), ♀, **5.2.** anterior view of head; **5.3.** lateral view of head; **5.4.** scape (and radicle), pedicel and flagellomeres 1 and 2; **5.5.** dorsal view of hind tarsal segments; **5.6.** lateral view of apex of mesosoma and ovipositor (Jennings and Austin 1997a). c = clypeus, es = epistomal suture, fc = frontal carina, g = gena, lmc = labio-maxillary complex, lp = labial palp, m = mandible, mep = metapleuron, mf = medial face, mp = maxillary palp, ms = malar space, pn = pronotum, pp = propleuron, pr = propodeum, ps = propodeal spiracle, r = radicle, t = torulus. Scale lines: *5.1-6*, 1 mm.



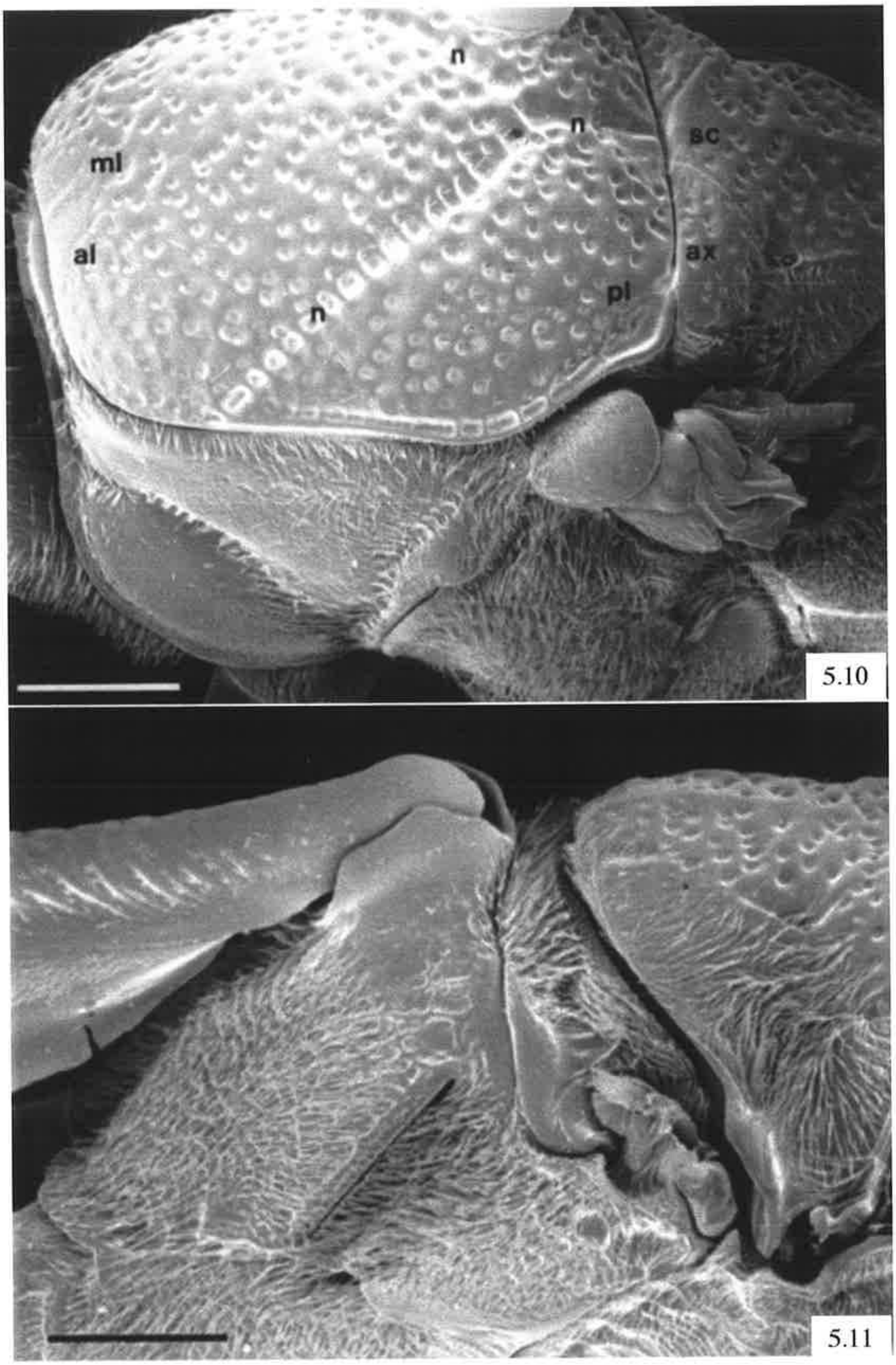
5.7

5.8



5.9

Figures 5.7-5.9. *Pseudofoenus unguiculatus* (Westwood), ♀. **5.7.** fore wing; **5.8.** hind wing (Jennings and Austin 1994b). *Crassifoenus houstoni* Jennings and Austin, paratype ♀. **5.9.** fore wing. Fore wing cells: 1, marginal; 2, submarginal; 3, discal; 4, discal; 5, costal; 6, basal; 7, subbasal; 8, plical (Jennings and Austin 1994a). Scale lines: *5.7-9,* 1mm.



Figuress 5.10-5.11. *Crassifoenus houstoni* Jennings & Austin, paratype ♀. **5.10.** dorso-lateral view of mesosoma (al = admedian line, ax = axilla, ml = median line, n = notaulus, pl = parapsidal line, sc = dorsal scutellum); **5.11.** lateral view of posterior mesosoma and T1 of metasoma. Scale lines: *5.10-11*, 1 mm. (Jennings and Austin 1994a - see Appendix A3).

Chapter 6.

Cladistics of the Hyptiogastrinae

6.1. Introduction

Relationships within the Gasteruptiidae, particularly the phylogenetic status of the subfamilies and genera, have not been examined previously, although Crosskey (1962) suggests that the Hyptiogastrinae is more 'primitive' than the Gasteruptiinae. Presented here are the results of cladistic analyses aimed at testing the monophyly of the Aulacidae and Gasteruptiidae, and the two subfamilies Gasteruptiinae and Hyptiogastrinae. This chapter also examines the relationships among genera and species of Hyptiogastrinae. It discusses the selection of taxa, characters and their states. Based on the results obtained here, a new classification for the Hyptiogastrinae is proposed which reflects their phylogenetic relationships.

6.2. Monophyly of the Hyptiogastrinae and outgroup determination

A total of 56 taxa (see Appendix A2.1) were included in the parsimony analyses to test the monophyly of the Aulacidae and Gasteruptiidae, and the two subfamilies Gasteruptiinae and Hyptiogastrinae. *Schlettererius cinctipes* (Cresson) (Stephanidae) was used as the outgroup because it is considered basal to the Evanioidea (see Dowton and Austin 1994). Six exemplar species of Aulacidae from Australia were selected, three each from *Aulacus* and *Pristaulacus*. Four Australian species of *Gasteruption* and one unidentified South American species were also included. Forty-two hyptiogastrines were included because of their morphological diversity and on the basis of both sexes being available for character analysis, viz. nine species of *Aulacofoenus*, three *Crassifoenus*, 23 *Eufoenus* (including nine undescribed species initially assigned to *Eufoenus* on the basis of the key in Crosskey (1962)), five *Hyptiogaster* and two *Pseudofoenus*. For *Pseudofoenus*, the two included species, *P. crassipes* and *P. unguiculatus*, were both female. The males of *Pseudofoenus* have not been associated with the females (Jennings and Austin 1994b; Austin *et al.* 1996, 1997), but of the male characters included, no differences between the species were observed.

A total of 58 characters (Appendix A2.1 and see below) were employed in these preliminary phylogenetic analyses, either because they showed some variation within and/or between the potential outgroups and the Hyptiogastrinae, or because they indicated variation within the Hyptiogastrinae. Female-based characters were used unless otherwise specified. Primary absence of a character was given a character state number '0'. Unknown states are scored as '?' and inapplicable as '_' in Appendix A2.1.

6.3. Character selection

Character 1. *Antennal insertion relative to eye:* **0)** well below eyes; **1)** level with base of eyes (Fig. 8.2); **2)** approximately half-way up eyes (Fig. 8.3; Appendix A4, Fig. 2).

Character 2. *Antennal segment number, female:* **0)** multi-segmented; **1)** 14.

Character 3. *Antennal segment number, male:* **0)** multi-segmented; **1)** 13; **2)** 14.

Character 4. *Width between antennal sockets:* **0)** wide apart (appendix A4, Fig. 2); **1)** close (Fig. 8.2). The latter state is found in aulacids (Crosskey 1962).

Character 5. *Clypeal margin:* **0)** sinuate (Appendix A6, Fig. 10); **1)** truncate lobe (Appendix A6, Figs 24, 50).

Character 6. *Clypeal ridge medially:* **0)** absent (Fig. 8.31); **1)** present (Appendix A6, Fig. 52).

Character 7. *Eye size and shape:* **0)** large and elliptical (Fig. 8.3); **1)** small and circular/sub-circular. This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 8. *Flagellomere 1 length relative to flagellomere 2:* **0)** first flagellomere greater in length than second; **1)** first flagellomere less than or equal to length second. Crosskey (1962) used this as one of the characters to distinguish *Hyptiogaster* from *Aulacofoenus* and *Eufoenus*.

Character 9. *Frontal carina:* **0)** absent (Fig. 8.59); **1)** present (Fig. 8.8).

Character 10. *Head width:length when viewed dorsally:* **0)** quadrate to lateral (Fig. 8.8); **1)** elongate (i.e. longer than wide) (Appendix A5, Fig. 31).

Character 11. *Lateral epistomal suture:* **0)** absent (Appendix A6, Figs 1, 10); **1)** present, at least in part (Fig. 8.116).

Character 12. *Malar space width:height of eye:* **0)** ≤ 0.15; **1)** > 0.15. Crosskey (1962) used this as one of the characters to distinguish *Crassifoenus* from *Aulacofoenus*, *Eufoenus* and *Hyptiogaster* .

Character 13. *Degree mandibles overlap:* **0)** slightly; **1)** broadly (Fig. 8.13). In *Gasteruption*, the mandibles overlap only slightly whereas they broadly overlap in the Hyptiogastrinae (Crosskey 1962).

Character 14. *Mandibular median teeth number:* **0)** one tooth (Appendix A5, Fig. 33); **1)** two teeth (Appendix A5, Fig. 32); **2)** three teeth.

Character 15. *Labio-maxillary complex:* **0)** fixed; **1)** extendible.

Character 16. *Occipital carina:* **0)** absent; **1)** incomplete (absent medially); **2)** complete. In Aulacidae, Townes (1950) distinguished between *Pristaulacus* and *Aulacus* by the latter lacking an occipital carina.

Character 17. *Occipital carina sculpturing:* **0)** sculptured (Fig. 8.17); **1)** smooth (Fig. 8.109).

Character 18. *Scape in lateral view:* **0)** convex; **1)** parallel-sided. This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 19. *Scape width: pedicel:width* **0)** scape much wider than pedicel; **1)** scape slightly wider than pedicel.

Character 20. *Subantennal groove:* **0)** absent; 10 present.

Character 21. *Dorsal tentorial pits:* **0)** absent; **1)** present.

Character 22. *Functional abdominal spiracles:* **0)** on three or more segments including 1 & 8; **1)** only on segments 1 and 8.

Character 23. *Median sulcus of mesoscutum:* **0)** absent; **1)** present.

Character 24. *Mesothorax anterior face in lateral view:* **0)** truncate; **1)** rounded (Fig. 5.10).

Character 25. *Notauli*: **0)** not percurrent; **1)** percurrent, not Y-shaped; **2)** percurrent, Y-shaped (Fig. 5.10). This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae. Crosskey distinguished between scutum 'divided' (not Y-shaped) or 'not fully divided by prescutum' (Y-shaped).

Character 26. *Prepectus:* **0)** absent; **1)** present.

Character 27. *Antero-dorsal pronotal processes:* **0)** absent; **1)** present (Appendix A6, Figs 25, 31, 47-48). Jennings and Austin (1997b) described these processes in some *Aulacofoenus* species.

Character 28. *Dorso-lateral pronotal processes:* **0)** absent; **1)** present (Appendix A6, Figs 25, 47). Jennings and Austin (1997b) described these processes in some *Aulacofoenus* species.

Character 29. *Propleural carina:* **0)** absent; **1)** present ventro-laterally (Appendix A3, Fig. 17; Appendix A6, Fig. 25).

Character 30. *Propleuron shape:* **0)** elongate (Fig. 5.1); **1)** short (Fig. 8.3).

Character 31. *Propodeal carina:* **0)** absent; **1)** present (Appendix A6, Fig. 27).

Character 32. *Propodeal spiracle:* **0)** glabrous or almost so; **1)** fringed with setae (Appendix A6, Fig. 26). When setae are present, they are generally long and found on both the anterior and posterior margins of the spiracle - only occasionally are the setae short. If only one or two setae are present, this was considered as state 0.

Character 33*. Shape of propodeum:* **0)** quadrate; **1)** pyramidal. This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 34*. Fore wing discal cell number:* **0)** 2 cells (Fig. 5.9); **1)** 1 cell (Fig. 5.7). Jennings and Austin (1994a & b, 1997 a & b) figured the discal cells of many included taxa.

Character 35*. Fore wing plication:* **0)** not plicate at rest; **1)** plicate at rest (Fig. 3.1). This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 36*. Fore wing vein r-m:* **0)** absent (Figs 5.7, 9); **1)** present (Fig. 8.1). This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 37*. Fore wing vein 1-Rs+M:* **0)** joins at M+Cu, 1-R; **1)** joins 1-M and 1-Rs; **2)** fused to form Rs+M+Cu(b). Jennings and Austin (1994b) discussed possible evolutionary pathways for this character (see Appendix A4, Figs 7-14).

Character 38*. Fore wing vein 2-M colour:* **0)** even; **1)** pale apically; **2)** pale basally. With state 2, the vein also becomes thinner apically.

Character 39*. Hind wing vein 1-Cu:* **0)** absent; **1)** present.

Character 40*. Submarginal cell number in fore wing:* **0)** 2 or 3 cells (Figs 5.7, 9); **1)** 1 cell. This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 41*. Groove on hind coxa:* **0)** absent; **1)** present. This character was used by Crosskey (1962) to distinguish between Aulacidae and Gasteruptiidae.

Character 42*. Groove on hind trochanter:* **0)** absent (Figs 8.25, 41); **1)** present (Appendix A6, Figs 33, 37, 41). This groove is found only in the Aulacidae and Gasteruptiidae, and is absent in all other Hymenoptera (Crosskey 1962). This character has been used by

Crosskey (1962) and Jennings and Austin (1994b) to distinguish between *Pseudofoenus* and *Eufoenus* which lack a dorso-ventral groove on the hind trochanter and other hyptiogastrine genera which have the groove. However, several described species of *Eufoenus* have a weak ill-defined groove on either the dorso-lateral surface or restricted to the inner lateral surface (e.g. Fig. 8.33).

Character 43. *Hind claw:* **0)** simple (Appendix A6, Figs 29-30); **1)** pectinate. These character states have been used by Townes (1950), Oehlke (1983a) and others to distinguish between *Aulacus* and *Pristaulacus* (Aulacidae). In *Aulacus*, the claws are apparently simple, but each has a single basal tooth which is difficult to see, whereas in *Pristaulacus*, two or more teeth are found.

Character 44. *Hind tarsal segment 1:* **0)** without projection, symmetrical (Appendix A5, Fig. 21); **1)** with lateral projection, highly asymmetrical (Appendix A5, Fig. 4).

Character 45. *Lateral projections on hind tarsal segments 2-4:* **0)** absent (Appendix A5, Fig. 21); **1)** present (Appendix A5, Fig. 4).

Character 46. *Length of hind tarsal segments:* **0)** normal (Appendix A3, Fig. 19); **1)** shortened (Appendix A3, Fig. 18). Jennings and Austin (1997b) have described shortened hind tarsal segments found in a small number of taxa.

Character 47. *Hind tibia with ventro-apical pecten of stout spines:* **0)** absent; **1)** present.

Character 48. *Mid tibial notch:* **0)** absent; **1)** present. The mid tibial notch is present in females of *Crassifoenus* (Jennings and Austin 1994a).

Character 49. *Prefemur on hind leg:* **0)** absent (Fig. 8.9); **1)** present (Fig. 8.5).

Character 50. *Trochantellus on hind leg:* **0)** absent; **1)** present.

Character 51. *Apical sternum:* **0)** incised (Fig. 8.6); **1)** not incised (Fig. 8.7).

Character 52. *Length of digitus length:length of basiparameres (male):* **0)** digitus length < basiparameres; **1)** digitus length ≥ basiparameres.

Character 53. *Metasomal insertion on propodeum:* **0)** low; **1)** high (Fig. 5.11).

Character 54. *Metasomal shape:* **0)** not thickening gradually towards the tip; **1)** sub-clavate.

Character 55. *Metasomal T1 and T2:* **0)** free; **1)** fused (Fig. 5.11).

Character 56. *Metasomal T1 median longitudinal ridge or line:* **0)** absent (Appendix A5, Fig. 45); **1)** present (Appendix A5, Fig. 46).

Character 57. *Ovipositor*: **0)** exserted; **1)** not exserted. Of the hyptiogastrines, only *Hyptiogaster* has an exserted ovipositor (Jennings and Austin 1997a).

Character 58. *Ovipositor sheath margin:* **0)** smooth; **1)** undulate or serrate. *Crassifoenus* species have the margins of the ovipositor sheaths undulate or serrate (see Appendix A3, Figs 4, 6, 8).

6.4. Preliminary phylogenetic analyses

6.4.1. Test for the monophyly of families and subfamilies

The first analysis weas conducted to test the monophyly of the Aulacidae and Gasteruptiidae and in particular the Hyptiogastrinae. Fifty four taxa were included, with the outgroup designated as *Schlettererius cinctipes*. *Aulacus atriceps* (Kieffer), *Aulacus* sp. 1 and 2, *Pristaulacus cinguiculatus*(Westwood), *P. variegatus* (Schuckard) and *Pristaulacus* sp. 1. *Gasteruption brachyurum* Schletterer, *G. fluviale* Turner, *G. spinigerum* Schletterer, *G. ?paradoxale* Pasteels and *Gasteruption* sp. 1 were included in the ingroup along with 47 species of Hyptiogastrinae (see Appendix A2.1).

An heuristic search of 100 random replicates with random addition sequence, tree-bisection-reconnection (TBR) branch swapping, steepest descent and MULPARS options was conducted with all character states unordered. 20,000 equally parsimonious trees each 124 steps in length were generated. Characters 2, 10, 19-23, 26, 49, 53, and 55 proved uninformative.

The strict consensus tree generated from these 20,000 trees (Fig. 6.1), resulted in a CI = 0.32, RI = 0.67 and RC = 0.22 (Table 6.1), indicating a high amount of homoplasy (see Section 4.5.4). This tree indicates that the Aulacidae, Gasteruptiidae and Hyptiogastrinae are all monophyletic. However, little resolution was achieved within the Hyptiogastrinae, although *Pseudofoenus* and *Crassifoenus* are shown to be monophyletic.

The data matrix was then manipulated in a number of ways to further explore the relationships between the taxa. These are elaborated below.

Table 6.1. Number of equally parsimonious trees generated, their number of steps and confidence index (CI), retention index (RI) and rescaled consistency index (RC) for the strict consensus trees generated in initial analyses (Section 6.4).

Analysis	# trees generated	# steps	CI	RI	RC
multiple outgroups	20,000	124	0.32	0.67	0.22
S. cinctipes as outgroup	20,000	124	0.32	0.67	0.22
characters weighted uninformative included	9,900	248	0.38	0.69	0.26
characters weighted uninformative excluded	7,500	230	0.33	0.68	0.23

6.4.2. Characters weighted

Swofford and Begle (1993) indicate that multi-state characters have a greater influence on an analysis than do binary characters. In this analysis, characters were weighted using a base weight of 2 to determine the influence of multi-state characters.

The data were re-analysed to determine the effect of excluding uninformative characters (i.e. autapomorphies) from the analysis. Using the same options as those above but excluding uninformative characters, the analysis generated 7,500 equally parsimonious trees with length 230, CI = 0.33, RI = 0.68 and RC = 0.23 (Table 6.2). The strict consensus tree had the same topology as in Figure 6.1, thus confirming that topology is unaffected by the inclusion of uninformative characters. Yeates (1992) and Bryant (1995) both indicate that CI should decrease with the removal of uninformative characters. When uninformative characters were included 9,900 equally parsimonious trees were generated with a tree length of 248, an increase of 18 steps. The topology of the strict consensus tree was identical to that found previously (Fig. 6.1), but with slightly lower CI, RI and RC values (Table 6.1), reflecting the inclusion of the uninformative characters. Strict consensus trees can therefore be compared for topology only and not tree length unless the analyses are identical.

A bootstrap analysis was also carried out on the same data excluding uninformative characters. 5,000 bootstrap replicates were generated using a random addition sequence each of two replicates. The bootstrap values are given in Figure 6.1 and confirm the monophyly of the Aulacidae (bootstrap value = 100). They also indicate good support for the monophyly of the Gasteruptiidae (92), the two subfamilies Gasteruptiinae (*Gasteruption* spp.) (75) and Hyptiogastrinae (75), and of *Crassifoenus* (99) and *Pseudofoenus* (66). Relationships among *Aulacofoenus*, *Eufoenus* and *Hyptiogaster* are not resolved.

6.4.3. Discussion and conclusions

In the above analyses, the monophyly of Aulacidae is supported by seven unequivocal character state changes, viz. the antennae are inserted level with base of eyes (character 1:state 1); antennal sockets wide apart (4:1); eye small and circular/sub-circular (7:1); notauli percurrent, Y-shaped (25:2) (see also Crosskey 1962); propleuron not elongate (30:1); propodeum not pyramidal (33:1) (see also Crosskey 1962); and the presence of a groove on the inner surface of the hind coxae of females (41:1) (see also Crosskey 1962). However, some *Aulacus* not included in this study, mostly those with short ovipositors, lack this groove (Townes 1951). Within the Aulacidae, the monophyly of *Aulacus* is supported by the absence of the occipital carina (16:0) whilst in *Pristaulacus* the occipital carina is incomplete (absent medially) (state 1) (see also Townes 1950). The monophyly of *Pristaulacus* is supported by the presence of pectinate hind claws (43:1). This character has been used previously by Townes (1950), Oehlke (1983b) and others to distinguish between *Aulacus* and *Pristaulacus*. In

Aulacus, the claws are apparently simple, but each has a single basal tooth which is difficult to see (Townes, 1950).

The monophyly of the Gasteruptiidae is supported by a single unequivocal character; the antennae inserted approximately half-way up the eyes (1:2). Within Gasteruptiidae, the monophyly of the Gasteruptiinae is supported by the mandibles overlapping only slightly (13:0), whereas they broadly overlap in Hyptiogastrinae (state 1) (see also Crosskey 1962), and fore wing vein 1-Rs+M joins at M+Cu, 1-R (37:0) (see also Jennings and Austin 1994b). Contrary to the view of Crosskey (1962), the Hyptiogastrinae are not more 'primitive' than the Gasteruptiinae. They clearly form a more apical clade. The monophyly of the Hyptiogastrinae is supported by the lack of a trochantellus on the hind leg (50:0) and they lack an incision or notch on the apical sternum (51:0). In *S. cinctipes*, Aulacidae and Gasteruptiinae, the trochantellus is present and the apical sternum is incised.

Relationships within the Hyptiogastrinae are largely unresolved. Of the five currently recognised hyptiogastrine genera, the monophyly only of *Crassifoenus* and *Pseudofoenus* are supported in this analysis. *Crassifoenus* is supported by the presence of hind wing vein 1-Cu (39:1), a mid tibial notch in females (48:1), and lateral ovipositor sheath margins that are either undulate or serrate (58:1) (see also Jennings and Austin 1994a). *Pseudofoenus* is supported by two reductional characters; the absence of discal cells in the fore wing (34:0) and fore wing vein 1-Rs+M fused to form Rs+M+Cu(b) (37:2).

6.5. Relationships within the Hyptiogastrinae

In an attempt to better resolve relationships within the Hyptiogastrinae, further analyses were conducted employing a separate matrix (Appendix A2.2). The characters used in the above analyses were re-examined and redefined where necessary, and a number of additional characters as well as additional species were included to better represent the morphological diversity within the subfamily. It should be noted that these species were tentatively assigned to *Eufoenus* on the basis of the generic descriptions and the key to genera in Crosskey (1962).

In the above analyses, the Gasteruptiinae (*Gasteruption*) was shown to be a monophyletic group and the sister group to the Hyptiogastrinae. *Gasteruption* sp. 1 was the most basal of the *Gasteruption* spp. included (i.e. it is the closest *Gasteruption* species to the Hyptiogastrinae), and it is therefore the most appropriate outgroup to use for analysis of hyptiogastrine relationships. The Aulacidae and *S. cinctipes* were also excluded from the analyses, and this led to a number of changes in character states and several additional characters became uninformative.

6.5.1. Additional characters included in the phylogenetic analyses

Several characters were revised to take into account the inclusion of additional taxa.

Character 5. *Clypeal margin:* **0)** sinuate; **1)** truncate lobe; **2)** convex. Several *Eufoenus* species have a distinctly convex clypeal margin.

Character 12. *Malar space width:height of eye:* **0)** ≥0.18; **1)** ≤0.17. Two of the additional *Eufoenus* had ratios >0.15 but ≤0.17.

Character 57. *Ovipositor:* Replaced by character 65 (see below).

Additional characters were included in the extended data matrix on the basis of they were potentially informative for the Hyptiogastrinae. Several characters such as body length were initially considered but were rejected on the basis that they were too variable. For example, body length of some species extends over 3 or 4 character states when the segment coding method of Chappill (1989) was used to assign character states.

Character 59. *Terminal flagellomere length:width*: **0)** ≤2.0; **1)** ≥2.1 - ≤2.7; **2)** ≥3.5 - ≤4.1; **3)** ≥4.2. Crosskey (1962) used the states 'quadrate' and 'elongate' to distinguish between various *Eufoenus* spp. However, after measuring all included taxa, it was found that they had elongate terminal flagellomeres. Mean terminal flagellomere length was coded using the segment coding technique of Chappill (1989) (see Appendix A2.3). States were assigned on the basis of one standard deviation (SD). It should be noted that none of the included taxa had ratios of 2.8 to 3.4. If in future taxa are found with these ratios, then this would become state 2, and the others revised.

Character 60. *Antennal length:lateral head length:* **0)** ≤1.74; **1)** ≥1.75 - ≤2.11; **2)** ≥2.12 - ≤2.48; **3)** ≥2.49 - ≤2.85; **4)** ≥2.86. Lateral head length was measured from the top of the vertex to the tip of the mandibles when in the closed position. Antennal length:lateral head length was coded using the segment coding technique of Chappill (1989) (see Appendix A2.4) and states were assigned on the basis of one standard deviation (SD).

Character 61. *Shape of propleural ventro-lateral carina:* **0)** normal; **1)** flange-like (Appendix A6, Fig. 25). Jennings and Austin (1994a) described a flange-like ventro-lateral propleural carina in species of *Crassifoenus* (see Appendix A3).

Character 62. *Hind tarsi, length segment 1:segment 2:* **0)** ≤1.91; **1)** ≥1.92 - ≤2.50; **2)** ≥2.51 - ≤3.09; **3)** ≥3.10 - ≤3.68; **4)** ≥3.69 The ratio of the length of hind tarsal segments 1:2 was coded using the segment coding technique of Chappill (1989) (see Appendix A2.5).

Character 63. *Hind tarsal claw length:hind tarsal segment 5 length:* **0)** ≤0.62; **1)** ≥0.63 - ≤0.83; **2)** ≥0.84 - ≤1.04; **3)** ≥1.05. The ratio of the hind tarsal claw length:length hind tarsal segment 5 was coded using the segment coding technique of Chappill (1989) (see Appendix A2.6) and states were assigned on the basis of one standard deviation (SD).

Character 64. *Metasoma length:mesosoma length:* **0)** ≤2.09; **1)** ≥2.10 - ≤2.38; **2)** ≥2.39 - ≤2.67; **3)** ≥2.68. Measurements were carried out in lateral view. The ratio of the metasomal length:mesosomal length was coded using the segment coding technique of Chappill (1989) (see Appendix A2.7) and states were assigned on the basis of one standard deviation (SD).

Character 65. *Ovipositor:metasoma length:* **0)** ≤0.23; **1)** ≥0.24 - ≤0.47; **2)** ≥0.48 - ≤0.71; **3)** ≥0.72. This is a replacement for character 57 above. Coding was carried out using the segment coding technique of Chappill (1989) (see Appendix A2.8) and states were assigned on the basis of one standard deviation (SD). Taxa with ovipositors not exserted were scored as zero. However, this character was later found to produce a strict consensus tree with an identical topology as that when this character was considered as binary.

Character 66. *Clypeal width:height:* **0)** ≤1.58; **1)** ≥1.59 - ≤1.97; **2)** ≥1.98 - ≤2.36; **3)** ≥2.37 - ≤2.5; **4)** ≥2.76. Coding was carried out using the segment coding technique of Chappill (1989) (see Appendix A2.9) and states were assigned on the basis of one standard deviation (SD).

Character 67. *Fore wing veins, length 1-M:1-Rs.* **0)** =0.0; **1)** ≥0.79 - ≤1.38; **2)** ≥1.39 - ≤2.08; **3)** ≥2.09 - ≤2.78; **4)** ≥2.79. This character is an extension of character 37 above. In most hyptiogastrines, 1-Rs+M intersects with 1-M and 1-Rs. In *Pseudofoenus*, 1-Rs+M is fused with 1-Cub to form Rs+M+Cu(b) and in *Gasteruption*, 1-Rs+M joins at M+Cu and 1-R (see Appendix A4, Figs 7-14). In both cases, the ratio of 1-M:1-Rs is therefore zero. Coding was carried out using the segment coding technique of Chappill (1989) (see Appendix A2.10) and states were assigned on the basis of one standard deviation (SD). It should be noted that none of the specimens measured had ratios of ≥0.1 - ≤0.72. This would normally be character state 1, but given no species examined have these ratios, the next ratio up becomes state 1.

Character 68. *Dense mat of hairs on ventral surface of hind tarsal segment 5:* **0)** absent; **1)** present. Jennings and Austin (1994a) referred to this character in species of *Crassifoenus*.

Characters 2-3, 10, 19-23, 26, 49, 53 and 55 were excluded as being uninformative (see above). With the removal of the previously used outgroups, a number of additional characters became invariant or uninformative and were excluded. These characters were 1, 4, 7, 13-16, 18, 25, 30-31, 33, 35-36, 40-41, 43, 50-52 and 54. Also, character 57 was revised and replaced by character 65. This left a total of 34 informative characters. For continuity, original character numbers were retained and additional characters numbered sequentially.

6.5.2. Results of analyses

6.5.2.1. Heuristic search

The modified data matrix (Appendix A2.2) was analysed using *Gasteruption* sp. 1 as the outgroup and with 51 taxa in the ingroup. An heuristic search using settings as in Section 6.4.1 was conducted on the modified data matrix. All character states were unordered and weighted using a base-weight of 60.

The heuristic search with character 65 as multi-state resulted in a strict consensus tree identical in topology as that when the character was binary (Fig. 6.2), and so further analyses were carried out with this character coded as binary. The latter analysis produced 1609 equally parsimonious trees each of length 7300. The strict consensus tree (Fig. 6.2) had a CI = 0.22, RI = 0.45 and RC = 0.10.

When the characters are traced in MacClade, a number of nodes are found to be supported by unequivocal character changes (Fig. 6.2). The clade constraining all ingroup taxa except for *Hyptiogaster* is supported by the ovipositor being short and hidden (character 65:state 1). *Hyptiogaster humeralis* + *H. kalbarrii* are united by the presence of pronotal processes (27:1 and 28:1), but *Hyptiogaster* is paraphyletic. The monophyly of *Crassifoenus* is supported by the presence of hind wing vein 1-Cu (39:1), a mid tibial notch in the female (48:1), and an undulate or serrate ovipositor sheath margin (58:1); while *Pseudofoenus* is supported by the presence of a single discal cell in the fore wing (34:1) and fore wing vein 1-Rs+M fused to form Rs+M+Cu(b) (37:2). However, neither *Aulacofoenus* nor *Eufoenus* are monophyletic, with species from both of these previously recognised genera falling out amongst each other (i.e. they are polyphyletic). Further, *Crassifoenus* and *Pseudofoenus* are clearly placed within this assemblage.

6.5.2.2. Bootstrap and Bremer support values

Bootstrapping of the modified matrix resulted in a number of nodes with bootstrap values ≥40 (Fig. 6.3). The monophyly of *Crassifoenus* is well supported with a bootstrap value of 100. Other nodes with reasonable support include those for *A. fletcheri* + *A. marionae* + *'Eufoenus' taylori* (40), *A. thoracicus* + *'Eufoenus' morganensis* (60), *E. crassitarsis* + *E. rieki* (40), *E. darwini* + *E. spinitarsis* + *'Eufoenus' crosskeyi* + *'Eufoenus'coorowensis* (40), *H. humeralis* + *H. kalbarrii* (80), *H. pinjarregaensis* + *H. rufus* (54), and *P. crassipes* + *P. unguiculatus* (75). Decay indices ('Bremer support values') also provide moderate support for these clades. An heuristic search of 50 random replicates for each node was conducted using the previous settings in PAUP. The characters were unordered and weighted using a base weight of 60. If the same analysis is carried out with fractional weighting (i.e. binary characters have a weight of 1.0 and multistate characters have fractional weights), the strict consensus tree produced is exactly the same in topology but the tree length is one-sixtieth of that produced previously. Thus, if the decay indices given in Figure 6.3 are divided by 60, then this better represents the number of steps. Only one node, that which includes three *Crassifoenus* species, has a low decay index (Fig. 6.3), but most nodes require a large number of extra steps to collapse them.

6.5.2.3. Successive weighting

In an attempt to further investigate the relationships among the hyptiogastrine taxa, successive weighting was undertaken. Two alternative techniques were explored; integer coding and additive binary coding (see Section 4.5.3).

The data matrix was converted to additive binary (i.e. multistate characters are divided into separate binary characters). The equally most parsimonious trees found in the heuristic search (Section 6.5.2.1 above), were reweighted using the maximum rescaled CI (i.e. 1000) of Farris (1989), and using the same options, successive heuristic searches of 100 random replicates were evaluated. This resulted in 9 trees of the same length and topology being found in replicates 5 to 7. The strict consensus tree in each of these replicates is shown in Figure 6.4. *Crassifoenus*, *Hyptiogaster* and *Pseudofoenus* are all resolved as monophyletic, but the monophyly of *Aulacofoenus* and *Eufoenus* is not supported. The main difference between the heuristic and successively weighted strict consensus trees is that *Hyptiogaster* is monophyletic whereas in the heuristic search this genus is paraphyletic. Also, the successive weighted tree has a large clade of 14 species which is supported unequivocally by the presence of sculpturing on the occipital carina (17:0).

6.5.3. Analyses with constraints

To further explore the status of *Aulacofoenus* and *Eufoenus*, heuristic analyses as in Section 6.5.2.1 were conducted by constraining them as monophyletic. An extra 4+ steps were required to force the monophyly of *Aulacofoenus*. Similarly, constraining *Eufoenus* as monophyletic required an additional 8+ steps. Based on these results and that of the previous analyses, monophyly of these two genera is clearly rejected.

6.5.4. New classification for the Hyptiogastrinae

Based on the successive weighting analysis above, a number of important outcomes are evident. Clearly the currently recognised genera *Crassifoenus*, *Hyptiogaster* and *Pseudofoenus* are monophyletic and are well supported by a number of characters. However, *Crassifoenus* and *Pseudofoenus* are contained within larger clades which encompass *Aulacofoenus* and *Eufoenus*, both of which are polyphyletic. These findings therefore affect how the classification of the subfamily should be viewed: two options are possible.

A conservative approach would be to continue to recognise the current five genera. The majority of known hyptiogastrine species, including those described here, can be placed within these genera based on particular distinguishing characters. However, a number of taxa cannot be readily accommodated in this framework in that several species possess character states that make them difficult to place. For example, according to Crosskey (1962), one of the major characters separating *Eufoenus* from *Aulacofoenus* is that the latter possesses a hind trochanteral groove. However, specimens of both *E. australis* and *E. patellatus* vary substantially, having either no groove through to a complete groove (see Chapter 8).

An alternative approach is to adopt a new classification recognising only monophyletic groups. The difficulty is that many of the clades presented in Figure 6.4 are not particularly stable and/or the species included within them lack easily recognisable characters to distinguish them. If a phylogenetic classification is adopted, and this would be the most desirable outcome in seeking to reflect natural groupings rather than a classification which is artificial, then only one arrangement seems possible; this would be to recognise two genera only. *Hyptiogaster* would remain as it is currently diagnosed, it forming a monophyletic group of species having an exserted ovipositor (character 65) and which forms the sister group to all remaining Hyptiogastrinae (Fig. 6.4). This latter group would be recognised as the second monophyletic group. The three genera *Aulacofoenus*, *Crassifoenus* and *Eufoenus* would be subsumed (synonymised) into this group. As the oldest available name, the genus would be referred to as *Pseudofoenus sensu lato.* This group could then be further divided into a number of monophyletic sub-groups.

On balance, the second option would appear to be the most logical and is adopted here to reclassify the Hyptiogastrinae. The new classification proposed for the Gasteruptiidae is summarised in Table 6.2, and is based on the strict consensus tree generated by successive weighting (Fig. 6.4). Most importantly, this classification recognises only monophyletic groups; it avoids the problem of establishing multiple genera in which the monophyly is not particularly stable, and should therefore provide a solid framework for future taxonomic and evolutionary studies, and a basis for a preliminary species-group classification.

6.5.4.1 Species-groups of *Pseudofoenus sensu lato*

Within *Pseudofoenus s.l.*, two monophyletic species groups can be recognised (Fig. 6.4). The first group is designated the *crassipes*-species group, and corresponds to *Pseudofoenus s. str.* It comprises two species in the analysis which are supported by two synapomorphies; the presence of a single discal cell in the fore wing (character 34: state 1) and fore wing veins 1-Rs+M and 1-Cu(b) fused to form Rs+M+Cu(b) (37:2). The second group is designated the *fletcheri*-species group and comprises 13 species supported by a single synapomorphy; the presence of sculpturing on the occipital carina (17:0). Within this latter group are recognised three subgroups. The first subgroup is designated the *thoracicus*-subgroup and comprises two species united by having lateral projections on hind tarsal segments 1-4 (44:1, 45:1). The second subgroup is designated the *macronyx*-subgroup and comprises three species which are united by the presence of hind wing vein 1-Cu (37:1), a notch on the mid tibia of females (48:1), an undulate or serrate lateral ovipositor sheath margin (58:1), and lack a median longitudinal ridge on metasomal segment T1 (56:0). They also lack an epistomal suture (11:0), a character state shared with *Hyptiogaster*. The *macronyx*-subgroup is synonymous with *Crassifoenus* Crosskey. The third subgroup is designated the *infumatus*-subgroup, and whilst it is not monophyletic, comprises the remaining nine species that lack lateral projections on the hind tarsal segments 1-4 (44:0, 45:0), lack hind wing vein 1-Cu (37:0), lack a notch on the mid tibia of females (48:0), have a smooth lateral ovipositor sheath margin (58:0), and have an epistomal suture (11:1).

The remaining 30 species within *Pseudofoenus s. l.* are not assigned to any species groups as there are no unequivocal character states which support their monophyly. Other described species not included in the above phylogenetic analyses are placed into the above generic and species-group classification in Chapter 8.

Table 6.2. Summary of the proposed reclassification of the Gasteruptiidae.

	Distribution	Number described species
Family Gasteruptiidae		
Subfamily Gasteruptiinae *Gasteruption* L.	cosmopolitan	c. 400
Subfamily Hyptiogastrinae *Hyptiogaster* Kieffer 1903 - *Odontofoenus* (in part) Kieffer 1910 - *Carinafoenus* Crosskey 1953a (syn. Crosskey 1962)	Australia	10
Pseudofoenus Kieffer 1902 - *Eufoenus* Szépligeti 1903. **syn. nov.** - *Aulacofoenus* Kieffer 1911. **syn. nov.** - *Hemifoenus* Kieffer 1911 (syn. Crosskey 1962) - *Trigonofoenus* Kieffer 1911 (syn. Crosskey 1962) - *Crassifoenus* Crosskey 1953a. **syn. nov.** - junior synonym of *Hyptiogaster*, Valentine & Walker, 1991	Australia, NZ, New Guinea, south-west Pacific, South America	68

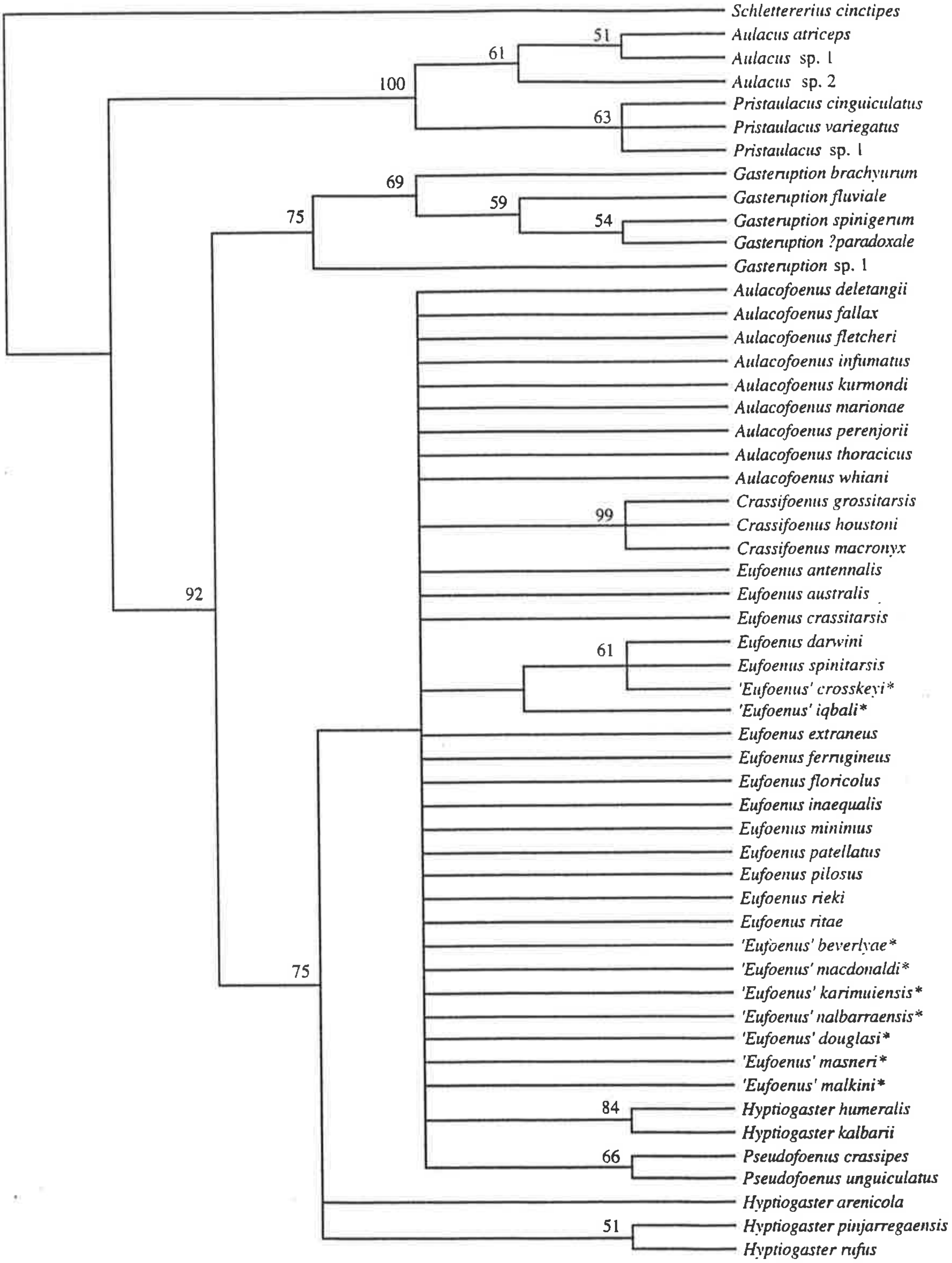


Figure 6.1. Strict consensus tree generated from multiple outgroup analysis resulting in 20,000 equally parsimonious trees (length = 124, CI = 0.32, RI = 0.67 and RC = 0.22). The figures represent bootstrap values. Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

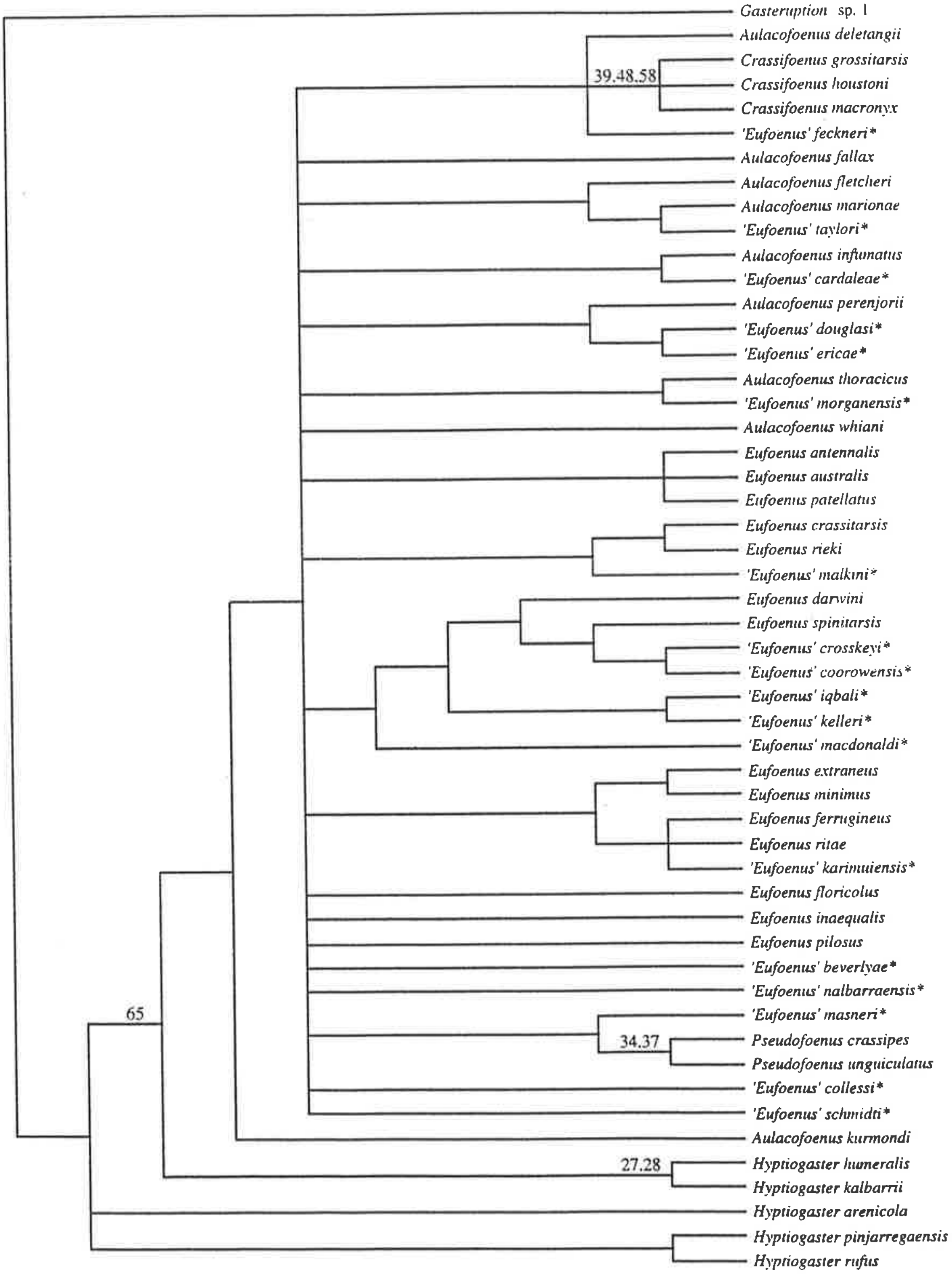


Figure 6.2. Strict consensus tree of 1609 equally parsimonious trees generated by an heuristic search of the modified data matrix (Table 6.4) (length = 7300, CI = 0.22, RI = 0.45 and RC = 0.10). Unequivocal character state changes are indicated by the character number. Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

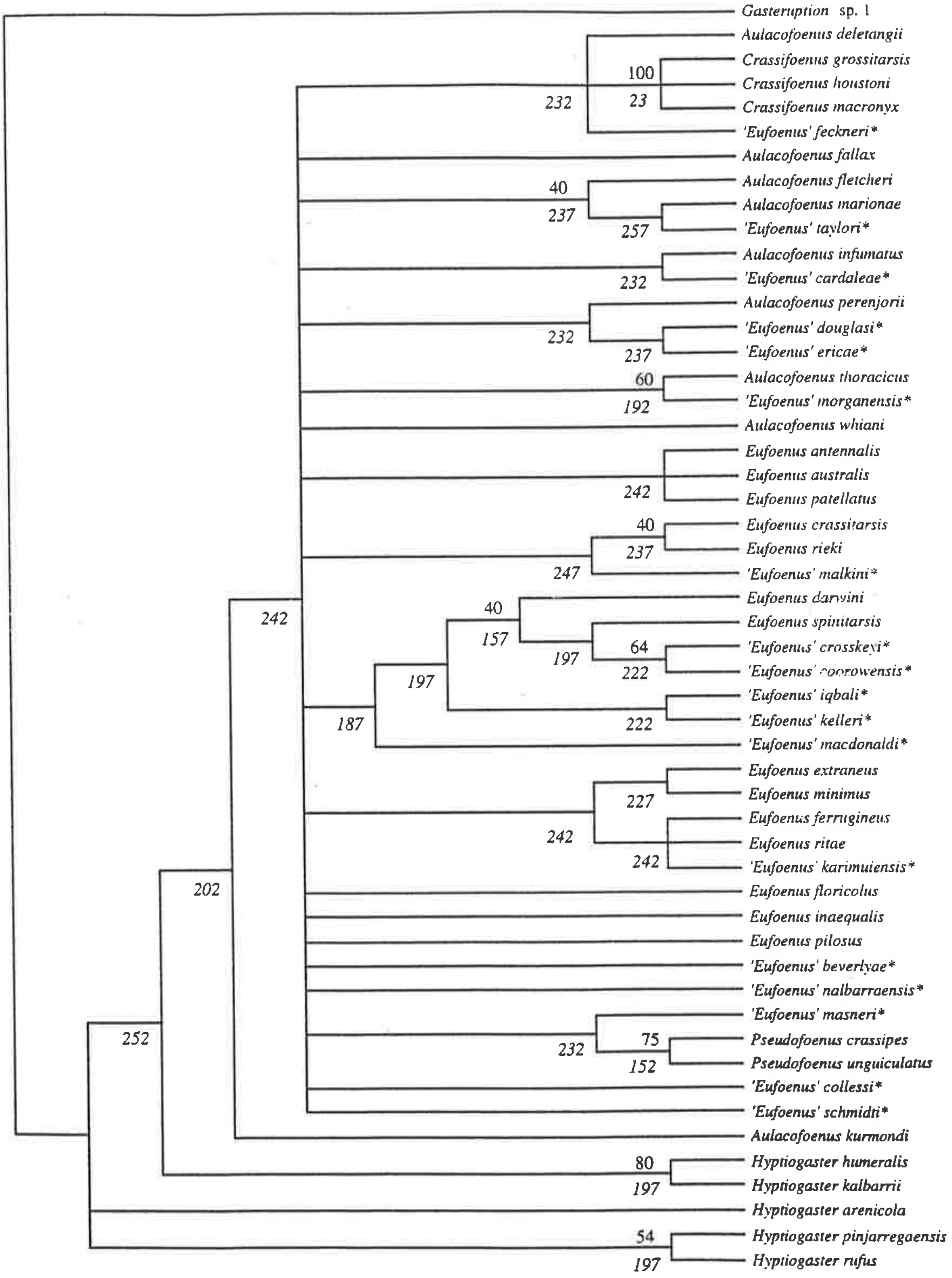


Figure 6.3. Strict consensus tree of 1609 equally parsimonious trees generated by an heuristic search of the modified data matrix (Table 6.4) indicating bootstrap values ≥40 (above line) and bremer support values (below line and italicised) (see section 6.5.2.2 for further explanation). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

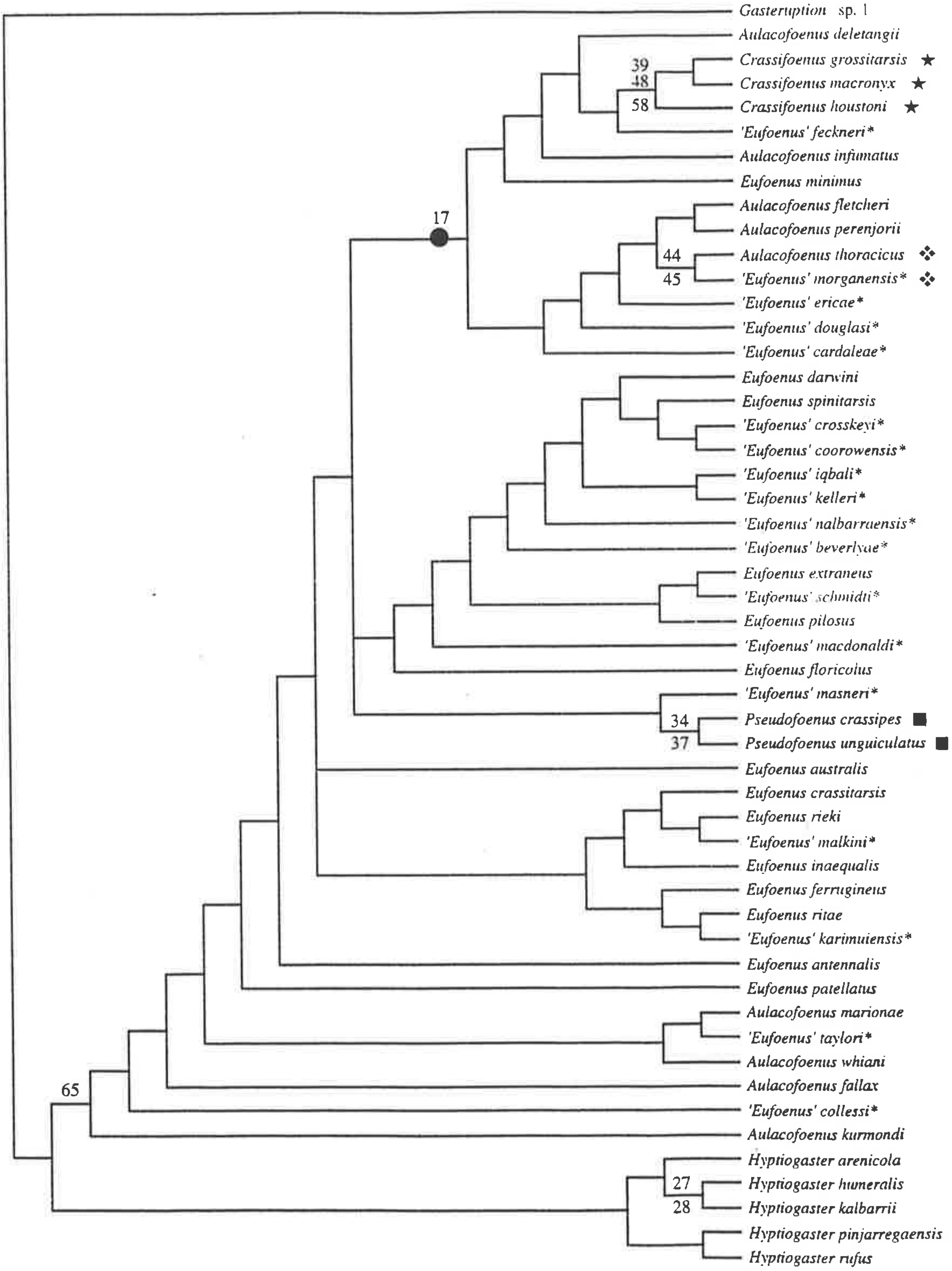


Figure 6.4. Strict consensus tree of 8 trees obtained in replicates 5 to 7, successive weighting - additive binary coded. Nodes supported by unequivocal character state changes are also indicated (see text for further details). ■ = *Pseudofoenus s. str.*; ● = *fletcheri*-group; ❖ = *thoracicus*-subroup; and ★ = *macronyx*-subgroup. Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Chapter 7.

Biogeography

Biogeographical studies rely heavily on systematic input. This chapter discusses the principles of biogeographical theory, the interrelationship of biogeography and systematics, and specifically examines the biogeography of the Hyptiogastrinae in light of the phylogenetic results presented in Chapter 6.

7.1. Biogeographical principles

Each organism has its own distribution or area of endemism. That is, it is endemic or restricted to a given region (Torre-Bueno 1989). There are, of course, many examples where species have been introduced to regions, either intentionally or otherwise, and are therefore not endemic. In spite of this, the distribution of many organisms can be more or less accurately determined. Global patterns of distribution for organisms can be demonstrated to show distinct and repetitive patterns between unrelated taxa. Biogeography is the study of these patterns and the ecological and historical reasons behind them (Kirsch 1984). On a broad scale, a number of regions of distinctive endemism (biogeographic regions) are generally recognised, namely the Nearctic, Palaearctic, Neotropical, Oriental, Australian, and Afrotropical regions (e.g. Cranston and Naumann 1991).

There are three partially overlapping biogeographical theories (e.g. Cranston and Naumann 1991):

i) ecological or physical biogeography,

ii) dispersal biogeography, and

iii) vicariance biogeography.

The latter two are usually considered as 'historical' biogeography (e.g. Ball 1975). These theories attempt to explain the distribution of taxa in different ways.

i) Ecological biogeography attempts to explain the distribution of organisms in terms of their biotic and abiotic requirements. Biotic variables include factors such as competition, predation and host distribution, whereas abiotic factors include climate, soil and topology. Ball (1975) indicated that most ecologists believe biogeography to be, at best, only part of ecology. He proposes, however, that ecology deals with distributions on a local scale and with community structure and trophic relationships, whereas biogeography is essentially the study of the distribution of living organisms in space and time, and of the principles, parameters and processes influencing this distribution.

Ecological factors are important in helping to explain the distribution of organisms. For example, Hopper (1979) considers that the high level of plant endemism in south-western Australia, is, in part, due to the susceptibility of plant populations to major climatic changes and year-to-year fluctuations. However, amongst a host of possible factors, tectonic stability, the existence of marine, edaphic, or climatic barriers, the formation and later weathering of lateritic soils, and various events in the late Tertiary and Quaternary are all considered important in creating the high levels of endemism found in this part of Australia. It is clear that the key factors involved in determining fundamental distribution patterns are historical.

ii) At the core of the theory of dispersal biogeography is the view that organisms have a centre of origin, from which they migrate or disperse to other areas across pre-existing barriers (e.g. Ball 1975; Kirsch 1984). Speciation occurs in isolation behind these barriers.

Dispersalism is characterised by a multiplicity of views. The centre of diversity is usually equated with the point of origin of the taxon. Various assumptions have been used to determine the centre of origin. For example, Cain (1944) put forward thirteen criteria for recognising the centre of origin. These included the location of the greatest variety of forms of the taxon, the location of the area of greatest dominance and density of distribution, and the location of the most primitive forms. Each of these may give a markedly different result (Humphries and Parenti 1986). There is also a range of arguments within dispersalism, sometimes contradictory. For example, the argument that the most derived taxa pushed out the more primitive ones to the perimeter of the distribution as they evolved (Darlington, 1970; Briggs 1974; Kirsch 1984), is the opposite of Hennig's (1966) 'progression rule', where it is the most ancestral (plesiomorphic) form that remained at, or near, the centre of origin, and that derived (apomorphic) forms were the furthest away.

Before the theory of continental drift was generally accepted, the only explanation for the occurrence of related taxa in different areas was by dispersal, even if it meant the proposal for ephemeral land bridges or lost continents (Archer 1984). The problem for dispersalists is to document routes which allow organisms to cross pre-existing barriers (Kirsch 1984). At some point, land bridges have been postulated as connecting most present-day continents in order to explain disjunct distributions. In only some cases is there geological evidence for them. For example, lower sea levels during the Pleistocene provided a possible means for human migration from Asia to Australia (Archer 1984). Similarly, there is some evidence for the 'lost' continent of Pacifica which existed about 225 million years ago and which subsequently disintegrated (Nur and Ben-Avraham 1977).

Using dispersal as the sole explanation for distributions creates a problem where similar distributions occur for unrelated organisms with very different abilities to disperse.

iii) In contrast to dispersal biogeography, vicariance biogeography, assumes that the barriers formed after dispersal (Kirsch 1984). With the wide acceptance of the plate tectonic theory of continental drift, Croizat (1964) and others have proposed the vicariance theory. Essentially, this theory suggests that ancient distribution patterns have been disrupted (vicariated) by tectonic movement that formed impassable barriers dividing many taxa, thus producing congruent patterns of speciation with similar geographic relationships. Because the barriers formed after dispersal, the taxa involved are of a similar age. If the barriers disappear, the range of the taxa can be expanded (Brundin 1981, 1988). It has also been proposed that taxa may disperse by chance, 'jump disperse', over pre-existing barriers (Brundin 1988).

Phylogenetic or cladistic biogeography (e.g. Humphries and Parenti 1986; Brundin 1988; Humphries *et al.* 1988) has emerged since Hennig (1966). Hennig's method of phylogenetic reconstruction has provided a framework within which biogeographic patterns can be examined. If terminal taxa in cladograms are replaced with areas in which the taxa occur, area cladograms result. Clades (or areas) can be monophyletic, paraphyletic or polyphyletic. Monophyletic groups indicate a shared common ancestor and hence areas of endemism.

7.2. Biogeography of the Hyptiogastrinae

The Gasteruptiidae now comprises three genera arranged in two subfamilies: the Gasteruptiinae, containing the almost cosmopolitan *Gasteruption* L. (absent from Polynesia and Hawaii (Crosskey 1962)), and the Hyptiogastrinae, which have a Gondwanan distribution (Crosskey 1962). In the latter subfamily, *Hyptiogaster* Kieffer is restricted to Australia (Jennings and Austin 1994a and 1997a), while *Pseudofoenus s.l.* is known from Australia, New Zealand, New Guinea, Fiji, New Caledonia and Vanuatu in the south-west Pacific, and South America (Jennings and Austin 1994a,b, 1997a,b).

7.2.1. Distribution of hyptiogastrines in Australia

Within Australia, several species of hyptiogastrine wasps have a broad distribution, for example, *P. floricolus* (Fig. 8.191) and *P. patellatus* (Fig. 8.196), but the majority of species are restricted in their distribution (Fig. 7.1). The Australian fauna shows a distinctly southern distribution with only three species endemic to the eastern and northern Torresian regions, and with no species shared with other regions. The south-west of Western Australia (western Bassian region), exhibits the highest level of endemism (12 spp.), with both the central arid and semi-arid regions of the continent (Eyrean region) (8 spp.) and the south-east of the continent (eastern Bassian region) (9 spp.) also having high endemism. As well, there are a large number of shared species between the western Bassian region and the Eyrean region (8 spp.), with most of these species found just outside of the boundary between these two regions. It is also evident that few species are shared between the south-western and south-eastern faunas (2 spp.), indicating that some speciation has occurred since the aridity of the Nullarbor region. There are no species endemic to Tasmania, although three species are shared with the eastern Bassian region.

7.2.2. Vicariance hypothesis

Given the restricted Gondwanan distribution of the Hyptiogastrinae, the hypothesis that the current distribution of the subfamily can be accounted for by vicariance events can be tested by examining the phylogenetic results in Figure 7.2. If a vicariance hypothesis is to be supported, then the New Zealand and South American taxa should be basal in the phylogeny reflecting the classical Gonwanan area cladogram. By the late Cretaceous (65-70 mya), New Zealand was separate from Australia+Antarctica+South America (Archer 1984). Hence the two *Pseudofoenus s.l.* from New Zealand should occur somewhat basally in the phylogeny and below those species from South America if the current distibution is to be explained by vicariance events. They occur somewhat apically and in a large clade in which the basal relationships are unresolved but which includes half of the Australian *Pseudofoenus* as well as species from South America.(Fig. 7.2). The separation of South America from Australia and Antarctica occurred about 50 mya in the middle Eocene (Owen 1983), and Australia became an island continent by the late Eocene (about 40-45 mya). The two species of *Pseudofoenus* endemic to South America should therefore represent a lineage which is the sister group to the Australasian taxa (excluding New Zealand) according to vicariance theory. However, in the successive weighting analysis, the two South American species are apical in the tree and have numerous Australian species as sister taxa (Fig. 7.2). This evidence suggests that their current distribution is possibly not determined by vicariance events. An alternative scenario might be that the two South American species are relicts of an earlier lineage, i.e. *Pseudofoenus s.l.* was in South America prior to its separation from Australia and Antarctica. However, there is no fossil evidence from South America to support this. Shaw (1990) encountered a similar situation where he used relicts to explain the current distribution of Megalyridae.

7.2.2.1. Phylogenetic constraints

Another approach to examine the hypothesis that the current distribution of the Hyptiogastrinae can be accounted for by vicariance events, is to constrain the strict consensus tree (Fig. 7.2) in various ways.

If both the New Zealand and South American taxa are placed basally, reflecting a strict Gondwanan cladogram (Fig. 7.3), this requires an additional 10 steps compared with the shortest tree generated by parsimony analysis. If only the two New Zealand taxa are placed basally in the tree below all other hyptiogastrine taxa, i.e. reflecting an hypothesis of a vicariance event in New Zealand but more recent dispersal to South America (Fig. 7.3), then an additional three steps are added to the tree length. On the other hand, if the two South American taxa are place basally (Fig. 7.4), then an additional eight steps are added to the length. This is further evidence to reject the vicariance hypothesis to explain the current distribution of the Hyptiogastrinae.

7.2.2.2. Dispersal ability of Hyptiogastrinae

If one takes a dispersalist view (e.g. Cain 1944), then given the high level of endemism in Australia, it would be considered as the 'centre of origin' for the Hyptiogastrinae. Among Cain's criteria for determining 'centres of origins' are the location of the greatest variety of forms of the taxon, and the location of the most primitive forms. The majority of hyptiogastrines (all but 8 species) are endemic to Australia, with many of these endemic to particular regions within Australia (Fig. 7.1).

Two species are endemic to New Guinea (Fig. 8.190). However, the lowland regions of New Guinea are part of the Australian plate and only separated from Australia by the narrow Torres Strait (Boucek 1988), and it is not possible to determine without fossil evidence whether the wasps dispersed to New Guinea before or after the recent separation of New Guinea from Australia (less than 5 mya - Burrett et al. 1991).

Several species are found on oceanic islands in the south-west Pacific, showing that hyptiogastrine wasps are capable of dispersal over at least intermediate distances. The barriers, in this case water, are relatively recent, Vanuatu and Fiji having emerged about 30 my BP (Burrett *et al.* 1991), and species occurring in these areas are expected to be more apical in any phylogeny. The evidence here is not clear cut given that some taxa are apical in the phylogeny, whereas others are more basal (Fig. 7.2). Of particular note is that the species from Vanuatu and Fiji are the sister taxa to two species from New Guinea, indicating that their origins are from this land mass, not from continental Australia. It is quite likely that they have arisen from species that have island-hopped form New Guinea and therefore species probably also exist on the islands of New Britain, New Ireland and the Solomon Islands, a proposition that can only be tested by future collecting. An undescribed male *Pseudofoenus* collected from New Britain has been recently been drawn to my attention, lending support to this proposition.

7.2.2.3. Hosts of Hyptiogastrinae

It is also useful to compare the numbers of hyptiogastrine wasps with the number of potential hosts in each of the major regions where the Hyptiogastrinae occur (Table 7.1). The potential hosts are ground nesting Colletidae, Stenotritidae and Halictidae (see Section 3.3). Although some colletids nest in rotting wood and some halictids nest in dead wood (Naumann 1991), no distinction has been made between those bees that are ground-nesting and those with other habits, and so the species numbers presented as potential hosts are an over-estimate of described species for each region.

Table 7.1. Distribution and number of described species of possible host bee families for Hyptiogastrinae. Note: Numbers of potential host species given are approximate total described species for the region. * = includes Halictinae only. Sources: a. Naumann 1991; b. Valentine & Walker 1991; c. Houston pers. comm. 1999; d. Michener 1965; e. Moure & Hurd 1987.

		No. potential host spp.				
Region	No. hyptiogastrine spp.	Colletidae	Stenotritidae	Halictidae	Total	Host: hyptiogastrine spp.
Australia	c.100	860[a]	30[a]	382[a]	1272	12.7:1
New Zealand	2	24[b]	0[b,c]	4[b]	28	14:1
South America	2	many[d]	0[c,e]	556[e]*		

With only two hyptiogastrine species in South America (Jennings and Austin 1997b), and a large number of potential hosts (Michener 1965), it is reasonable to conclude that they have not speciated to any degree and therefore one can postulate that they are recent arrivals to South America. If the South American taxa were "old" species in an evolutionary sense or evolved from relict taxa (see above), more speciation might be expected to have occurred. On the other hand, there are 14 potential host species per hyptiogastrine species in New Zealand (Table 7.1), with a slightly higher proportion in Australia where there are about 12.7 potential host species for each species of hyptiogastrine wasp. The degree of radiation of the hyptiogastrine fauna is greatest in Australia with New Zealand slightly less so, but it is much lower in South America. These data also do not support the hypothesis that the current distribution of the Hyptiogastrinae can be accounted for by vicariance events.

7.2.3. Discussion

The hypothesis that the distribution of hyptiogastrine wasps has been determined by vicariance events can be rejected on the basis of two independent pieces of information: 1) phylogenetic results do not match a Gondwanan area cladogram, and 2) the group has not speciated in New Zealand and South America, indicating that they have arisen from more a recent arrival of ancestors. In the light of this evidence, it seems more likely that hyptiogastrine wasps have an Austral centre and that the group has reached New Zealand and South America by dispersal more recently than the break-up of the Australian+Antarctic+South American connection. Their apparent lack of speciation in New Zealand and South America, in spite of numerous potential hosts, support this, along with the fact that some species have clearly dispersed into the south-west Pacific. As far as is known, this is the first time a vicariance hypothesis has been rejected for any group of animals that show such a restricted Gondwanan distribution.

A number of other Hymenopteran groups also display restricted Gondwanan distributions (Table 7.2), but whether these distributions can be explained by vicariance events or dispersal, generally remain untested. Of these groups, Shaw (1990) was able to use the results of a phylogenetic study to explain the present-day distribution of Megalyridae by continental drift (i.e. vicariance events), although none of the megalyrid genera are common to both Australia and South America. The remainder remain untested. For example, Naumann (1985) indicted that for the Monomachidae, where the family is known only from Australia and South America, it was reasonable to assume that the family has a Gondwanan origin.

Table 7.2. Hymenopteran groups with known restricted Gondwanan (Australasian-South American) distributions.

Family (Superfamily)	Distribution/comments	Reference(s)
Coelocybinae (Chalcidoidea)	Australia (13 genera), New Zealand (2 genera, 1 shared with Australia), South America (1 genus).	Boucek 1988
Colotrechninae (Chalcidoidea)	Australia (6 genera), New Zealand (2 genera), South America (3 genera).	Boucek 1988
Crabroninae (Sphecoidea)	Ground nesting *Podagritus* occurs in South America, Australia and New Zealand	Naumann 1991
Diapriidae (Proctotrupoidea)	Ambositrinae; about 20 spp. with Gondwanan distribution.	Naumann 1988; Masner 1993
Melophorini (Vespoidea)	This tribe of ants consists of 5 genera in Australia (although one genus also found in New Guinea) and one genus in temperate South America	Ward, pers. comm.
Megalyridae (Megalyroidea)	Gondwanan distribution. Includes genera endemic to Chile (*Rigel* Shaw, *Neodinapsis* Shaw), and Brazil (*Cryptalyra* Shaw).	Shaw 1990
Monomachidae (Proctotrupoidea)	*Monomachus* Klug; Australia (3 spp.), South America (10 spp.).	Naumann 1985
Nyssoninae (Sphecoidea)	*Clitemnestra*; Australia (9 spp.) and Chile (3 spp.)	Bohart and Menke 1976
Pergidae (Tenthredinoidea)	Except for a small lineage of 4 spp. in North America, pergids are restricted to Australia and Central and South America. Philomastiginae (2 spp.) restricted to Australia and South America.	Goulet 1993; Naumann 1991
Platygasteridae (Platygasteroidea)	*Parabaeus* and several other genera show essentially Gondwanan distributions.	Naumann 1991
Scelionidae (Platygasteroidea)	*Archaeoteleia*; New Zealand (1 sp.), Chile (4 spp.)	Masner 1968, 1976
Rotoitidae (Chalcidoidea)	New Zealand, Chile.	Gibson 1993
Tiphiidae (Vespoidea)	Thyninae; 715 Australian spp. Largely restricted to Australia and South America, but do not share genera.	Naumann 1991

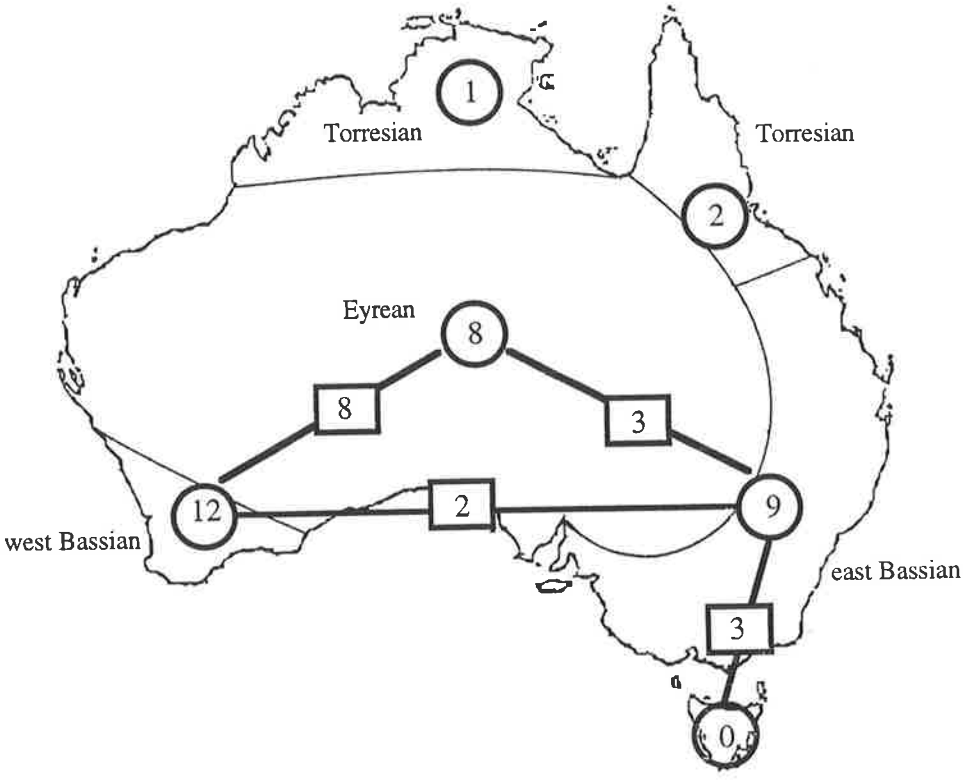


Figure 7.1. Number of hyptiogastrine species endemic (in circles) to particular biogeographic regions of Australia, and numbers of species shared between them (in boxes). Species which occur in more than two regions not indicated, as are species shared between disjunct regions.

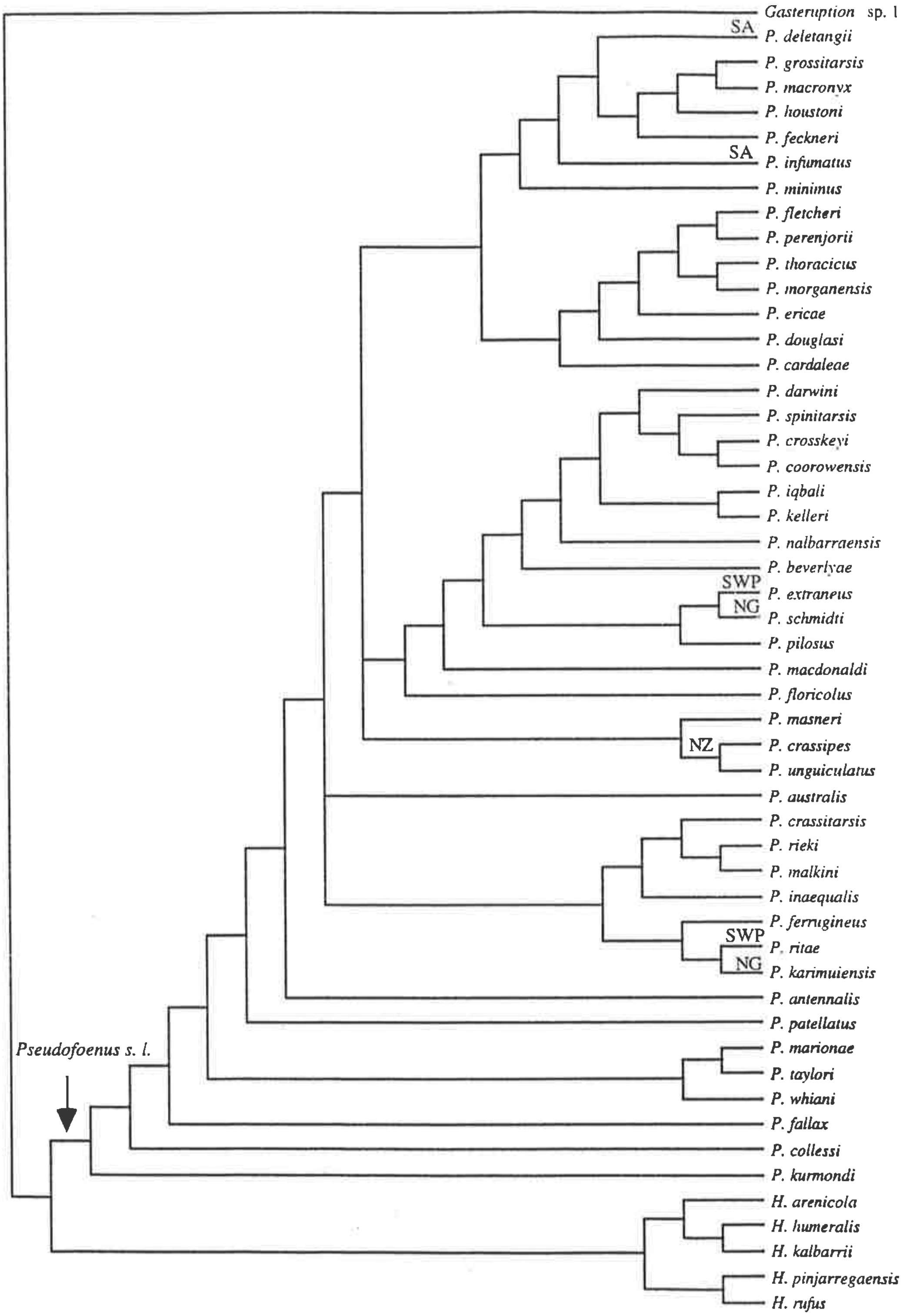


Figure 7.2. Strict consensus tree after successive weighting (Fig. 6.4) with non-Australian taxa indicated. NG = New Guinea, NZ = New Zealand, SA = South America, SWP = south-west Pacific.

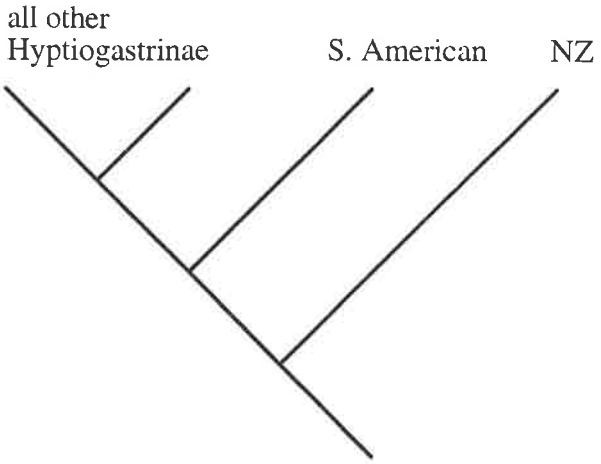


Figure 7.3. A strict Gondwanan cladogram requires an additional 10 steps compared with the shortest tree generated by parsimony analysis.

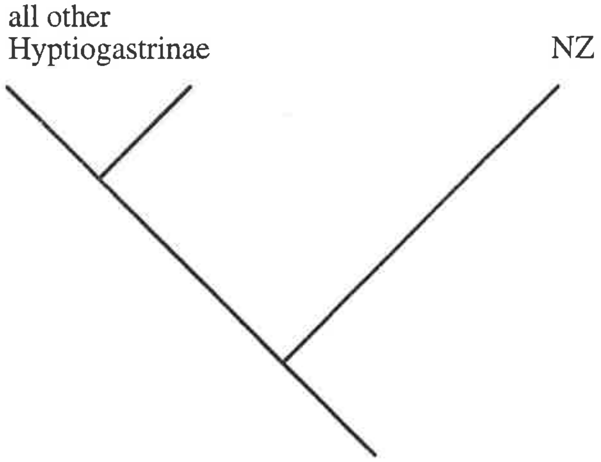


Figure 7.4. A cladogram that reflects a vicariance event in New Zealand but more recent dispersal to South America requires an additional three steps compared with the shortest tree generated by parsimony analysis.

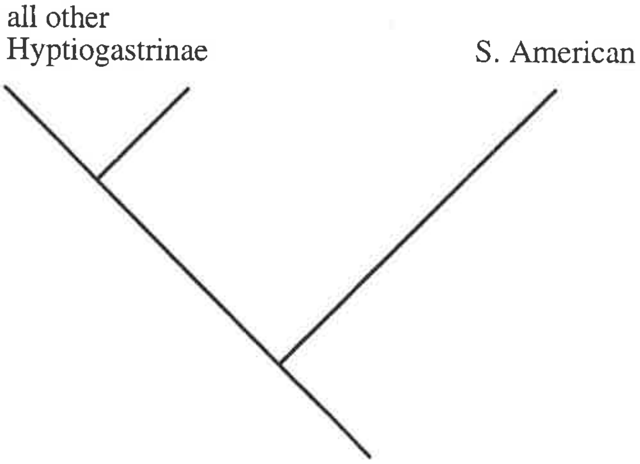


Figure 7.5. A cladogram where the two South American taxa are place basally requires an additional eight steps compared with the shortest tree generated by parsimony analysis.

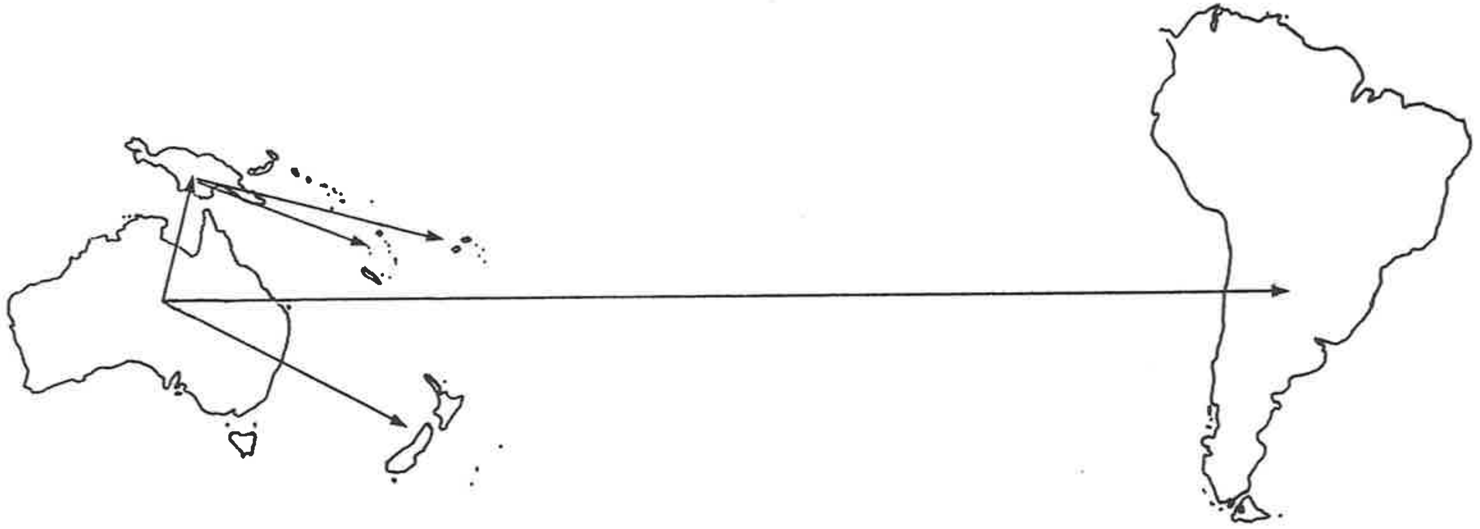


Figure 7.6. Map of southern Pacific showing possible dispersal of hyptiogastrine wasps.

Chapter 8.

Synopsis of Gasteruptiidae and revision of Hyptiogastrinae

8.1. Introduction

Based on the phylogenetic analyses discussed in Chapter 6, two hyptiogastrine genera are now recognised: *Hyptiogaster* Kieffer, which forms a monophyletic group of species diagnosed by the presence of an exserted ovipositor, and *Pseudofoenus sensu lato* Kieffer 1902. Three genera *Aulacofoenus* Kieffer, *Crassifoenus* Crosskey and *Eufoenus* Szépligeti, are synonymised under the latter genus which is further divided into a number of species-groups and subgroups (see Section 6.5.5.1). In this chapter, the taxonomy of the Hyptiogastrinae are revised and the means to identify the family, subfamilies, genera, species groups and subgroups, and species are provided in the form of separate dichotomous keys.

8.2. Families of Evanioidea

The superfamily Evanioidea traditionally comprises three families united by the high insertion point of the metasoma (e.g. Naumann 1991) (see also Chapter 2). The following key to evanioid families is modified from Naumann (1991) and Gauld and Bolton (1996).

1. Fore wing with vein 2m-cu present (Fig. 8.1); antennal insertion low on face, near lower margin of eyes (Fig. 8.2) .... **AULACIDAE**

\- Fore wing with vein 2m-cu absent (e.g. Appendix A6, Fig. 6); antennal insertion about mid level of eyes (e.g. Appendix A6, Fig. 1; Fig. 8.3) 2

2. Metasomal segment 1 slender (petiolate) and the remaining segments forming a short, ovate structure (Fig. 8.3); malar space large (longer than basal width of mandible); propleura not elongate, not meeting dorsally and not forming a neck (Fig. 8.4); hind wing with jugal lobe .... **EVANIIDAE**

\- Metasoma elongate and subclavate; malar space generally small; propleura elongate, meeting dorsally and forming a neck; hind wing without jugal lobe .... **GASTERUPTIIDAE**

8.3. Subfamilies of Gasteruptiidae

The two subfamilies of gasteruptiid wasps are both monophyletic (Fig. 6.1), and can be readily separated by the following key.

1. Mandibles long and broadly overlapping when in closed position; prefemur absent; first discal cell formed by fore wing vein 1-Rs+M intersecting basal cell about one-quarter to one-third distance from M+Cu (Appendix A5, Fig. 6) or first discal cell absent and veins 1-Rs+M and 1-Cu(b) fused to form Rs+M+Cu(b), veins 1-M and m-cu absent (Appendix A5, Fig. 3); female subgenital sternite simple (Fig. 8.7); hind trochanter with (Appendix A6, Figs 3, 33) or without a groove (Fig. 8.10); ovipositor usually hidden, not exserted, except in *Hyptiogaster* where it is exserted .... **Hyptiogastrinae**

\- Mandibles short and not broadly overlapping when in closed position; prefemur generally present (Fig. 8.5), sometimes indicated by a slightly differentiated basal swelling; first discal cell formed by fore wing vein 1-Rs+M forming node at 1-Rs, M+Cu and 1-Cu, vein 1-M absent (Appendix A4, Fig. 8) [several species with 1m-cu absent or nearly so such that the first discal cell is triangular (Appendix A4, Figs 9-13)]; female subgenital sternite notched or slit (Fig. 8.6); hind trochanter with a groove (Fig. 8.5); ovipositor exserted .... **Gasteruptiinae** .... ***Gasteruption*** L.

8.3.1. Diagnosis of subfamilies

Subfamily Gasteruptiinae

Gasteruptioninae Ashmead: 1900: 7. - Crosskey 1962: 394; Naumann 1991; 942.

Type genus *Gasteruption* Latreille 1796.

Diagnosis

Small to large gasteruptiid wasps; head about equal in width to or slightly wider than mesosoma; head elongate ventrally, length of malar space plus mandibles about as long or longer than height of eye; mandibles short, not overlapping when closed, inner margin with or without one medial tooth; labio-maxillary complex elongate, protruding well below mandibles; frontal carina either present or absent; dorsal tentorial pits present on frons, one each above toruli; sub-antennal sutures present, indistinct to clearly visible, defining small triangular subantennal area on medial face; female antenna 14-segmented, male antenna 13-segmented; pronotum without processes; mesoscutum almost as broad as long; notauli percurrent, punctate or scrobiculate; parapsidal lines indistinct; pit of metapleural apophysis deep; propodeal spiracle elongate; propodeum separated from metapleuron by carinate furrow, with short or percurrent medial longitudinal carina; inner surface of mid tibia without subapical notch; prefemur on hind leg (Fig. 8.5), rarely indistinct; hind trochanter with transverse groove (Fig. 8.5); hind femur and tibia strongly incrassate, about equal in length; outer hind tibial spur shorter and more robust than inner spur; first discal cell formed by fore wing vein 1-Rs+M joining M+Cu (Appendix A4, Fig. 8), 1m-cu absent or nearly so such that the first discal cell is triangular (Appendix A4, Figs 9-13); female subgenital sternite notched or slit (Fig. 8.6); ovipositor exserted, protruding well beyond apex of metasoma.

Comments

The subfamily currently comprises some 400 species all belonging to a single genus, *Gasteruption* L. (e.g. Crosskey 1963). Crosskey (1963) has outlined the taxonomic history of the subfamily.

Subfamily Hyptiogastrinae Crosskey 1963

Hyptiogastrinae Crosskey 1953: 351. - Crosskey 1962: 389; Naumann 1991: 942.

Type genus *Hyptiogaster* Kieffer 1903.

Diagnosis

Small to large gasteruptiid wasps; head about equal in width to or slightly wider than mesosoma; head elongate ventrally, length of malar space plus mandibles about as long or longer than height of eye (Appendix A6, Fig. 1); mandibles elongate, about as long as clypeus; labio-maxillary complex elongate, protruding well below mandibles (Appendix A6, Fig. 1);

frontal carina either present (Appendix A6, Fig. 23) or absent; dorsal tentorial pits present on frons, one each above toruli; sub-antennal sutures present, indistinct to clearly visible, defining small triangular subantennal area on medial face (Appendix A6, Fig. 1); female antenna 14-segmented, male antenna usually 13-segmented, rarely 14-segmented; pronotum without processes, rarely with processes (Appendix A6, Figs 25, 31); propleuron with prominent ventro-lateral carina (Appendix A6, Fig. 25) or without carina; mesoscutum almost as broad as long; notauli percurrent, punctate or scrobiculate; parapsidal lines indistinct; pit of metapleural apophysis deep; propodeal spiracle elongate (Appendix A3, Figs 11-12); propodeum separated from metapleuron by carinate furrow, with short or percurrent medial longitudinal carina; inner surface of mid tibia in female with or without subapical notch, absent in male; prefemur on hind leg absent (Appendix A3, Fig. 13); hind trochanter with transverse groove (Appendix A3, Figs 13-14) or without groove (Fig. 8.61); hind femur and tibia strongly incrassate, about equal in length; outer hind tibial spur shorter and more robust than inner spur; fore wing vein 1-Rs+M intersecting basal cell about one-quarter to one-third distance from M+Cu (Appendix A3, Fig. 15; Appendix A5, Fig. 6) or first discal cell absent, and veins 1-Rs+M and 1-Cu(b) fused to form Rs+M+Cu(b), veins 1-M and m-cu absent (Appendix A4, Fig. 3); female subgenital sternite simple (Fig. 8.7); ovipositor either short, robust, upwardly curved (Appendix A3, Figs 3,5,7), normally hidden by ovipositor sheaths (Appendix A3, Figs 26-27), or exserted, protruding well beyond apex of metasoma.

8.4. Treatment of genera and species of Hyptiogastrinae

The key to genera given below allows the user to key out female hyptiogastrine wasps to genus. It should be noted that males of some species cannot be keyed out as there lack distinguishing generic level characters. However, males that lack a groove on the hind trochanter are all placed in *Pseudofoenus s.l.*, and those which have pronotal processes are placed in *Hyptiogaster*.

Key to hyptiogastrine genera

1. Ovipositor exserted, protruding well beyond apex of metasoma; pronotum either without processes or with processes (Appendix A6, Figs 25, 31, 47-48); hind trochanter with a groove .... ***Hyptiogaster*** Kieffer

Ovipositor short, robust, upwardly curved (Appendix A3, Figs 3, 5, 7), normally hidden by ovipositor sheaths (Appendix A3, Figs 26-27); pronotum without processes; hind trochanter either with (Appendix A2, Figs 13-14) or without a groove (Fig. 8.10) .... ***Pseudofoenus*** *sensu lato* Kieffer

8.4.1. *Hyptiogaster* Kieffer

Genus ***Hyptiogaster*** Kieffer

Hyptiogaster Kieffer, 1903: 93. [Type species: *Gasteruption crassiceps* Schletterer, 1889, by original designation (junior synonym of *Foenus rufus* Westwood); not *Gasteruption antennale* Schletterer, 1889, by erroneous subsequent designation of Bradley, 1908 or *Foenus australis* Westwood, 1835, by erroneous designation of Crosskey, 1953]; Bradley, 1908: 108; Kieffer, 1912: 194; Hedicke, 1939: 47; Crosskey, 1962: 393; Jennings and Austin, 1997b: 1534.

Odontofoenus (in part) Kieffer, 1910: 77; synonymy by Crosskey, 1962: 393.

Carinafoenus Crosskey, 1953a: 104; synonymy by Crosskey, 1962: 393.

Diagnosis

Medium to large sized wasps (length 12.0-20.0 mm), generally red-brown in colour with black markings; head in dorsal view slightly wider than mesosoma, slightly longer than wide in lateral view (Appendix A6, Fig. 2); malar space short, 0.1-0.2 x height of eye; length of malar space plus mandibles less than height of eye; medial epistomal suture indistinct; lateral epistomal suture absent so that clypeus is continuous with gena (Appendix A6, Fig. 10); clypeus 1.3-2.5 x as wide as high, clypeal margin either sinuate (Appendix A6, Fig. 10) or with truncate medial lobe (Appendix A6, Fig. 24); mandibles elongate, generally with 2 but sometimes 3 medial teeth; labio-maxillary complex retractable, when extended protruding well below mandibles (Appendix A6, Figs 1-2); frontal carina distinct (Appendix A6, Fig. 23); antennal scrobes slightly excavate; subantennal sutures distinct; distance from lateral ocellus to eye margin 0.5-0.7 x distance between lateral ocellus and occipital carina; antenna 14-segmented in female, 13-segmented in male, first flagellomere about same length as second, terminal flagellomere much longer than wide; basal mandibular tooth triangular; pronotum with or without antero-dorsal and antero-lateral tooth-like processes (Appendix A6, Figs 25, 31, 47-48); pronotal depressions carinate; propleuron with ventro-lateral carina (Appendix A6, Fig. 25); mesoscutum slightly longer than broad, distinctly truncate anteriorly (Appendix A6, Figs 54, 57, 63), with distinct or indistinct admedial lines, with or without medial line; notauli percurrent, scrobiculate (Appendix A6, Fig. 63), or sometimes indistinct and hidden by coarse sculpturing; parapsidal lines present, sometimes indistinct and obscured by sculpturing; propodeal spiracle elongate (Appendix A6, Fig. 26), with or without fringe of setae; propodeum separated from metapleuron by carinate furrow; fore and mid tarsi pubescent; inner surface of mid tibia without subapical notch; hind trochanter with distinct groove (e.g. Appendix A6, Fig. 13); femur shorter than tibia; inner hind tibial spur about 1.5 x as long as outer spur, outer spur more robust (sometimes spurs broken off or worn); hind tarsal segments 1-4 with ventro-apical pecten of short spines (Appendix A6, Fig. 5), these spines sometimes absent; fore wing generally pale brown, veins dark brown except for M+Cu, 2cu-a, 2-1A, 3-1A, 2-cu(b) pale brown; hind wing generally pale brown; hind wing vein 1-Cu (and 1-M) absent (Appendix A6, Fig. 7); metasoma 2.0-3.3 x length of mesosoma; ovipositor exserted, elongate, at least 0.25 x length metasoma, apex slightly curved upwards, lateral margins of ventral ovipositor valves smooth.

Comments

Hyptiogaster was erected without description by Kieffer (1903), although he provided a key to genera and included 11 species. *Gasteruption crassiceps* Kieffer was designated by him as the type species. However, subsequent authors confused the type species with *Gasteruption antennale* Schletterer, 1889, designated in error by Bradley (1908), and *Foenus australis* Westwood, 1835, designated in error by Crosskey (1953a). In his key, Kieffer distinguished *Hyptiogaster* and *Gasteruption* from *Pseudofoenus* on the basis of the latter genus lacking a closed discal cell and he distinguished *Hyptiogaster* from *Gasteruption* primarily on wing venation, i.e. *Hyptiogaster* having the first discal cell located before the sub-marginal cell (Appendix A6, Fig. 6).

Hedicke (1939) included 24 species in *Hyptiogaster*, while Crosskey (1953a) accommodated 23 species under this generic name. At the same time, Crosskey removed five species (see below) previously included in *Hyptiogaster* and erected a new genus, *Carinafoenus*, which differed from *Hyptiogaster* in all possessing a groove on the hind trochanter, the fourth antennal segment being as long as the third, a long ovipositor, and a greater number of hamuli. He later added four more species to *Hyptiogaster* (Crosskey 1956), but they were subsequently removed to *Eufoenus* (Crosskey 1962). It was not until Crosskey (1962) revised the Hyptiogastrinae and stabilised the genera that all of the species he had previously included in *Hyptiogaster* (Crosskey 1953a, 1956), were assigned to other genera. At the same time, he placed *Carinafoenus* as a junior synonym of *Hyptiogaster* and transferred its five species to *Hyptiogaster*, i.e. *H. crassiceps*, *H. arenicola* Turner, *H. flavosignata*, *H. humeralis* and *H. rufus*. The genus has remained unstudied until Jennings and Austin (1997b), undertook a complete revision of the group. Seven species were added and two synonymies, *H. flavosignata* (Kieffer) with *H. humeralis* (Schletterer) and *H. crassiceps* (Schletterer) with *H. rufus* (Westwood), were proposed (see Appendix A6).

Preliminary studies by Jennings and Austin (1997b), indicated that the monophyly of *Hyptiogaster* was supported by at least two apomorphic characters: the anterior mesothorax truncate in lateral view and hind wing vein M (2-M in *Crassifoenus* - Jennings and Austin 1994a) being nebulous and barely pigmented (Appendix A6, Fig. 7). The sister-group to

Hyptiogaster was not resolved, but superficially it was most similar to *Aulacofoenus* and *Crassifoenus*. However, phylogenetic analysis (Fig. 6.4) indicates that these characters do not support the monophyly of *Hyptiogaster*. *Hyptiogaster* includes all species that have an elongate exserted ovipositor, although this character state is also shared by *Gasteruption* and Aulacidae. It is also the only genus in which at least some species possess tooth-like pronotal processes, this character state probably being apomorphic (see Appendix A6).

8.4.1.1. Included species

The 10 included *Hyptiogaster* species (Table 8.1) were recently described in Jennings and Austin (1997b) (see Appendix A6).

Table 8.1. List of species included in *Hyptiogaster* Kieffer.

Hyptiogaster arenicola Turner
Hyptiogaster cobarensis Jennings and Austin
Hyptiogaster hulli Jennings and Austin
Hyptiogaster humeralis (Schletterer)
Hyptiogaster kalbarrii Jennings and Austin
Hyptiogaster kiefferi Jennings and Austin
Hyptiogaster naumanni Jennings and Austin
Hyptiogaster pinjarregaensis Jennings and Austin
Hyptiogaster rufus (Westwood)
Hyptiogaster weowaniensis Jennings and Austin

8.4.2. *Pseudofoenus sensu lato* Kieffer

Genus *Pseudofoenus* Kieffer

Pseudofoenus Kieffer, 1902: 6. [Type species *Foenus unguiculatus* Westwood, 1841, by subsequent designation of International Commission on Zoological Nomenclature, 1998]. - Kieffer, 1903: 93; Szépligeti, 1903: 365; Bradley, 1908: 109; Kieffer, 1911b: 176; Kieffer, 1912: 204; Turner, 1918a: 413; Hedicke, 1939: 45; Crosskey, 1962: 392; Valentine and Walker, 1991: 31 (junior synonym of *Hyptiogaster* Kieffer); Jennings and Austin, 1994b: 1290.

Aulacofoenus Kieffer, 1911b: 177. - Kieffer, 1912: 193; Hedicke, 1939: 50; Crosskey, 1962: 393; Jennings and Austin, 1997a: 945. **Syn. nov.**

Crassifoenus Crosskey 1953: 355-356. - Muesebeck and Walkley 1956: 344; Crosskey 1962: 389; Jennings and Austin 1994a: 576. **Syn. nov.**

Eufoenus Szépligeti, 1903: 365. - Bradley, 1909, 38 (syn. with *Hyptiogaster*); Crosskey, 1962: 392. **Syn. nov.**

Hemifoenus Kieffer, 1911: 182. - Turner, 1918a: 410 (syn. with *Hyptiogaster*); Hedicke, 1939: 50; Crosskey, 1962: 392, 398.

Trigonofoenus Kieffer, 1911: 177. - Hedicke, 1939: 42; Crosskey, 1962: 392, 398 (syn. with *Eufoenus*).

Diagnosis

Small to large wasps, length 3-23 mm; head about equal in width to or slightly wider than mesosoma; head generally slightly longer than wide in dorsal view (Appendix A5, Fig. 30), rarely obviously elongate (Appendix A3, Fig. 1; Appendix A5, Fig. 31); malar space short, 0.03-0.3 x height of eye; length of malar space plus mandibles less than height of eye; epistomal suture distinct medially, rarely absent, distinct laterally, rarely absent; clypeus wider than high, sometimes with a slightly raised median carina; clypeus generally flat, sometimes raised and dome-like; clypeal margin sinuate (Fig. 8.13); mandibles elongate, strongly curved distally, basal tooth triangular (Appendix A4, Figs 26-29); labio-maxillary complex retractable, when extended protruding well below mandibles (Appendix A5, Figs 2-3); frontal carina either present (Appendix A5, Figs 2, 30, 31) or absent; dorsal tentorial pits present; subantennal sutures present, indistinct to clearly visible, defining small triangular subantennal area on medial face (Appendix A3, Fig. 1), or absent (Appendix A4, Fig. 2); antennal scrobes slightly excavate; antenna 14-segmented in female, generally 13-segmented in male, sometimes 14-segmented; first flagellomere longer than second (Appendix A5, Fig. 5); terminal flagellomere longer than wide; pronotum without processes; pronotal depressions carinate; propleuron with or without ventro-lateral carina; mesoscutum slightly longer than broad, with admedian lines anteriorly, with or without medial lines; notauli percurrent, scrobiculate or punctulate; parapsidal lines indistinct; propodeal spiracle elongate, either fringed with long hairs or not so; propodeum separated from metapleuron by carinate furrow, short median propodeal carina posteriorly; inner surface of mid tibia with or without subapical notch; hind trochanter with or without distinct trochanteral groove (Appendix A3, Figs, 9-10; Appendix A5, Figs 60-64), sometimes indistinct (Appendix A5, Figs 57-58); inner hind tibial spur about 1.5 x as long as outer spur, outer spur more robust (sometimes spurs broken off or worn); hind tarsal segments 2-4 not greatly shortened in male; hind tarsal segments 1-4 with ventro-apical pecten of short spines (Appendix A5, Fig. 4), these spines sometimes absent; hind tarsal claws about as long as or shorter than hind tarsal segment 5; fore wing with two discal cells, fore wing vein 1-Rs+M intersecting basal cell about one-quarter to one-third distance from M+Cu (Appendix A5, Fig. 6) or first discal cell absent, and veins 1-Rs+M and 1-Cu(b) fused to form Rs+M+Cu(b) (Appendix A4, Fig. 3); hind wing with 2-7 hamuli, Cu present (Appendix A3, Fig. 15) or absent (Appendix A4, Fig. 4); fore wing generally pale brown, veins dark brown, except M+Cu, 2-1A, 3-1A and 2cu-a pale brown; hind wing generally pale brown, vein M+Cu pale brown (Appendix A5, Fig. 7); metasoma 1.75-3.10 x length of mesosoma; ovipositor short, robust, upwardly curved, normally hidden by ovipositor sheaths (Appendix A4, Fig. 5); lateral margins of ventral ovipositor valves generally smooth, sometimes undulate or serrate (Appendix A3, Figs 4, 6, 8); digitus (male) about the same length as basiparamere (Appendix A5, Figs 65-68).

Comments

The phylogenetic analyses (Figs 6.2 and 6.4) indicate that the monophyletic sister group to *Hyptiogaster* is supported by short, hidden ovipositor. As a consequence of expanding the limits of *Pseudofoenus* to include all members of the subfamily other than Hyptiogaster, the three genera *Aulacofoenus*, *Crassifoenus* and *Eufoenus* are here synonymised, and those species formerly included in them are transferred to *Pseudofoenus s.l.* The strict consensus tree generated after successive weighting (Fig. 6.4) was used to divide *Pseudofoenus s.l.* into species groups and subgroups. Two monophyletic or informal species groups based on unequivocal character states are recognised; the *crassipes*-group and the *fletcheri*-species group, with the latter divided into the *thoracicus-*, *macronyx-*, and *infumatus*-subgroups. The remaining taxa considered in the analysis are not assigned to any species groups as there are no unequivocal character states which support their monophyly. Other species not included in the data matrix are placed into the generic and species-group classification on the basis of the character states they possess.

Recent studies by Jennings and Austin (Appendices A3-A5) have revised the species of *Aulacofoenus*, *Crassifoenus* and *Pseudofoenus s. str.*

Table 8.1. Classification of *Pseudofoenus s. l.* by species-group.

***crassipes*-group**

P. crassipes (Smith)
P. nocticolor Kieffer
P. pedunculatus (Schletterer)
P. unguiculatus (Westwood)

***fletcheri*-group**

***thoracicus*-subgroup**

P. morganensis sp. nov.
P. thoracicus (Guérin Menéville) comb. nov.

***macronyx*-subgroup**

P. grossitarsis (Kieffer) comb. nov.
P. houstoni (Jennings & Austin) comb. nov.
P. macronyx (Schletterer) comb. nov.

***infumatus*-subgroup**

P. bungeyi (Jennings & Austin) comb. nov.
P. cardaleae sp. nov.
P. deletangi (Schletterer) comb. nov.
P. douglasi sp. nov.
P. ericae sp. nov.
P. feckneri sp. nov.
P. fletcheri (Jennings & Austin) comb. nov.
P. goonooensis (Jennings & Austin) comb. nov.
P. infumatus (Schletterer) comb. nov.
P. microcephalus (Crosskey) comb. nov.
P. minimus (Turner) comb. nov.
P. perenjorii (Jennings & Austin) comb. nov.
P. wubinensis (Jennings & Austin) comb. nov.

Other species

P. antennalis (Schletterer) comb. nov.
P. australis (Westwood) comb. nov.
P. beverlyae sp. nov.
P. collessi sp. nov.
P. coorowensis sp. nov.
P. crassitarsis (Kieffer) comb. nov.
P. crosskeyi sp. nov.
P. darwini (Westwood) comb. nov.
P. extraneus (Turner) comb. nov.
P. fallax (Schletterer) comb. nov.
P. ferrugineus (Crosskey) comb. nov.
P. floricolus (Turner) comb. nov.
P. inaequalis (Turner) comb. nov.
P. iqbali sp. nov.
P. karimuiensis sp. nov.
P. kelleri sp. nov.
P. kurmondi (Jennings & Austin) comb. nov.
P. loxleyi (Jennings & Austin) comb. nov.
P. macdonaldi sp. nov.
P. malkini sp. nov.
P. marionae (Jennings & Austin) comb. nov.
P. masneri sp. nov.
P. nalbarraensis sp. nov.
P. nitidiusculus (Turner) comb. nov.
P. patellatus (Westwood) comb. nov.
P. pilosus (Kieffer) comb. nov.
P. reticulatus (Crosskey) comb. nov.
P. rieki (Crosskey) comb. nov.
P. ritae (Cheesman) comb. nov.
P. schmidti sp. nov.
P. spinitarsis (Westwood) comb. nov.
P. swani (Jennings & Austin) comb. nov.
P. taylori sp. nov.
P. whiani (Jennings & Austin) comb. nov.

8.4.2.1. Key to species-groups and subgroups and species of *Pseudofoenus sensu lato* Kieffer

1. Fore wing with single discal cell (Appendix A4, Fig. 3); fore wing vein 1-Rs+M fused to form Rs+M+Cu(b) (Appendix A4, Fig. 3) .... ***crassipes*****-group** 2

Fore wing with two discal cells (Appendix A3, Fig. 15); fore wing vein 1-Rs+M with joins 1-M and 1-Rs (Appendix A3, Fig. 15) 5

2 (1). Antenna 14-segmented; metasoma about 1.8 x length of mesosoma; ovipositor present and enclosed by sheaths (Appendix A4, Fig. 5) .... (female) 3

Antenna 13-segmented; metasoma about 2.4 x length of mesosoma; digitus and penis valves present (Appendix A4, Figs 31-34) .... (male) 4

3 (2). Hind claws long (Appendix A4, Figs 17, 21); hind tarsal segment 5 with dense setae (Appendix A4, Fig. 17) .... ***P. unguiculatus*** (Westwood)

Hind claws short (Appendix A4, Figs 19, 22); hind tarsal segment 5 with scattered setae (Appendix A4, Fig. 19) .... ***P. crassipes*** (Smith)

4 (2). Digitus much longer than penis valves; basal lobe of basiparamere with imbricate microsculpturing medially and with small pit; base of penis valves narrow and elongate (Appendix A4, Figs 31-32) .... ***P. nocticolor*** Kieffer

Digitus only slightly longer than penis valves; basal lobe of basiparamere smooth medially, small pit absent; base of penis valves short and broad (Appendix A4, Figs 33-34) .... ***P. pedunculatus*** (Schletterer)

5 (1). Occipital carina sculptured (Fig. 8.17), with at least a carina medially .... ***fletcheri*****-group** 6

Occipital carina smooth 23

6 (5). Hind wing vein 1-Cu present (Appendix A3, Fig. 16); subapical notch on inner surface of the mid tibia of females, absent in males; dentate or undulate lateral margins of the ventral ovipositor valves (Appendix A3, Figs 4, 6, 8) .... ***macronyx*****-subgroup** 7

Hind wing vein 1-Cu absent; subapical notch on the inner surface of the mid tibia absent in both sexes; lateral margins of ventral ovipositor valves smooth 9

7 (6). Mandible with two distinct medial teeth (Appendix A3, Figs 21-22); mat of long setae present on ventral surface of hind tarsal segment 5; vertex finely scrobiculate or punctate-reticulate adjacent to occipital carina; predominantly reddish species ... 8

Mandible with indistinct medial teeth (Appendix A3, Fig. 20); without mat of long setae on ventral surface of hind tarsal segment 5; vertex coarsely scrobiculate adjacent to occipital carina; predominantly black species .... ***P. houstoni*** (Jennings and Austin) comb. nov.

8 (7). Proepisternal carina oblique, short and fine; vertex finely scrobiculate adjacent to occipital carina .... ***P. macronyx*** (Schletterer) comb. nov.

Proepisternal carina oblique, long and enlarged; vertex punctate-reticulate adjacent to occipital carina .... ***P. grossitarsis*** (Kieffer) comb. nov.

9 (6). Hind tarsal segment 1 asymmetrical, sometimes with broad lateral projection (Appendix A5, Fig. 4); hind tarsal segments 2-3 and sometimes segment 4 with lateral projections (Appendix A5, Fig. 4) .... ***thoracicus***-subgroup 10

Hind tarsal segments 1-4 without lateral projections (Appendix A5, Figs 13-25) .... ***infumatus***-subgroup 11

10 (9). Hind tarsal segments 1-3 asymmetrical, segment 1 deeply incised, with stout lateral projection, segments 2-3 and sometimes segment 4 with stout lateral spine-like projections (Appendix A5, Figs 4, 14); frontal carina very strong and horn-like; ; metasomal T1 punctate-rugulose anteriorly to punctate-imbricate posteriorly (Appendix A5, Fig. 46) ....***P. thoracicus*** (Guérin Menéville) comb. nov.

Hind tarsal segments 1-4 somewhat dorso-ventrally flattened, segments 1-3 somewhat asymmetrical (Fig. 8.147); frontal carina strong, not horn-like (Fig. 8.8); metasomal T1 imbricate (Fig. 8.10); mandibles narrow .... ***P. morganensis*** sp. nov.

11 (9). Hind trochanter without a groove 12

Hind trochanter with a groove 16

12 (11). Malar space small, < 0.1 x height of eye 13

Malar space large, 0.2 x height eye; metasomal T1 imbricate, some underlying rugosity (Fig. 8.29) .... ***P. minimus*** (Turner) comb. nov.

13 (12). Hind tarsal claw large, ≥0.8 x length hind tarsal segment segment 5 14

Hind tarsal claw small, <0.8 x length hind tarsal segment segment 5 15

14 (13). Hind tarsal claw 1.00 (0.80-1.30) x length hind tarsal segment 5 (Fig. 8.151); metasomal T1 punctate-imbricate, almost smooth medially (Fig. 8.22); first flagellomere 3.00 (2.75-3.60) x as long as scape, 1.87 (1.50-2.30) x as long as second flagellomere .... ***P. feckneri*** sp. nov.

Hind tarsal claw 0.8 x length hind tarsal segment 5 (Fig. 8.152); metasomal T1 imbricate-rugose (Fig. 8.26); first flagellomere 1.5 x as long as scape, 1.7 x as long as second flagellomere .... ***P. microcephalus*** (Crosskey) comb. nov.

15 (13). Hind tarsal claw 0.52 (0.46-0.58) x length hind tarsal segment segment 5 (Fig. 8.148); ventro-apical pecten of spines on hind tarsal segments 1-4 extremely short; metasomal T1 rugulose, with some punctures laterally (Fig. 8.14) .... ***P. cardaleae*** sp. nov.

Hind tarsal claw 0.65 (0.62-0.67) x length hind tarsal segment 5 (Fig. 8.149); metasomal T1 rugulose dorsally to imbricate laterally (Fig. 8.16) .... ***P. douglasi*** sp. nov.

16 (11). Head wider than long (Appendix A5, Fig. 26) or somewhat quadrate (Appendix A5, Fig. 30) when viewed dorsally 17

Head elongate when viewed dorsally (Appendix A5, Fig. 31) [fore wing vein 2-M pale in apical three-fifths; slightly raised longitudinal median ridge on T1] .... ***P. fletcheri*** (Jennings & Austin) comb. nov.

17 (16). Frontal carina absent 18

Frontal carina present 19

18 (17). Hind tarsal segment 1 deeply incised, segments 2-4 greatly shortened (Appendix A5, Fig. 24); hind tarsal claw long, 1.1 (1.0-1.3) x length hind tarsal segment 5

(Appendix A5, Fig. 24); metasomal T1 strigate dorsally, smooth laterally (Appendix A5, Fig. 52) [South America] .... ***P. deletangi*** (Schletterer) comb. nov.

Hind tarsal segment 1 not deeply incised, segments 2-4 not greatly shortened (Appendix A5, Fig. 25); hind tarsal claw 0.5 (0.46-0.56) x length hind tarsal segment 5 (Appendix A5, Fig. 25); metasomal T1 smooth dorsally, rugose laterally (Appendix A5, Fig. 53) [South America] . ***P. infumatus*** (Schletterer) comb. nov.

19 (17). Two medial mandibular teeth present 20

One medial mandibular tooth present (Appendix A5, Fig. 33); frontal carina weak (Appendix A5, Fig. 29); metasomal T1 rugose-imbricate (Appendix A5, Fig. 52) [length 8 mm] .... ***P. goonooensis*** (Jennings & Austin) comb. nov.

20 (19). Frontal carina strong, not horn-like 21

Frontal carina raised and horn-like; metasomal T1 punctate-imbricate (Appendix A5, Fig. 55) ....***P. perenjorii*** (Jennings & Austin) comb. nov.

21 (20). Anterior clypeal margin sinuate 22

Anterior clypeal margin convex; hind trochanter with indistinct groove on inner lateral surface (Fig. 8.18); metasomal T1 rugose, almost striate dorsally, imbricate laterally (Fig. 8.19) .... ***P. ericae*** sp. nov.

22 (21). Face punctulate-imbricate, pubescence short; occipital carina broad; metasomal T1 punctulate-imbricate (Appendix A5, Fig. 54) .... ***P. wubinensis*** (Jennings & Austin) comb. nov.

Face rugulose medially to rugulose-punctulate laterally, pubescence long; occipital carina narrow; metasomal T1 imbricate dorsally, punctate-imbricate laterally .... ***P. bungeyi*** (Jennings & Austin) comb. nov.

23 (5). Frontal carina absent 24

Frontal carina present 39

24 (23). Malar space length : eye length <0.1 25

Malar space length : eye length ≥0.1 29

25 (24). Epistomal suture present medially 26

Epistomal suture absent medially (sometimes indicated by a faint line) (Fig. 8.73); hind trochanteral groove absent (Fig. 8.74); mesoscutum rugose, medial line present; metasomal T1 smooth except for a few small shallow punctures posteriorly (Fig. 8.75) .... ***P. floricolus*** (Turner) comb. nov.

26 (25). Occipital carina narrow 27

Occipital carina broad (Fig. 8.132); malar space small (0.04 x height of eye); metasomal T1 smooth, with a few shallow punctures (Fig. 8.134) [Irian Jaya] .... ***P. schmidti*** sp. nov.

27 (26). Medial line on mesoscutum present 28

Medial line on mesoscutum absent; face, frons, vertex and gena smooth; metasomal T1 imbricate (Fig. 8.42) .... ***P. beverlyae*** sp. nov.

28 (27). Clypeus broad, 1.20 x as wide as high, imbricate; metasomal T1 imbricate (Fig. 8.84) [Papua New Guinea] .... ***P. karimuiensis*** sp. nov.

Clypeus narrow, 2.86 x as wide as high, smooth; metasomal T1 punctate-imbricate (Fig. 8.104) .... ***P. nalbarraensis*** sp. nov.

29 (24). Hind tarsal segments 1 and 2 highly asymmetrical, each segment with a stout apical spine (Figs 8.161, 180) 30

Hind tarsal segments 1 and 2 either symmetrical or somewhat asymmetrical, without stout apical spines 31

30 (29). Metasomal T1 smooth medially, imbricate laterally (Fig. 8.62); mesepimeron narrow; small species, length 5.4 mm (4-6 mm) .... ***P. darwini*** (Westwood) comb. nov.

Metasomal T1 punctate-imbricate (Fig. 8.138); mesepimeron broad; larger species, length 9 mm (7-11 mm) .... ***P. spinitarsis*** (Westwood) comb. nov.

31 (29). Hind tarsi asymmetrical (eg Fig. 8.158) 32

Hind tarsi more or less symmetrical 34

32 (31). Clypeus more or less flat 33

Clypeus somewhat dome-shaped; anterior clypeal margin convex; face, frons, vertex and gena smooth (very weakly imbricate under high magnification); hind coxae, trochanters, femora and tibiae smooth (very weakly imbricate under high magnification); metasomal T1 smooth (Fig. 8.57) .... ***P. crosskeyi*** sp. nov.

33 (32). Anterior clypeal margin convex; mesoscutum smooth, with a few shallow punctures; malar space 0.27 (0.26-0.30) x length eye; metasomal T1 smooth (Fig. 8.50) [punctate-imbricate in male] .... ***P. coorowensis*** sp. nov.

Anterior clypeal margin sinuate; mesoscutum imbricate, with a few scattered shallow punctures; malar space 0.15 x height eye; metasomal T1 smooth medially to weakly imbricate laterally (Fig. 8.88) .... ***P. kelleri*** sp. nov.

34 (31). Metasoma with short setae; occipital carina narrow 35

Metasoma with long setae [long setae on most parts of the body giving a pilose appearance]; occipital carina broad (Fig. 8.115); epistomal suture absent medially (Fig. 8.116); metasomal T1 imbricate with a few punctures laterally (some sometimes smooth medially) (Fig. 8.117) .... ***P. pilosus*** (Kieffer) comb. nov.

35 (34). Hind tarsal claw short, <0.75 x length segment 5 36

Hind tarsal claw long, 1.0 x length segment 5 (Fig. 8.176); malar space 0.14 x height eye; epistomal suture absent (Fig. 8.119); mesoscutum imbricate, with scattered shallow punctures; metasomal T1 imbricate, with a few scattered shallow punctures (Fig. 8.120); small species, 5 mm long ....
.... ***P. reticulatus*** (Crosskey) comb. nov.

36 (35). Mandible with two prominent medial teeth 37

Mandible with single weak medial tooth (Fig. 8.129); face imbricate; [13-segmented antennae in male; Vanuatu and New Caledonia] .. ***P. ritae*** (Cheesman) comb. nov.

37 (36). Frons punctulate-imbricate or imbricate 38

Frons strigate; length 7.0 (5.5-7.5) mm [14-segmented antennae in male; Fiji]
.... ***P. extraneus*** (Turner) comb. nov.

38 (37). Frons punctulate-imbricate; scutellum, axillae and metanotum imbricate; length 3 (2.5-3.5) mm .... ***P. macdonaldi*** sp. nov.

Frons imbricate; scutellum, axillae and metanotum smooth, with a few shallow punctures; length 5 mm .... ***P. iqbali*** sp. nov.

39 (23). Malar space large, ≥ 0.1 x height eye 40

Malar space small, < 0.9 x height eye 42

40 (39). Mandible with medial teeth not widely separated; hind tarsal segments 2-4 not greatly shortened in female 41

Mandible with two widely separated medial teeth (Appendix A5, Fig. 35); hind tarsal segments 2-4 greatly shortened in female (Appendix A5, Fig. 17); metasomal T1 smooth .... ***P. kurmondi*** (Jennings & Austin) comb. nov.

41 (40). Hind tarsal claw long, 1.17 (1.10-1.25) x length hind tarsal segment 5 (Fig. 8.154); metasomal T1 rugose-imbricate (Fig. 8.34) .... ***P. antennalis*** (Schletterer) comb. nov.

Hind tarsal claw short, 0.65 (0.6-0.7) x length hind tarsal segment 5 (Fig. 8.157); metasomal T1 imbricate (Fig. 8.45) .... ***P. collessi*** sp. nov.

42 (39). Ventro-lateral propleural carina present 43

Ventro-lateral propleural carina absent 49

43 (42). Hind tarsal claw short, ≤ 1.0 x length hind tarsal segment 5 44

Hind tarsal claw long, 1.3 (1.2-1.4) x length hind tarsal segment 5 (Appendix A5, Fig. 21); propleural ventro-lateral carina prominent, flange-like .... ***P. swani*** (Jennings & Austin) comb. nov.

44 (43). Hind tarsal segments 2-4 not compressed 45

Hind tarsal segments 2-4 compressed (Appendix A5, Fig. 13); fore wing vein 2-M pale in apical two-thirds .... ***P. fallax*** (Schletterer) comb. nov.

45 (44). Hind tarsal segments predominantly red-brown 46

Hind tarsal segments predominantly white; metasomal T1 imbricate with a few punctures laterally (Fig. 8.113); hind trochanter with (Figs 8.111-112) or without groove; length 14 mm (11-18 mm) .... ***P. patellatus*** (Westwood) comb. nov.

46 (45). Metasomal T1 sculptured dorsally 47

Metasomal T1 smooth dorsally, with a few scattered setae (Fig. 8.99); hind trochanter without groove (Fig. 8.98); length 7.5 mm (6-8 mm) .... ***P. masneri*** sp. nov.

47 (46). Metasomal T1 imbricate, with either underlying rugosity or with a few shallow punctures laterally 48

Metasomal T1 rugulose-punctate (Appendix A5, Fig. 47); hind trochanter with a groove; length 12 mm .... ***P. loxleyi*** (Jennings & Austin) comb. nov.

48 (47). Metasomal T1 imbricate with underlying rugosity (Fig. 8.38); hind trochanter with or without groove; large wasp, length 13.5 mm (12-15 mm) .... ***P. australis*** (Westwood) comb. nov.

Metasomal T1 imbricate, with a few shallow punctures laterally (Fig. 8.108); hind trochanter without groove (Fig. 8.107); medium sized wasp, 9.6 mm (9-10 mm) .... ***P. nitidiusculus*** (Turner) comb. nov.

49 (42). Large species, ≥ 8 mm in length 50

Small species, length 4 mm [5 mm in male]; male with stout setae on hind tarsal segment 1 (Fig. 8.96); body pale orange .... ***P. malkini*** sp. nov.

50 (49). Sculpturing of frons other than striate 51

Frons distinctly striate (Fig. 8.51); hind tarsal claw long, 0.95 (0.8-1.0) x length segment 5 (Fig. 8.159); inner tibial spur on hind leg almost same length as outer spur .... ***P. crassitarsis*** (Kieffer) comb. nov.

51 (50). Mandible with two medial teeth, both distinct 52

Mandible with two medial teeth, but more apical tooth indistinct; apex of hind tarsal segment 1 and segments 2-5 cream .... ***P. marionae*** (Jennings & Austin) comb. nov.

52 (51). Clypeus sculptured 54

Clypeus smooth; hind trochanter with weak groove (Fig. 8.69) .... ***P. ferrugineus*** (Crosskey) comb. nov.

53 (52). Hind trochanter without groove 54

Hind trochanter with groove, sometimes weak and on inner lateral surface of hind trochanter only 55

54 (53). Metasoma broad, 2.08 (1.87-2.25) x length mesosoma; hind tibia without ventro-apical pecten of short robust spines; medium sized wasp, 10.4 (9 -12) mm in length .... ***P. inaequalis*** (Turner) comb. nov.

Metasoma narrow, 2.36 (2.15-2.57) x length mesosoma; hind tibia with ventro-apical pecten of short robust spines; large wasp, 13 (11-14) mm; [14-segmented antennae in male] .... ***P. rieki*** (Crosskey) comb. nov.

55 (53). Hind trochanter with distinct groove (Appendix A5, Fig. 62); hind tarsal segments 1-2 not flattened .... ***P. whiani*** (Jennings & Austin) comb. nov.

Hind trochanter with weak groove on inner lateral surface (Fig. 8.141); hind tarsal segments 1-2 somewhat flattened (Fig. 8.181) .... ***P. taylori*** sp. nov.

8.4.2.2. Treatment of species

8.4.2.2.1. *crassipes*-species group

The *crassipes* species group is supported by the presence of a single discal cell in the fore wing and fore wing vein 1-Rs+M being fused to form Rs+M+Cu(b) (see Jennings and Austin 1994b). Two female species, *P. crassipes* (Smith) and *P. unguiculatus* (Westwood), are included in this group, as are two male species which have yet to be associated with the female species, *P. nocticolor* Kieffer and *P. pedunculatus* (Schletterer) (Jennings and Austin 1994b, Austin *et al.* 1996, 1997). The four included species were recently revised by Jennings and Austin (1994b) (see Appendix A4).

Pseudofoenus crassipes (Smith)
Pseudofoenus nocticolor Kieffer
Pseudofoenus pedunculatus (Schletterer)
Pseudofoenus unguiculatus (Westwood)

8.4.2.2.2. *fletcheri*-species group

The *fletcheri*-species group comprises 18 species supported by a single synapomorphy; the presence of sculpturing on the occipital carina. Within this group are recognised three species subgroups; the *thoracicus*-subgroup, *macronyx*-subgroup and the *infumatus*-subgroup (see Chapter 6 and Table 8.1).

8.4.2.2.2.1. *thoracicus*-subgroup

Pseudofoenus morganensis sp. nov.

(Figs. 8.8-8.11, 8.147. 8.195)

Material Examined

Holotype. ♀, "26-1-[19]65, Morgan S.A., hovering near aggregation, T.F.H. [Houston]" (SAMA).

Paratypes. **South Australia:** 2♂, same data as holotype (SAMA).

Female

Length. 15 mm.

Colour. Body generally red, flagellomeres and apex of hind tibiae dark brown, last few metasomal tergites black dorsally.

Head. Wider than long when viewed dorsally (Fig. 8.8); face rugulose medially, imbricate laterally, pubescence short; frons punctate-imbricate, pubescence short; frontal carina strong; vertex punctate-imbricate, slightly rugose near frontal carina, almost glabrous, with scattered short setae; gena imbricate, with scattered short setae; occipital carina carinate; malar space 0.03 x height eye; clypeus 1.5 x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.25 x distance between lateral ocellus and occipital carina; scape 3.57 x length pedicel; first flagellomere 1.20 x as long as scape, 1.76 x as long as second flagellomere; mandible narrow (specimens well worn at apex), with two medial teeth, basal tooth triangular.

Mesosoma. Propleuron punctate-imbricate, ventro-lateral carina present, pubescencc long laterally; lateral pronotum rugose-imbricate; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, longer and more dense ventrally, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, pubescence short; propodeum rugose, posterior margin, without median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa imbricate, strigate in coxal depression, with scattered long setae; hind trochanter without groove, imbricate, with several shallow punctures laterally, with scattered long setae (Fig. 8.9); hind femur imbricate, pubescence short; hind tibia imbricate, pubescence short, with scattered emergent setae; hind femur 4.15 x as long as wide, 0.84 x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 somewhat flattened ventrally and with ventro-apical pecten of short robust spines, segments 1-3 asymmetrical (Fig. 8.147), segment 1, 1.60 x length segment 2; segment 2, 0.56 x length segment 3; segment 3, 1.78 x length segment 4; segment 4, 0.56 x length segment 5 (Fig. 8.147); hind tarsal claw 0.56 x length segment 5 (Fig. 8.147); hind wing with 3 hamuli.

Metasoma. 2.32 x length of mesosoma; T1 imbricate, longitudinal median ridge absent (Fig. 8.10).

Male

Similar to female except: digitus 0.95 x length basiparamere; basiparameres smooth (Fig. 8.11); genitalia red except tip of basiparameres black.

Comments

Pseudofoenus morganensis is similar in appearance to *P. thoracicus* comb. nov., and the two can be separated by the characters given in the key. It is also superficially similar to *P. australis*comb. nov., but the two can be readily separated by the nature of the hind tarsal segments. *P. morganensis* has somewhat dorso-ventrally flattened segments 1-4 (Fig. 8.147), whereas in *P. australis* they are not flattened (Fig. 8.147). This species has only been collected from Morgan, South Australia (Fig. 8.195), and is named after this locality.

Pseudofoenus thoracicus (Guérin Menéville) comb. nov.

Comments

This species was recently redescribed by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

8.4.2.2.2.2. *macronyx*-subgroup

The three included species in the *macronyx*-subgroup were formerly included in *Crassifoenus* (see Appendix A3), and are hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus grossitarsis (Kieffer) comb. nov.
Pseudofoenus houstoni (Jennings and Austin) comb. nov.
Pseudofoenus macronyx (Schletterer) comb. nov.

8.4.2.2.2.3. *infumatus*-subgroup

Pseudofoenus bungeyi (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus cardaleae sp. nov.

(Figs 8.12-8.14, 8.148, 8.184)

Material Examined

Holotype. ♀, "22km N Bullfinch, 30.59S 119.06E, Western Australia, 2-3.x.1981, T.F. Houston" "Hovering near nests of bee *Nomia australica*" (WAMA).

Paratypes. **Western Australia:** 1♀, same data as holotype (WAMA); 2♀, 11km ENE Ankatell HS, 28.02S 118.51E, 4-8.ix.1981, T.F. Houston (WAMA).

Female

Length. 10.5 mm (10-11 mm).

Colour. Body generally red brown, head black except for small red patches near eye margin between antennal sockets and eye and between lateral ocelli and eye, with variable amounts of black on propleuron, mesoscutum, axillae, tegulae of hind wings and ventral mesepisternum, with variable amounts of dark brown on ventral metapleuron, dorsal surface of mid and hind trochanters and apical flagellomeres.

Head. Wider than long when viewed dorsally (Fig. 8.12); face rugulose, pubescence short; frons rugulose, with a few shallow punctures near eye margin, with striae radiating from median ocellus, pubescence short, denser near antennal scrobes; frontal carina present; vertex rugulose medially to rugulose-punctate laterally, with shallow groove behind lateral ocelli, not reaching past ocelli, with scattered short setae; gena smooth except for a few shallow punctures, pubescence long; occipital carina weakly carinate; malar space 0.07 (0.06-0.08) x height eye; clypeus 2.63 x as wide as high, smooth except for a few shallow punctures; distance from lateral ocellus to eye margin 0.72 (0.64-0.77) x distance between lateral ocellus and occipital carina; scape 2.40 (2.14-2.57) x length pedicel; first flagellomere 1.25 (1.17-1.37) x as long as scape, 1.46 (1.40-1.62) x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.13).

Mesosoma. Propleuron rugulose tending to smooth posteriorly, ventro-lateral carina weak, pubescence long, denser laterally; lateral pronotum rugulose; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line absent; scutellum, axillae and metanotum rugose; dorsal part of mesepisternum rugulose, with scattered short setae, separated from ventral part by carinate depression, ventral part rugulose, with median transverse carina, pubescence long; mesepimeron broad, carinate; dorsal part of metapleuron rugulose, almost glabrous, ventral part rugose, pubescence long; propodeum coarsely rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, margins glabrous; hind coxa strigate dorsally, imbricate laterally, pubescence long laterally; hind trochanter without groove, almost glabrous, with a few short setae; hind femur imbricate, pubescence short; hind tibia imbricate, with a few shallow punctures, pubescence short, with a few scattered emergent stout setae; hind femur 3.89 (3.71-4.15) x as long as wide, 0.79 (0.76-0.82) x length hind tibia; hind tibia with a weak ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of very short robust spines (Fig. 8.148), segment 1, 2.00 (1.88-2.14) x length segment 2; segment 2, 1.24 (1.15-1.50) x length segment 3; segment 3, 1.61 (1.43-1.86) x length segment 4; segment 4, 0.59 (0.54-0.64) x length segment 5; hind tarsal claw 0.52 (0.46-0.58) x length segment 5 (Fig. 8.148); hind wing with 4 hamuli.

Metasoma. 2.19 (2.03-2.27) x length of mesosoma; T1 rugulose, with a few punctures laterally, longitudinal median ridge absent (Fig. 8.14).

Male

Unknown.

Comments

Pseudofoenus cardaleae sp. nov. can be separated from other *Pseudofoenus* by the ventro-apical pecten of spines on hind tarsal segments one to four being extremely short (Fig. 8.148). It can be further distinguished by the characters given in the key. Specimens from Bullfinch, Western Australia were observed around a nest of *Ctenocolletes ordensis* Michener (Stenotritidae) (Houston 1984) and specimens from Ankatell Homestead, Western Australia were observed hovering near a nest of *Nomia australica* Smith (Halictidae). This species has been collected from south-west Western Australia (Fig. 8.184), and is named after Dr Josephine Cardale, Australian National Insect Collection.

Pseudofoenus deletangi (Schletterer) comb. nov.

Comments

This species was recently redescribed by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus douglasi sp. nov.

(Figs 8.15-8.16. 8.149, 8.183)

Material Examined

Holotype. ♀, "Great Northern Highway, 13km N Kalbarri Reserve, Western Australia, 11.ix.1977, A.M. & M.J. Douglas" (WAMA).

Paratypes. **Western Australia:** 2♀, same data as holotype (WAMA).

Female

Length. 9 mm.

Colour. Body generally red brown, face, frons, vertex, gena, clypeus, scape, pedicel and propleuron black, with variable amounts of black on mesoscutum, scutellum, axillae, metanotum, mesepisternum, mesepimeron, metapleuron, propodeum and metasomal T1, and antennal flagellomeres, coxae, trochanters, fore and mid femora, and metasoma dark brown.

Head. Wider than long when viewed dorsally (Fig. 8.15); face rugulose medially, punctulate laterally, pubescence short; frons rugose-punctate, radiating striae from median ocellus, with scattered short setae, denser near antennal scrobes; frontal carina present; vertex rugose-punctate tending to rugulose near occipital carina, radiating striae from lateral ocelli, with scattered short setae; gena imbricate, pubescence short; occipital carina carinate medially, otherwise smooth; malar space 0.09 (0.08-0.10) x height eye; clypeus 1.72 (1.40-2.00) x as wide as high, punctulate; distance from lateral ocellus to eye margin 0.63 (0.59-0.67) x distance between lateral ocellus and occipital carina; scape 2.56 (2.45-2.73) x length pedicel; first flagellomere 1.39 (1.33-1.44) x as long as scape, 1.73 (1.67-1.77) x as long as second flagellomere; mandible with two prominent medial teeth, basal tooth triangular.

Mesosoma. Propleuron rugulose, ventro-lateral carina weak, pubescence long laterally; lateral pronotum rugulose in dorsal part, ventral part imbricate; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugulose, with short pubescence; propodeum coarsely rugose, posterior margin, median longitudinal carina posteriorly, reaching about one third height of propodeum; propodeal spiracle elongate, fringed with long setae; hind coxa rugulose to strigate in coxal depression, imbricate laterally, pubescence short; hind trochanter without groove, imbricate, with scattered minute punctures, these associated with short setae; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered stout emergent setae; hind femur 4.16 (4.12-4.25) x as long as wide, 0.83 (0.80-0.89) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.19 (2.08-2.36) x length segment 2; segment 2, 1.30 (1.22-1.44) x length segment 3; segment 3, 1.53 (1.50-1.66) x length segment 4; segment 4, 0.46 (0.42-0.50) x length segment 5 (Fig. 8.149); hind tarsal claw 0.65 (0.62-0.67) x length segment 5 (Fig. 8.149); hind wing with 3 hamuli.

Metasoma. 2.42 (2.20-2.56) x length of mesosoma; T1 rugulose dorsally to imbricate laterally, longitudinal median ridge present (Fig. 8.16).

Male

Unknown.

Comments

Pseudofoenus douglasi is superficially similar to *E. melanopleurus* Crosskey *incertae sedis* but the gena is not bulbous behind the eyes (Fig. 8.15) as is the case with the latter species (Fig. 8.144). Also, *E. melanopleurus* has larger hind tarsal claws, 1.0 x length hind tarsal segment 5 (Fig. 8.182), whereas in *P. douglasi* they are 0.65 (0.62-0.67) x length hind tarsal segment 5 (Fig. 8.149). This species has only been collected from the type locality, 13km N Kalbarri Reserve, Western Australia (Fig. 8.183), and is named after the collectors, Athol and Marion Douglas.

Pseudofoenus ericae sp. nov.

(Figs 8.17-8.19, 8.150, 8.183)

Material Examined

Holotype. ♀, "25 [40km] S Nannup, Western Australia, 12.xi.1958. E.F. Riek" (ANIC).

Paratypes. **Western Australia:** 5♀, same data as holotype (ANIC).

Female

Length. 10.6 mm (10-11 mm).

Colour. Body generally red, with variable amounts of black around ocelli and on propleuron and mesoscutum.

Head. Wider than long when viewed dorsally (Fig. 8.17); face punctulate, with scattered short setae; frons coarsely rugose, with scattered long setae, denser near antennal scrobes; frontal carina strong; vertex rugose, with scattered long setae; gena imbricate, with a few shallow punctures near eye margin, pubescence long; occipital carina carinate (Fig. 8.17); malar space 0.19 (0.17-0.20) x height eye; clypeus 1.27 (1.20-1.37) x as wide as high, imbricate, with a few shallow punctures, anterior margin convex; distance from lateral ocellus to eye margin 0.70 (0.61-0.80) x distance between lateral ocellus and occipital carina; scape 2.87 (2.67-3.08) x length pedicel; first flagellomere 1.25 (1.20-1.30) x as long as scape, 2.05 (1.92-2.17) x as long as second flagellomere; mandible with two prominent medial teeth.

Mesosoma. Propleuron rugulose, ventro-lateral carina present, pubescence long, denser laterally; lateral pronotum rugulose in dorsal part, ventral part imbricate; medial and lateral lobes of mesoscutum coarsely rugose, with scattered short setae, medial line absent; scutellum, axillae and metanotum coarsely rugose; mesepisternum with long pubescence, denser ventrally, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with long, denser ventrally pubescence, dorsal part rugulose, ventral part rugose; propodeum areolate, with median longitudinal carina; propodeal spiracle elongate, fringed with long setae; hind coxa strigate dorsally, rugulose-imbricate laterally, pubescence long laterally; hind trochanter with indistinct groove on inner lateral surface, imbricate, pubescence long (Fig. 8.18); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent stout setae; hind femur 4.62 (4.32-4.83) x as long as wide, 0.80 (0.75-0.85) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.41 (2.13-2.73) x length segment 2; segment 2, 1.13 (1.00-1.36) x length segment 3; segment 3, 1.60 (1.57-1.71) x length segment 4; segment 4, 0.46 (0.44-0.53) x length segment 5 (Fig. 8.150); hind tarsal claw 0.65 (0.63-0.69) x length segment 5 (Fig. 8.150); hind wing with 3 hamuli.

Metasoma. 2.41 (2.22-2.58) x length of mesosoma; T1 rugose, almost striate dorsally, imbricate laterally, longitudinal median ridge present (Fig. 8.19).

Male

Unknown.

Comments

The anterior clypeal margin in this species is convex, a character shared by *P. coorowensis* sp. nov. and *P. crosskeyi* sp. nov. *Pseudofoenus ericae*, however, has a strong frontal carina (Fig. 8.17), which is lacking in the other two species. It is known only from the type locality, south of Nannup, Western Australia (Fig. 8.183), and is named in memory of my mother, Erica Jennings, late of Waikerie, South Australia.

Pseudofoenus feckneri sp. nov.

(Figs 8.20-8.22, 8.151, 8.184)

Material Examined

Holotype. ♀, "Rottnest Island, 37-3375" [1937, L. Glauert] (WAMA).

Paratypes. **Western Australia:** 19♀, 2♂, Rottnest Island, 1937, [L. Glauert] (WAMA, WARI); 6♀, 5♂, Broomehill, 1944, [L. Glauert] (WAMA); 2♀, 19km SSW Grass Patch, 33.23S 121.40E, 19-20.ix.1981, I.D. Naumann & J.C. Cardale (ANIC); 2♀, 23km E by N Dongara, 29.12S 115.10E, 30.ix.1981, I.D. Naumann & J.C. Cardale (ANIC).

Other specimens examined. **New South Wales:** 1♀, Lane Cove, 12.ix.1943, no collector (AMSA); 1♀, Colo R., 25km N Windsor, 9.x.1974, Z. Liepa (ANIC). **South Australia:** 2♀, Pelican Point, 16.ix.1973, T.F. Houston (SAMA); 1♀, 11km E Narrung, 16.ix.1973, T.F. Houston (WAMA); 1♀, 20-25km W Vokes Hill, 22.viii.1980, J. Forrest (SAMA); 1♀, 60-120km S Vokes Hill Corner, 28.viii.1980, J. Forrest (SAMA); 1♀, Mt Lofty, no date, A.M. Lea (SAMA). **Victoria:** 2♀, L. Merton, 15.xii.1946, R.T. (MVMA). **Western Australia:** 2♀, Darlington, 137m, 5.ix.1962, E.S. Ross & D.Q. Cavagnaro (CASC); 1♀, 16km W Euela, 13.ix.1964, G.L. Bush (MCZC); 1♀, 8km E Waikiki, S Fremantle, 1.x.1970, D.H. Colless (ANIC); 1♂, Stirling NP 12.x.1970, D.H. Colless (ANIC); 3♀, 2♂, Drummonds Cove nr Geraldton, ix.1972, N. McFarland (ANIC); 1♀, East Bunjil, 3.ix.1975, R.P. McMillan (WAMA); 3♀, 4♂, W Wannamai, 8.x.1977, A.M. & M.J. Douglas (WAMA); 1♂, Wannamai, 23.ix.1976, S.M. Postmus (WAMA); 1♀, 50km NW Yuna, 6.ix.1981, G.A. Holloway (AMSA); 1♀, 12km E Carrabin, 31.23S 118.48E, 9.x.1981, I.D. Naumann & J.C. Cardale (ANIC); 1♀, 13km S Wannoo, 26.45S 114.37E, 1.viii.1985, T.F. Houston (WAMA).

Female

Length. 9.4 mm (8-11 mm).

Colour. Body generally red brown, with variable amounts of black on face, frons, vertex gena, clypeus, propleuron, pronotum, mesoscutum, scutellum, axillae, metanotum, mesepisternum, mesepimeron, metapleuron, propodeum, coxae and trochanters, and flagellomeres and metasoma brown.

Head. Wider than long when viewed dorsally (Fig. 8.20); face imbricate, pubescence short; frons rugulose medially, imbricate near eyes, with radiating striae from median ocellus, with scattered short setae or with long setae, denser near antennal scrobes; frontal carina present; vertex rugulose-imbricate, with radiating striae from lateral ocelli, with scattered short setae or with long setae; gena imbricate, pubescence short or with long setae; occipital carina carinate (Fig. 8.20); malar space 0.07 (0.06-0.09) x height eye; clypeus 1.92 (1.70-2.20) x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.78 (0.71-0.86) x distance between lateral ocellus and occipital carina; scape 2.85 (2.50-3.30) x length pedicel; first flagellomere 3.00 (2.75-3.60) x as long as scape, 1.87 (1.50-2.30) x as long as second flagellomere; mandible with two prominent medial teeth.

Mesosoma. Propleuron imbricate dorso-anteriorly to punctulate-imbricate dorso-posteriorly, rugulose laterally, ventro-lateral carina present, pubescence long laterally; lateral pronotum rugulose-imbricate; medial and lateral lobes of mesoscutum coarsely rugose-punctate, with scattered short setae or with long setae, medial line present; scutellum, axillae and metanotum coarsely rugose-punctate; mesepisternum with short pubescence, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, pubescence short; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa rugulose dorsally, strigate in coxal depression, pubescence long laterally; hind trochanter without groove, imbricate, with scattered short setae (Fig. 8.21); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent stout setae; hind femur 3.33 (3.08-3.52) x as long as wide, 0.83 (0.78-0.87) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines, or with several such spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.89 (2.40-3.43) x length segment 2; segment 2, 1.44 (1.29-1.67) x length segment 3; segment 3, 1.33 (1.17-1.50) x length segment 4; segment 4, 0.28 (0.22-0.33) x length segment 5 (Fig. 8.151); hind tarsal claw 1.00 (0.80-1.30) x length segment 5 (hind claw sometimes worn) (Fig. 8.151); hind wing with 2-4 hamuli (87% of specimens with 3/3 and 13% with number variable between each wing).

Metasoma. 2.34 (2.13-2.57) x length of mesosoma; T1 punctate-imbricate, almost smooth medially, longitudinal median ridge absent (Fig. 8.22).

Male

Similar to female except: hind trochanter without groove, or with a weak groove on inner lateral surface (about 30% of specimens); hind segment 1, 2.62 (2.33-2.80) x length segment 2; segment 2, 1.33 (1.13-1.50) x length segment 3; segment 3, 1.15 (1.00-1.33) x length segment 4; segment 4, 0.40 (0.32-0.47) x length segment 5; hind tarsal claw 0.66 (0.63-0.67) x length segment 5; digitus 0.9 x length basiparamere; basiparameres imbricate.

Variation

Several specimens have long setae on the frons, vertex and gena; several have a number of short robust spines ventro-apically on the hind tibia; about 30% of males have a weak groove on the inner lateral surface of the hind trochanter.

Comments

The male of this species has much smaller hind claws than those found in the female. The female is superficially similar to that of *P. inaequalis* comb. nov. However, they differ in sculpturing patterns on the face, frons, vertex and occipital carina, and the ratio of the length of flagellomere 1 to the length of the scape is much smaller in *P. inaequalis* comb. nov. than in *P. feckneri*.

Pseudofoenus feckneri is widespread across the southern Australian mainland (Fig. 8.184), whereas *P. inaequalis* comb. nov. is confined to south-western Western Australia (Fig. 8.192), where the species are sympatric.

Based on observations and specimens from Jamberoo, Illawarra Range, NSW, Parrott (1955) indicated that *Eufoenus inaequalis* was parasitic on the larvae of *Cladocerapis persooniae* Rayment (Colletidae). However, these specimens have not been located and, this species is not found in NSW (Fig. 8.192). As indicated below, these specimens are probably *P. feckneri*, although this host relationship cannot be confirmed. *Pseudofoenus feckneri* has also been observed near nests of *Notocolletes* sp. (Colletidae) (WAMA).

This species has been collected on dandelion (*Taraxacum officinale* Weber) (Asteraceae) in South Australia (SAMA) and flowers of *Thryptomene* sp. (Myrtaceae) and white myrtle (*Hypocalymma angustifolium* (Endl.) Schauer (Myrtaceae)) in Western Australia (WAMA). It is named after Terry Feckner, Laboratory Manager, Department of Applied and Molecular Ecology, Waite Campus, The University of Adelaide.

Pseudofoenus fletcheri (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus goonooensis (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus infumatus (Schletterer) comb. nov.

Comments

This species was recently redescribed by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus microcephalus (Crosskey) comb. nov.

(Figs 8.23-8.26, 8.152, 8.185)

Hyptiogaster microcephala Crosskey, 1953: 379.

Material Examined

Holotype. ♀, "Dongarra, 245 miles north of Perth, 20-25.ix.1935, R.E. Turner" (BMNH, No. 3 c. 325). Tip of metasoma damaged and glued to point. Left antenna and right antennal segments 6-14 missing.

Female

Length. 8 mm.

Colour. Body generally black, with variable amounts of red on anterior clypeus, scutellum, pronotum and mesopleuron, propodeum and ventral surfaces of hind leg red, posterior margins of metasoma yellow brown.

Head. Wider than long when viewed dorsally (Fig. 8.23); face rugulose-punctate, pubescence short; frons rugose-punctate, striate near ocelli, with scattered short setae, denser near antennal scrobes; frontal carina weak; vertex rugose, striate near ocelli, with scattered short setae; gena imbricate, pubescence long; occipital carina weakly carinate (Fig. 8.23); malar space 0.06 x height eye; clypeus 1.67 x as wide as high, punctulate, pubescence short; distance from lateral ocellus to eye margin 1.0 x distance between lateral ocellus and occipital carina; scape 1.8 x length pedicel; first flagellomere 1.5 x as long as scape, 1.7 x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.24).

Mesosoma. Propleuron rugulose, ventro-lateral carina present, pubescence long; lateral pronotum rugulose; medial and lateral lobes of mesoscutum rugose with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with long pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugulose dorsally, smooth ventrally, with median transverse carina; mesepimeron broad, carinate; metapleuron rugulose, pubescence long; propodeum rugose, without median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa strigate medially, rugulose laterally, pubescence long laterally; hind trochanter without groove, imbricate, with scattered long setae (Fig. 8.25); hind femur imbricate, pubescence short hind tibia punctate-imbricate, pubescence short, with scattered stout emergent setae; hind femur 4.8 x as long as wide, equal in length to hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-3 with ventro-apical pecten of short robust spines, segment 1, 2.0 x length segment 2; segment 2, 1.1 x length segment 3; segment 3, 1.4 x length segment 4; segment 4, 0.8 x length segment 5 (Fig. 8.152); hind tarsal claw 0.8 x length segment 5 (Fig. 8.152); hind wing with 3 hamuli .

Metasoma. 2.7 x length of mesosoma; T1 imbricate-rugulose, longitudinal median ridge absent (Fig. 8.26).

Comments

Crosskey (1962) overlooked *microcephalus* in his revision of gasteruptiid wasps. *Pseudofoenus microcephalus* comb. nov. lacks a groove on the hind trochanter and the female does not have an exserted ovipositor, and therefore clearly does not belong in *Hyptiogaster*. This species is similar in appearance to *P. feckneri* sp. nov., but the latter has larger hind claws (Fig. 8.151) and differs in the sculpturing pattern of metasomal T1 (Fig. 8.22). This species has only been collected from south-west Western Australia (Fig. 8.185).

Pseudofoenus minimus (Turner) comb. nov.

(Figs 8.27-8.29, 8.153, 8.185)

Hyptiogaster minima Turner, 1918a: 412. - Hedicke, 1939: 49; Crosskey, 1953a: 381.

Eufoenus minimus Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Mt. Wellington, Tasmania, 15.i.1913, R.E. Turner, taken at 2,300 ft." (BMNH, No. 3 a. 144).

Other specimens examined. **Australian Capital Territory:** 1♂, Cotter River, 5.ii.1947, E.F. Riek (ANIC); 1♂, Blundells, 30.iii.1948, E.F. Riek (ANIC). **Tasmania:** 1♀, Hobart, 4.i.1951, E.F. Riek (ANIC).

Female

Length. 6.0 mm.

Colour. Body generally red brown, antennae dark brown, posterior margins of metasomal segments 2-7 white, giving a banded appearance.

Head. Wider than long when viewed dorsally (Fig. 8.27); face punctulate-imbricate, pubescence short; frons punctulate-imbricate, pubescence short; frontal carina absent; vertex imbricate, with scattered punctures and several striations behind lateral ocelli, with scattered short setae; gena imbricate, with scattered long setae; occipital carina weakly carinate medially; malar space 0.2 x height eye; clypeus 2.08 (2.00-2.22) x as wide as high, punctulate-imbricate, pubescence short; distance from lateral ocellus to eye margin 0.9 x distance between lateral ocellus and occipital carina; scape 2.2 x length pedicel; first flagellomere 1.0 x as long as scape, 1.4 x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.28).

Mesosoma. Propleuron punctate-imbricate, weak ventro-lateral carina present, pubescence long; lateral pronotum punctate-imbricate, pubescence long; medial lobe of mesoscutum rugose-punctate, lateral lobes tending to punctate posteriorly, with scattered long setae, medial line absent; scutellum, axillae and metanotum punctate; mesepisternum with long pubescence, dorsal part imbricate, separated from ventral part by carinate depression, ventral part punctate-imbricate, with median transverse carina; mesepimeron broad, carinate; metapleuron rugulose-punctate, pubescence long; propodeum rugose, short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa imbricate pubescence short; hind trochanter without groove, imbricate, pubescence short; hind femur imbricate, pubescence short and with few emergent setae; hind tibia imbricate, pubescence short and with few emergent setae; hind femur 4.1 x as long as wide, 0.9 x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-3 with ventro-apical pecten of short robust spines, segment 1, 2.6 x length segment 2; segment 2, 1.1 x length segment 3; segment 3, 1.2 x length segment 4; segment 4, 0.6 x length segment 5 (Fig. 8.153); hind tarsal claw 0.65 x length segment 5 (Fig. 8.153); hind wing with 3 hamuli.

Metasoma. 2.0 x length of mesosoma; T1 imbricate (some underlying rugosity), longitudinal median ridge absent (Fig. 8.29).

Male

Similar to female except: mean length 7.0 mm; variable amounts of black on propleuron, lateral pronotum, mesoscutum and propodeum; digitus 0.9 x length basiparamere: basiparameres smooth.

Comments

Pseudofoenus minimus comb. nov. is one of several species with a large malar space. It can be distinguished from these by the characters given in the key. Nothing is know about the biology of this species and it has only been collected from a few sites in the Australian Capital Territory and Tasmania (Fig. 8.185).

Pseudofoenus perenjorii (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus wubinensis (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

8.4.2.2.3. Species not assigned to species groups

The following 35 species (see Table 8.2) are not placed into species groups. Undoubtedly as further species are described, other affinities are likely to emerge that would enable this large group to be further divided into additional species groups.

Pseudofoenus antennalis (Schletterer) comb. nov.

(Figs 8.30-8.34, 8.154, 8.186)

Gasteruption antennale Schletterer, 1889: 386.

Hyptiogaster antennalis Kieffer, 1903: 9. - Kieffer, 1904: 16; Kieffer, 1912: 195, 202; Hedicke, 1939: 47; Crosskey, 1953a: 378.

Eufoenus antennalis Szépligeti, 1903: 365. - Crosskey, 1962: 398.

Material Examined

Holotype. ♂ "Australia" (ZMHB).

Other specimens examined. **Australian Capital Territory:** 1♀, 19.ix.1951, Jervis Bay, T.G. Campbell (ANIC). **New South Wales:** 1♀, Gordon, ix.1955, D.F. Waterhouse (ANIC). **Victoria:** 1♀, Grampians, x.1928, F.E. Wilson (MVMA); 2♂, Frankston, 28.9.?1918, C.E. Cole (MVMA); 1♀, 12.5km NNE Mitre, 36.37S 141.49E, 22.x.1983, I.D. Naumann & J.C. Cardale (ANIC). **Western Australia:** 2♂, Carnac Island, 19.ix.1934, K.R. Norris (ANIC); 1♂, Hovea, 14.ix.1936, K.R. Norris (ANIC); 1♂, Dryandra, 11.x.1965, A. Douglas (WAMA); 1♀, 4♂, Wannamal, 23.ix.1976, S.M. Postmus (WAMA); 1♂, Torndirrup, 35.06S 117.54E, 7.x.1981, I.D. Naumann & J.C. Cardale (ANIC). **Other:** 1♂, no data (ANIC).

Female

Length. 11 mm (10-11 mm).

Colour. Body generally red brown, face, frons, vertex and gena black, with variable amounts of black on clypeus, propleuron, mesoscutum, scutellum, axillae, mesepimeron, metapleuron and propodeum.

Head. Wider than long when viewed dorsally (Fig. 8.30); face rugose, pubescence long; frons rugose and with striations radiating from median ocellus, with scattered long setae, denser near antennal scrobes; frontal carina weak (Fig. 8.30); vertex rugose and with striations radiating from lateral ocelli, with scattered long setae; gena punctulate, with scattered long setae; occipital carina smooth, narrow; malar space 0.15 x height eye; clypeus 1.43 (1.41-1.47) x as wide as high, punctulate; distance from lateral ocellus to eye margin 0.77 x distance between lateral ocellus and occipital carina; scape 2.9 (2.7-3.0) x length pedicel; first flagellomere 1.23 (1.21-1.26) x as long as scape, 1.80 (1.62-1.91) x as long as second flagellomere; mandible with two medial teeth (Fig. 8.31).

Mesosoma. Propleuron rugulose, ventro-lateral carina present, pubescence long; lateral pronotum rugulose; medial and lateral lobes of mesoscutum rugose, with scattered long setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with long pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with long pubescence, dorsal part strigate, ventral part rugose; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa strigate, pubescence long laterally; hind trochanter imbricate, with weak groove on inner lateral surface (Figs 8.32-33), pubescence short; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent setae; hind femur 4.24

(3.83-4.65) x as long as wide, 0.86 (0.85-0.87) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.8 (2.7-2.9) x length segment 2; segment 2, 1.1 (1.0-1.2) x length segment 3; segment 3, 1.4 x length segment 4; segment 4, 0.28 (0.25-0.30) x length segment 5 (Fig. 8.154); hind tarsal claw 1.17 (1.10-1.25) x length segment 5 (Fig. 8.154); hind wing with 3-4 hamuli (one specimen with 3/3, one with 4/4 and two with number variable between each wing).

Metasoma. 2.51 (2.23-2.80) x length mesosoma; T1 rugose-imbricate dorsally, sometimes smoother medially, longitudinal median ridge absent (Fig. 8.34).

Male

Similar to female except: length 9.5 mm (9-10 mm); hind tarsal segment 1, 1.91 (1.86-2.00) x length segment 2; segment 2, 1.21 (1.10-1.25) x length segment 3; segment 3, 1.6 x length segment 4; segment 4, 0.4 x length segment 5; hind tarsal claw 0.6 x length segment 5; T1 imbricate, with slight rugosity laterally, weak longitudinal ridge present; digitus 0.8 x length basiparamere; basiparameres smooth.

Comments

The female of *P. antennalis* comb. nov. has long claws (Fig. 8.154), whereas the male has much shorter claws. They also differ in hind tarsal segment lengths, males tending to be smaller.

Crosskey (1953a) indicated that the frontal carina was absent in this species. However, all specimens observed have a weak frontal carina (Fig. 8.34). *Pseudofoenus antennalis* is superficially similar to *P. rieki* comb. nov., *P. morganensis* sp. nov., and *P. australis* comb. nov., but these three species have a strong frontal carina. Other characters used to separate these species can be found in the key.

Pseudofoenus antennalis has been collected from the southern Australian mainland on both sides of the continent, but not from South Australia (Fig. 8.186).

Pseudofoenus australis (Westwood) comb. nov.

(Figs 8.35-8.39, 8.155, 8.186)

Foenus australis Westwood, 1835: 51. - Westwood, 1843: 259.

Gasteruption australe Schletterer, 1885: 303. - Schletterer, 1889: 459.

Hyptiogaster australis Kieffer, 1903: 94. - Kieffer, 1904: 16; Kieffer, 1912: 195; Hedicke, 1939: 47; Crosskey, 1953a: 370; Crosskey, 1956: 124.

Gasteruption trianguliferum Kieffer, 1911a: 195.

Trigonofoenus triangulifer Kieffer, 1911a: 177. - Kieffer, 1912: 199; Hedicke, 1939: 42; Crosskey, 1953: 370 (syn. *H. australis*)

Eufoenus australis Crosskey, 1962: 398.

Material Examined

Holotype. *australis* : ♀, "Australia" (OXUM). *triangulifer*: ♀, "South Australia" (BMNH, No. 3 a. 163)

Other specimens examined. **Australian Capital Territory:** 1♀, Cotter, 30.i.1948, E.F. Riek (ANIC); 1♀, Bendora, 10.ii.1948, E.F. Riek (ANIC); 1♀, 1♀, Mt. Franklin, 24.i.1950, E.F. Riek (ANIC); 1♀, Bendora, 13.ii.1950, E.F. Riek (ANIC); 1♀, 1♀, Gingera, 31.1.1952, E.F. Riek (ANIC); 4♀, Bendora, 5.ii.1952, E.F. Riek (ANIC, BMNH); 1♀, Mt. Gingera, 4.ii.1953, I.F.B. Common (BMNH); 2♀, Corin Dam, 18.i.1970, H. Evans & R.W. Matthews (MCZC); **New South Wales:** 1♀, Lane Cove, 3.i.1944, no collector (AMSA); 1♀, Blackheath, 24-27.i.1948, R.T.M.P. & A.N.B. (MVMA); 1♀, Kiandra, 23.ii.1952, B. Given (ANIC); 2♀, Kosciusko, 28.ii.1952, B. Given (ANIC, BMNH); 1♀, Huonbrook, nr Mullumbimby, 4.xii.1961, McAlpine & Lossin (AMSA); 1♀, Wilsons Valley, 16.ii.1963, D.K. McAlpine (AMSA); 1♀, 8km S Mendooran, 12.viii.1973, G. Daniels (AMSA); 1♀, Mooney Mooney Creek, nr Gosford, 6.xii.1975, G. Daniels (AMSA); 1♀, Carrington Falls, 20.i.1979, G. Daniels (AMSA); 1♀, 1♀, Clarence, nr Lithgow, 18.i.1990, D.K. McAlpine, B. Day & J. Martin (AMSA); 2♀, no data label (MAMU); 1♀, Blue Mountains, no other data (MAMU). **Queensland:** 1♀, Meteor Downs, nr Springsure, 18.xi-3.xii.1930, I.M. Mackerras (ANIC). **Victoria:** 2♀, 1♂, Glen Wills, 22.ii.1952, AB [Burns]

(MVMA); 1♀, Mt Buffalo NP, 16.i.1966, T. Weir (UQBA); 1♀, no data label (MVMA). **Western Australia:** 1♀, Deep Dene, Karridale, 8.xi.1963, L.M. O'Halloran (ANIC); 1♀, 10km ESE Meedo HS, 25.40S 114.37E, 23-26.viii.1980, C.A. Howard & T.F Houston (WAMA); 1♂, Yarriigil 4P Catchment via Dwellingup, 11-18.xii.1980, A. Postle (QPIM); 1♂, 50km E Mullewa, 3.ix.1981, G.A. Holloway (AMSA); 1♂, 13km S Wannoo, 26.49S, 114.37E, 21-23.viii.1985, T.F. Houston (WAMA).

Female

Length. 13.5 mm (12-15 mm).

Colour. Body generally red brown, with variable amounts of black on face, frons, vertex, propleuron, mesoscutum, axillae, propodeum and T1, antennae dark brown except inner surface of scape red, dorsal surface of coxae, trochanters, femora, tibiae and metasoma with variable amounts of dark brown.

Head. Wider than long when viewed dorsally (Fig. 8.35); face imbricate, pubescence short; frons rugulose-imbricate medially, imbricate laterally, with scattered short setae, denser near antennal scrobes; frontal carina strong, reaching to median ocellus; vertex imbricate, with shallow lateral groove behind ocelli, not reaching eyes, a few shallow punctures near groove, with scattered short setae; gena imbricate, pubescence short; occipital carina smooth; malar space 0.055 (0.05-0.06) x height eye; clypeus 1.92 (1.67-2.10) x as wide as high, imbricate, with a short median carina anteriorly, pubescence short; distance from lateral ocellus to eye margin 0.6 (0.56-0.62) x distance between lateral ocellus and occipital carina; scape 2.5 (2.33-2.88) x length pedicel; first flagellomere 1.4 (1.23-1.55) x as long as scape, 1.47 (1.38-1.55) x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.36)

Mesosoma. Propleuron rugulose-imbricate, ventro-lateral carina weak, pubescence long; lateral pronotum imbricate; medial and lateral lobes of mesoscutum rugose-strigate, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, denser ventrally, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, with short pubescence, denser ventrally;

propodeum rugose, short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa imbricate, pubescence long laterally; hind trochanter imbricate, with scattered short setae, a weak ill-defined groove may be present on dorsal and inner lateral surface one or both trochanters, on inner surface only, or absent (Fig. 8.37); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with stouter emergent setae; hind femur 3.84 (3.35-4.00) x as long as wide, 0.76 (0.63-0.82) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.78 (2.43-3.33) x length segment 2; segment 2, 1.32 (1.20-1.50) x length segment 3; segment 3, 1.46 (1.29-1.57) x length segment 4; segment 4, 0.5 x length segment 5 (Fig. 8.155); hind tarsal claw 0.5 x length segment 5 (Fig. 8.155); hind wing with 3-4 hamuli (only one specimen with 4 hamuli on left wing).

Metasoma. 2.6 (2.35-2.80) x length of mesosoma; T1 imbricate dorsally, with underlying rugosity, longitudinal median ridge absent (Fig. 8.38).

Male

Similar to female except: digitus 0.9 x length basiparamere; basiparameres smooth (Fig. 8.39).

Variation

Approximately 30% of female specimens have no groove on either hind trochanter, 16% have a groove on one trochanter only, and 54% have a groove on both. Males show similar variation.

Comments

The groove on the hind trochanter of some *Pseudofoenus*, as well as *Hyptiogaster* and *Gasteruption*, is generally well-defined and occurs dorsally and on both lateral surfaces of the hind trochanter. About 70% of the specimens of *P. australis* possess a weak ill-defined groove on the hind trochanter. When present, the groove varies from being a weak ill-defined groove on the inner surface only to being well defined and on both the dorsal and inner lateral surfaces of the hind trochanter. This species is similar to *P. nitidiusculus* comb. nov., but the two are readily separated as the latter species is much smaller.

Little is known about the biology of *P. australis* comb. nov. although it has been collected from the flowers of *Calytrix oldfieldii* Benth. (Myrtaceae) and *Hakea* sp. (Proteaceae) in Western Australia. This species is widely distributed on both the west and east coasts of mainland Australia (Fig. 8.186). It is also recorded from central-southern Australia - the holotype of *triangulifer* was recorded from South Australia (OXUM), but this has not been plotted because of a lack of precise locality data.

Pseudofoenus beverlyae sp. nov.

(Figs 8.40-8.42, 8.156, 8.187)

Material Examined

Holotype. ♀, "Emily Gap, 7mi [11km] E Alice Springs, N.T., 22-23.ix.1972, H. Evans & R.W. Matthews" (MCZC).

Paratypes. **Northern Territory:** 3♀, same data as holotype (MCZC, ANIC).

Female

Length. 6.5 mm (6-7 mm).

Colour. Body generally red brown, head brown black, posterior margins of metasomal segments white, giving a banded appearance.

Head. Wider than long when viewed dorsally; face smooth, pubescence short; frons smooth, pubescence short, denser near antennal scrobes; frontal carina absent; vertex smooth, with scattered short setae; gena smooth, pubescence long; occipital carina smooth; malar space 0.05 (0.045-0.067) x height eye; clypeus 1.67 (1.50-1.90) x as wide as high, smooth; distance from lateral ocellus to eye margin 0.56 (0.52-0.64) x distance between lateral ocellus and occipital carina; scape 2.50 (2.20-2.75) x length pedicel; first flagellomere 0.96 (0.85-1.05) x as long as scape, 2.0 (1.64-2.20) x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.40).

Mesosoma. Propleuron rugulose, ventro-lateral carina weak, pubescence long; lateral pronotum imbricate in dorsal part, ventral part rugulose; medial lobe of scutellum rugose-punctate, less rugose posteriorly, with scattered short setae, medial line absent; lateral lobes of mesoscutum punctate, faint rugosity anteriorly, with scattered short setae; scutellum smooth, with a few shallow punctures; axillae rugose-punctate, almost smooth; metanotum rugose; mesepisternum with scattered short setae, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugulose, with median transverse carina; mesepimeron broad, carinate; dorsal part of metapleuron rugulose, with long pubescence, ventral part rugulose, with scattered long setae; propodeum rugose, median lateral carina and median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa strigate dorsally, imbricate laterally, pubescence long laterally; hind trochanter without groove, imbricate, with a few long setae (Fig. 8.41); hind femur imbricate pubescence long; hind tibia punctate-imbricate, pubescence short, with scattered long emergent setae; hind femur 3.76 (3.3-4.1) x as long as wide, 0.89 (0.84-0.97) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 3.42 (3.30-3.64) x length segment 2; segment 2, 1.2 (1.1-1.4) x length segment 3; segment 3, 1.3 (1.2-1.4) x length segment 4; segment 4, 0.5 (0.44-0.54) x length segment 5 (Fig. 8.156); hind tarsal claw 0.7 x length segment 5 (Fig. 8.156); hind wing with 3 hamuli.

Metasoma. 1.93 (1.75-2.08) x length of mesosoma; T1 imbricate, longitudinal median ridge absent (Fig. 8.42).

Male

Unknown.

Comments

The female of *P. beverlyae* sp. nov. is superficially similar to *P. iqbali* sp. nov. They can be separated by a number of features; *P. iqbali* sp. nov. is slightly larger (5 mm in length), and there are many differences in sculpturing patterns. For example, *P. beverlyae* has a smooth head whereas in *P. iqbali* sp. nov. it is punctulate-imbricate. *P. beverlyae* is also superficially similar to *P. karamuiensis* sp. nov. and *P. nalbarraensis* sp. nov., but can be separated by the characters given in the key. It is known only from the type locality, Emily Gap, east of Alice Springs Northern Territory (Fig. 8.187), and is named after my wife, Beverly Jennings.

Pseudofoenus collessi sp. nov.

(Figs 8.43-8.46, 8.157, 8.187)

Material Examined

Holotype. ♀, "William Bay, W Denmark, W. A., 10.x.1970, D.H. Colless" (ANIC).

Paratypes. **Western Australia:** 1♀, 7♂, same data as holotype (ANIC, WARI).

Female

Length. 8 mm.

Colour. Body generally red brown, head black except for malar space and anterior margin of clypeus red, with variable amounts of black on propleuron, mesoscutum, scutellum, axillae, mesepisternum, mesepimeron, metapleuron, dark brown on antennae except for scape with red patch apically and radicle red, and dark brown on dorsal surface of coxae, trochanters, femora and metasomal tergites, posterior margins of metasomal segments pale brown, basal third of hind tarsal segments pale.

Head. Wider than long when viewed dorsally (Fig. 8.43); face punctate medially, punctulate laterally, pubescence short; frons rugose-punctate, short radial striations near median ocellus, with scattered short setae, denser near antennal scrobes; frontal carina present; vertex rugose-punctate, short radial striations near lateral ocelli, with scattered short setae; gena smooth, pubescence longer than on vertex; occipital carina smooth; malar space 0.1 x height eye; clypeus 1.67 x as wide as high, punctulate; distance from lateral ocellus to eye margin 0.67 x distance between lateral ocellus and occipital carina; scape 2.5 x length pedicel; first flagellomere 1.3 x as long as scape, 1.9 (1.8-2.0) x as long as second flagellomere; mandible with two medial teeth, the most basal of these less prominent.

Mesosoma. Propleuron rugulose, ventro-lateral carina present, pubescence long; lateral pronotum rugulose, pubescence short; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line absent; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, denser ventrally, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence dorsally, longer and denser ventrally, dorsal part rugulose, almost smooth medially, ventral part rugose; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa strigate dorsally and on inner lateral surface, imbricate on outer lateral surface, pubescence long laterally; hind trochanter with ill-defined groove on inner lateral surface (Fig. 8.44), imbricate, almost smooth, pubescence short; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered stout emergent setae; hind femur 3.6 x as long as wide, 0.8 x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.6 (2.45-2.80) x length segment 2; segment 2, 1.25 (1.10-1.38) x length segment 3; segment 3, 1.45 (1.3-1.6) x length segment 4; segment 4, 0.5 x length segment 5 (Fig. 8.157); hind tarsal claw 0.65 (0.6-0.7) x length segment 5 (Fig. 8.157); hind wing with 3 hamuli.

Metasoma. 2.25 (2.2-2.3) x length of mesosoma; T1 imbricate, longitudinal median ridge absent (Fig. 8.45).

Male

Similar to female except: length 8.5 mm (8-9 mm); hind wing with 2-4 hamuli (five specimens with 3/3, one specimen with 2/3 and one with 4/3 hamuli); metasoma 2.7 (2.5-2.9) x length mesosoma; digitus broad at base, 0.7 x length basiparamere; basiparameres smooth (Fig. 8.46).

Comments

The ill-defined groove on the inner lateral surface of the hind trochanter of this species is clearly visible only under SEM, although it appears similar to that found in *P. australis* comb. nov. and *P. patellatus* comb. nov. *Pseudofoenus collessi* sp. nov. can be distinguished from other species by the characters given in the key. This species is named after the collector Dr Donald Colless, CSIRO Division of Entomology, Canberra. It is known only from the type locality, William Bay, west of Denmark, Western Australia (Fig. 8.187).

Pseudofoenus coorowensis sp. nov.

(Figs 8.47-8.50, 8.158, 8.188)

Material Examined

Holotype. ♀, "Pinjarrega Lake Nature Res., ca 24km SW of Coorow, Western Australia, 17-18.xii.1995, T.F. Houston" (WAMA).

Paratypes. **Western Australia:** 1♂, Pinjarrega Lake Nature Res., ca 25km SW of Coorow, 25-27.xi.1995, T.F. Houston" (WAMA); 3♀, 1♂, same data as holotype (WAMA).

Female

Length. 8 mm.

Colour. Body red brown.

Head. Much wider than long when viewed dorsally (Fig. 8.47); face weakly imbricate with scattered punctures, with scattered short setae; frons weakly imbricate with scattered punctures, almost glabrous, with a few scattered short setae; frontal carina absent; vertex weakly imbricate with scattered punctures, with scattered short setae (Fig. 8.47); gena weakly imbricate with scattered punctures, with scattered long setae; occipital carina smooth; malar space 0.27 (0.26-0.30) x height eye; clypeus 1.60 (1.50-1.70) x as wide as high, smooth with scattered punctures, with scattered long setae; distance from lateral ocellus to eye margin 1.13 (1.07-1.27) x distance between lateral ocellus and occipital carina; scape 3.15 (2.88-3.43) x length pedicel; first flagellomere 0.75 (0.70-0.78) x as long as scape, 1.55 (1.45-1.64) x as long as second flagellomere; mandible with two prominent medial teeth, basal tooth triangular, very short.

Mesosoma. Propleuron imbricate, weakly rugulose anteriorly, ventro-lateral carina absent, with scattered long setae; lateral pronotum imbricate, with a few shallow punctures; medial and lateral lobes of mesoscutum smooth, with scattered shallow punctures, almost glabrous except for a few short setae, medial line present; scutellum, axillae and metanotum smooth, with scattered shallow punctures; mesepisternum with short pubescence dorsally, long ventrally, dorsal part rugulose, separated from ventral part by carinate depression, ventral part smooth, with a few shallow punctures, without median transverse carina; mesepimeron narrow, weakly carinate; metapleuron almost glabrous dorsally, with short pubescence ventrally, dorsal part smooth, ventral part strigate; propodeum rugose, almost strigate medially, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with short setae; hind coxa weakly strigate dorsally, outer lateral surface rugulose basally to smooth and with a few shallow punctures apically, pubescence long laterally; hind trochanter without groove, smooth, with a few long setae (Fig. 8.48); hind femur weakly imbricate and with a few shallow punctures, with scattered long setae; hind tibia smooth, with a few shallow punctures, with scattered long setae except inner lateral surface with short pubescence; hind femur 2.72 (2.62-2.90) x as long as wide, 0.80 (0.75-0.84) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-2 asymmetrical, segment 2 tipped with stout seta (Figs 8.49, 8.158), segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.07 (1.82-2.19) x length segment 2; segment 2, 1.58 (1.50-1.70) x length segment 3; segment 3, 1.67 x length segment 4; segment 4, 0.6 x length segment 5; hind tarsal claw 0.7 x length segment 5; hind wing with 3-4 hamuli (75% of specimens with 3/3 and 25% with number variable between each wing).

Metasoma. 2.23 (1.98-2.65) x length of mesosoma; T1 smooth, with a few shallow punctures laterally, longitudinal median ridge absent (Fig. 8.50).

Male

Similar to female except: T1 punctate-imbricate; digitus and basiparameres not visible.

Comments

Pseudofoenus coorowensis sp. nov. has asymmetrical hind tarsi (Fig. 8.158), similar to those found in *P. crosskeyi* sp. nov. (Fig. 8.160) and *P. kelleri* sp. nov. (Fig. 8.168). This species, however, differs in having a very large malar space (0.27 (0.26-0.30) x length eye).

the sculpturing patterns on the body sclerites are generally smooth, and the basal tooth on the mandibles is short. Both *P. coorowensis* and *P. crosskeyi* have a convex anterior clypeal margin, whereas in *P. kelleri* it is sinuate. Other characters used to separate the species are given in the key. *Pseudofoenus spinitarsis* comb. nov. and *P. darwini* comb. nov. also have asymmetrical hind tarsi, but in these, the hind tarsal segments 1 and 2 are tipped with a stout spine that is lacking in *P. coorowensis*. This species is named for the locality of the type series, Coorow, Western Australia (Fig. 8.188).

Pseudofoenus crassitarsis (Kieffer) comb. nov.

(Figs 8.51-8.54, 8.159, 8.188)

Hyptiogaster crassitarsis Kieffer, 1906: 271. - Kieffer, 1911a: 210; Kieffer, 1912: 198; Hedicke, 1939: 48; Crosskey, 1953a: 383.

?*Eufoenus crassitarsis* Crosskey, 1962: 398.

Material Examined

Holotype. ♂, "Subiaco, Western Australia, Sept." (ZMHB).

Other specimens examined. **Northern Territory:** 1♀, 32km SbyE Alice Springs, 23.59S 133.56E, 23.ix.1978, J.C. Cardale (ANIC); 2♀, 41km SbyE Alice Springs, 24.03S 133.59E, 4.x.1978, J.C. Cardale (ANIC). **Queensland:** 1♀, 80km S Nappamerry, 5.xi.1949, E.F. Riek (ANIC). **Western Australia:** 1♀, Nilemah Station, 80km S Denham, 8-9.xi.1969, H. Evans & R.W. Matthews (MCZC).

Female

Length. 10.8 mm (10.0-11.0 mm).

Colour. Body generally red, with variable amounts of black on frons, vertex, propodeum, fore coxae, mesoscutum and metapleuron.

Head. Wider than long when viewed dorsally (Fig. 8.51); face imbricate with a few striations medially, pubescence short; frons striate, imbricate near eye margins, with scattered short setae; frontal carina strong; vertex strigate-imbricate, with scattered short setae (Fig.

8.51); gena imbricate, pubescence short; occipital carina smooth, broad; malar space 0.05 x height eye; clypeus 1.67 (1.64-1.75) x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.57 (0.55-0.59) x distance between lateral ocellus and occipital carina; scape 3.0 (2.67-3.50) x length pedicel; first flagellomere 1.16 (1.10-1.20) x as long as scape, 2.1 (1.90-2.50) x as long as second flagellomere; mandible with two prominent medial teeth (sometimes slightly worn, indicated by dull surface) (Fig. 8.52).

Mesosoma. Propleuron imbricate, ventro-lateral carina absent, pubescence long; lateral pronotum imbricate; medial and lateral lobes of mesoscutum strigate with scattered short setae, medial line absent; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, dorsal part rugulose-imbricate, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence, dorsal part rugulose, ventral part rugose; propodeum rugose, median longitudinal carina absent; propodeal spiracle elongate, anterior margin fringed with very short setae, posterior margin glabrous; hind coxa finely strigate dorsally, pubescence short laterally; hind trochanter without groove, imbricate, with scattered short setae (Fig. 8.53); hind femur imbricate, pubescence short; hind tibia punctate-imbricate pubescence short, with stouter emergent setae; hind femur 3.12 (2.96-3.30) x as long as wide, 0.9 (0.85-1.00) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines, inner tibial spur almost same length as outer spur; hind tarsal segments 1-4 asymmetrical, with ventro-apical pecten of short robust spines, segment 1, 2.3 (2.04-2.45) x length segment 2; segment 2, 1.2 (1.1-1.5) x length segment 3; segment 3, 1.65 x length segment 4; segment 4, 0.4 x length segment 5 (Fig. 8.159); hind tarsal claw 0.95 (0.8-1.0) x length segment 5 (Fig. 8.159); hind wing with 3 hamuli.

Metasoma. 2.3 (2.15-2.42) x length of mesosoma; T1 rugose-imbricate dorsally, longitudinal median ridge absent (Fig. 8.54).

Male

Similar to female; digitus 0.9 x length basiparamere; basiparameres smooth.

Comments

Pseudofoenus crassitarsis comb. nov. was doubtfully included in *Eufoenus* by Crosskey (1962), and is here transferred to *Pseudofoenus* based on the results of the phylogenetic analyses. It has striate sculpturing of the frons (Fig. 8.51), a feature not found in any other *Pseudofoenus* spp. examined. It has been collected from several widely separated localities across central and south-western Western Australia (Fig. 8.188).

Pseudofoenus crosskeyi sp. nov.

(Figs 8.55-8.58, 8.160, 8.189)

Material Examined

Holotype. ♀, "25 [40km] S Coolgardie, 28 Oct 1958, E.F. Riek, W A " (ANIC).

Paratypes. **Western Australia:** 5♀, 4♂, same data as holotype (ANIC, WARI); 1♀, 24km W Southern Cross, 30.x.1958, E.F. Riek (ANIC); 1♀, Wongan Hills, 31.x.1958, E.F. Riek (ANIC); 4♀, 2♂, East Yuna Nature Reserve, 34km WNW Mullewa, 12-14.ix.1987, T.F. Houston (WAMA).

Female

Length. 6.9 mm (6-8 mm).

Colour. Body generally red, with variable amounts of brown black on mesoscutum and dorsally on last few metasomal segments.

Head. Wider than long when viewed dorsally (Fig. 8.55); face, frons, vertex. gena and clypeus smooth (very weakly imbricate) with a few scattered shallow punctures, almost glabrous except for a few scattered long setae; frons with shallow median groove reaching from median ocellus to about half way to antennal scrobes; frontal carina absent; occipital carina smooth, broad (Fig. 8.55); malar space 0.33 (0.31-0.34) x height eye; clypeus somewhat dome-shaped, 1.92 (1.80-2.30) x as wide as high; distance from lateral ocellus to eye margin 1.28 (1.22-1.35) x distance between lateral ocellus and occipital carina; scape 3.11 (2.65-3.91) x length pedicel; first flagellomere 0.66 (0.60-0.72) x as long as scape, 1.36 (1.29-1.55) x as long as second flagellomere; mandible with two prominent medial teeth.

Mesosoma. Propleuron rugulose, ventro-lateral carina absent, with scattered long setae; lateral pronotum, mesoscutum, scutellum, axillae and metanotum smooth (very weakly imbricate) with a few scattered shallow punctures, almost glabrous except for a few scattered long setae; medial line on mesoscutum absent; mesepisternum with scattered short setae dorsally, scattered long setae ventrally, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose dorsally to smooth ventrally, without median transverse carina; mesepimeron broad, carinate; metapleuron imbricate in dorsal part, glabrous, ventral part rugose, pubescence short; propodeum strigate medially, rugose laterally, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa smooth (very weakly imbricate) with a few scattered shallow punctures, almost glabrous except for a few scattered long setae, longer laterally; hind trochanter without a groove; hind trochanter, femur and tibia smooth (very weakly imbricate), almost glabrous except for a few scattered long setae; hind femur 2.70 (2.46-2.88) x as long as wide, 0.74 (0.70-0.80) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segment 1-2 with marked asymmetry (Fig. 8.56), segment 3 asymmetrical, but less so (Fig. 8.160), segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 1.77 (1.56-2.10) x length segment 2; segment 2, 1.65 (1.55-1.78) x length segment 3; segment 3, 1.59 (1.36-1.73) x length segment 4; segment 4, 0.63 (0.57-0.67) x length segment 5; hind tarsal claw 0.68 (0.63-0.76) x length segment 5 (Fig. 8.160); hind wing with 3-4 hamuli (58% of specimens with 3, 33% with 4 and 9% with number variable between each wing).

Metasoma. 1.94 (1.78-2.11) x length of mesosoma; T1 smooth, longitudinal median ridge absent (Fig. 8.57).

Male

Similar to female except: length 7.8 mm (7-8 mm); generally more pubescent; and darker in colour, flagellomeres, scutellum, axillae, lateral pronotum, mesepisternum, metapleuron, coxae, trochanters, femora and tibiae with variable amounts of dark brown, propleuron, face, frons, vertex, gena, clypeus, scape and pedicel with variable amounts of black; hind femur narrower, 3.61 (3.43-3.82) x as long as wide; digitus 0.9 x length basiparamere; basiparameres smooth (Fig. 8.58).

Comments

This species is similar to *P. coorowensis* sp. nov. and *P. kelleri* sp. nov. in that they all have somewhat asymmetrical hind tarsi (see comments under *P. coorowensis* sp. nov.). Both *P. crosskeyi* and *P. coorowensis* have convex anterior clypeal margins whereas in *P. kelleri* the margin is sinuate. It is also similar to *P. ericae* sp. nov. which also has a convex anterior clypeal margin, but this species has a strong frontal carina which is lacking in the other species.

Little is known of the biology of *P. crosskeyi* sp. nov. Specimens collected from the East Yuna Nature Reserve (WAMA), were all associated with *Euryglossa (Dermatonesma)* sp. (Colletidae). One female was collected from a nest of this bee whilst the remaining specimens of both sexes were collected whilst flying over the bee nests. This species is confined to south-west Western Australia (Fig. 8.189) and has been named after Dr Roger Crosskey, The Natural History Museum, London, who carried out a major revision of the hyptiogastrine wasps.

Pseudofoenus darwini (Westwood) comb. nov.

(Figs 8.7, 8.59-8.63, 8.161, 8.189)

Foenus darwinii Westwood, 1841: 537. - Westwood, 1843: 259.

Gasteruption darwinii Schletterer, 1885: 305. - Schletterer, 1889; 465; Froggatt, 1891: 716.

Hyptiogaster darwinii Kieffer, 1903: 94.

Pseudofoenus darwinii Kieffer, 1912: 205.

Hyptiogaster darwinii Turner, 1918a: 411. - Brues, 1922: 12; Hedicke, 1939: 48; Crosskey 1953a: 373; Crosskey, 1956: 125.

Eufoenus darwinii Crosskey, 1962: 398.

Material Examined

Holotype. ♂, "Australia, C. Darwin" (BMNH, No. 3 a. 142). Metasoma missing.

Other specimens examined. **Australian Capital Territory:** 1♀, Blundells, 18.ii.1931, L.F. Graham (ANIC); 1♀, Canberra, 7.xii.1953, E.F. Riek (ANIC); 1♀, Bendora, 24.ii.1959, E.F. Riek (ANIC). **New South Wales:** 3♀, 1♂, 32-39km W Batemans Bay, 23.xii.1969, H. Evans & R.W. Matthews (MCZC). **Queensland:** 2♀, Murphys Ck., nr Helidon, 25.xi.1966, J.C. Cardale (UQIC); 1♀, Eidsvold, 25.22S 151.07E, 11.x.1984, I. Naumann & J. Cardale (ANIC). **South Australia:** 1♀, Adelaide, 11.ii.1990, R. Wharton (TAMU); 2♀, Waite Institute, 20-28.iii.1990, R. Wharton (WARI); **Tasmania:** 1♀, Huon-Picton Junction, 17.ii.1967, E.F. Riek (ANIC); 2♂, Rosebery, 24.1-8.ii.no year, no collector (AEIC); 2♀, 1♂, Strahan, 8-14.iii.no year, no collector (AEIC). **Victoria:** 1♀, Growler Ck., Lind NP, 26.ii.1980, I.D. Naumann & J.C. Cardale (ANIC).

Female

Length. 5.4 mm (4.0-6.0 mm).

Colour. Body generally red brown, with variable amounts of black on face, frons, vertex, gena, clypeus, propleuron and mesoscutum, antennae, legs and dorsal surface of metasoma generally darker brown, posterior margins of metasomal segments white, giving a banded appearance.

Head. Wider than long when viewed dorsally (Fig. 8.59); face rugulose-punctate, pubescence short; frons rugulose-punctate medially to punctate-imbricate near eyes, with shallow median groove near median ocellus, pubescence short; frontal carina absent; vertex rugulose-punctate medially to punctate-imbricate near eyes, with scattered short setae; gena punctate-imbricate, pubescence short; occipital carina smooth; malar space 0.17 (0.150-0.190) x height eye; clypeus 2.22 (2.00-2.50) x as wide as high, punctate; distance from lateral ocellus to eye margin 0.78 (0.74-0.86) x distance between lateral ocellus and occipital carina; scape 2.37 (2.25-2.56) x length pedicel; first flagellomere 0.90 (0.83-0.96) x as long as scape, 1.43 (1.26-1.86) x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.60).

Mesosoma. Propleuron rugulose, ventro-lateral carina absent, pubescence short; lateral pronotum rugulose; medial and lateral lobes of mesoscutum strigate anteriorly, strigate-punctate medially, punctate posteriorly, with scattered short setae, medial line absent; scutellum, axillae and metanotum rugose-punctate, some specimens scutellum and axillae almost smooth; mesepisternum with short pubescence, dorsal part rugulose separated from ventral part by carinate depression, ventral part rugulose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugulose, with short pubescence, with scattered emergent setae ventrally; propodeum rugose (almost strigate), with median lateral carina and short median longitudinal carina posteriorly; propodeal spiracle elongate, glabrous; hind coxa imbricate, weakly strigate in coxal depression, pubescence long laterally; hind trochanter without groove, imbricate, with scattered long setae (Fig. 8.61); hind femur imbricate, with a few scattered shallow punctures, pubescence short dorsally, long ventrally; hind tibia punctate-imbricate, pubescence short, with scattered emergent setae; hind femur 3.45 (2.80-4.30) x as long as wide, 0.79 (0.70-0.86) x length hind tibia; hind tibia punctate-imbricate, pubescence short, with emergent setae, without ventro-apical pecten of short robust spines; hind tarsal segments 1-2 asymmetrical, segments 1-4 with stout latero-apical spines and ventro-apical pecten of short robust spines, segment 1, 2.5 (2.0-2.7) x length segment 2; segment 2, 1.34 (1.17-1.50) x length segment 3; segment 3, 1.44 (1.25-1.50) x length segment 4; segment 4, 0.55 (0.45-0.67) x length segment 5 (Fig. 8.161); hind tarsal claw 0.64 (0.45-0.75) x length segment 5 (claw sometimes worn) (Fig. 8.161); hind wing with 3-4 hamuli (81% of specimens with 3/3 and 19% with number variable between each wing).

Metasoma. 2.0 (1.89-2.07) x length of mesosoma; T1 smooth medially, imbricate laterally, longitudinal median ridge absent (Fig. 8.62).

Male

Similar to female except: hind tarsal segment 1 not markedly asymmetrical and segment 2 not asymmetrical, segments 1-4 without latero-apical spine; digitus 0.95 x length basiparamere; basiparameres smooth (Fig. 8.63).

Comments

The females of *P. darwini* are similar in appearance to those of *P. spinitarsis*. Both species have highly asymmetrical hind tarsal segments 1 and 2, each with a stout apical spine (Figs), and a large malar space, but they differ in that the latter is a larger wasp (mean 9 mm), has different sculpturing patterns, the scape is much longer than the pedicel, and has a narrow mesepimeron. *P. darwini* is also similar to *P. crosskeyi* sp. nov., but the latter is generally much smoother on the head, mesoscutum, etc., and lacks the pronounced spines on hind tarsal segments 1 and 2 (Fig. 8.161). It has been collected from the south-eastern part of mainland Australia and from Tasmania (Fig. 8.189).

Pseudofoenus extraneus (Turner) comb. nov.

(Figs 8.64-8.67, 8.162, 8.190)

Hyptiogaster extranea Turner, 1918b: 342

Hemifoenus extraneus Brues, 1922: 11. - Hedicke, 1939: 50; Crosskey, 1953a: 377.

Eufoenus extraneus Crosskey, 1962: 398.

Material Examined

Holotype. ♂, "Cuvu, [Viti Levu], Fiji, 17.vi.1915, R. Veitch" (BMNH, No. 3 a. 156). Metasoma missing.

Other specimens examined. **Fiji: Tavenui:** 1♀, Songgulu, 27.vi.1938, R.A. Lever (BMNH). **Viti Levu:** 1♀, Madaevatu, 1932, H.W. Simmonds (BMNH); 3♀, 1♂, Nanggaranambuluti, 3.x.1942, R.A. Lever (BMNH); 1♀, Suva, Colo-I-Suva, 7.ii.1969, J.E. Tobler (CASC); 1♀, Suva, Mt. Korobab, 17.ii.1969, J.E. Tobler (CASC); 1♀, 1♂, Korolevu, 10-15.vii.1970, T.W. Davies (CASC); 2♀, 1♂, Nandi, 20.vii.1972, J.F. McAlpine (CNCI); 1♀, 10km N Galoa, 29.viii-1.ix.1978, S. & J. Peck (CNIC); 1♀, Nadarivatu, 21-23.iv.1981, R.A. Beaver (FIJI); 1♂, Savura Ck, 8-13.ix.1981, R.A. Beaver (FIJI).

Female

Length. 7.0 mm (5.5-7.5 mm).

Colour. Body generally red brown, with some metasomal segments darker brown (older specimens appear darker generally), edges of mandibles dark brown.

Head. Wider than long when viewed dorsally (Fig. 8.64); face imbricate, pubescence long; frons strigate with lateral striations near median ocellus, pubescence short, denser near antennal scrobes; frontal carina absent; vertex with lateral striations behind ocelli (Fig. 8.64), a few shallow punctures near eyes, with scattered long setae; gena imbricate, pubescence long; occipital carina smooth; malar space 0.08 (0.06-0.09) x height eye; clypeus 1.43 (1.25-1.55) x as wide as high, smooth, pubescence long; distance from lateral ocellus to eye margin 0.7 (0.5-0.8) x distance between lateral ocellus and occipital carina; scape 2.8 (2.2-3.3) x length pedicel; first flagellomere 1.1 (1.00-1.27) x as long as scape, 1.6 (1.4-2.0) x as long as second flagellomere: mandible with two prominent medial teeth (sometimes slightly worn, indicated by dull surface), the most apical tooth more prominent (Fig. 8.65).

Mesosoma. Propleuron imbricate, ventro-lateral carina present, pubescence long; lateral pronotum imbricate in dorsal part, ventral part strigate; medial and lateral lobes of mesoscutum strigate, with scattered long setae, medial line present; scutellum rugose-strigate; axillae smooth; metanotum rugose; mesepisternum with long pubescence, dorsal part rugulose separated from ventral part by carinate depression, ventral part rugulose and with median transverse carina; mesepimeron broad, carinate; metapleuron almost glabrous, with a few short setae posteriorly, dorsal and ventral parts smooth; propodeum areolate, with median lateral carina and with a short medial longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa strigate dorsally, imbricate laterally, pubescence long laterally; hind trochanter without groove, imbricate, with scattered long setae (Fig. 8.66); hind femur imbricate, pubescence long; hind tibia punctate-imbricate, pubescence short, with emergent stout setae; hind femur 4.7 (4.2-4.9) x as long as wide, 0.9 (0.85-0.97) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments pubescent with long dark brown setae, segments 1-4 with ventro-apical pecten of short robust spines, segment 1 3.1 (2.7-3.3) x length segment 2; segment 2, 1.5 (1.2-1.8) x length segment 3;

segment 3, 1.4 (1.3-1.5) x length segment 4; segment 4, 0.45 x length segment 5 (Fig. 8.162); hind tarsal claw 0.65 x length segment 5 (Fig. 8.162); hind wing with 3-4 hamuli (77% of specimens with 3/3, 11% with 4/4 and 11% with number variable between each wing).

Metasoma. 2.0 (1.77-2.32) x length of mesosoma; T1 smooth dorsally and with a few scattered short setae, imbricate laterally, longitudinal median ridge absent (Fig. 8.67).

Male

Similar to female except; body generally less robust, length 6.6 mm (6.0-8.0 mm); antennae 14-segmented; digitus 0.9 x length basiparamere; basiparameres smooth.

Comments

Pseudofoenus extraneus is one of two known species where both the females and males have 14-segmented antennae, the other being *P. rieki* comb. nov. This feature is also not known from *Hyptiogaster* (Crosskey 1962; Jennings and Austin 1997b).

The females are similar in appearance to those of *P. ritae* comb. nov. which is endemic to New Caledonia and Vanuatu. The two species differ in a number of characters, but are most readily separated by the mandible having a single weak medial tooth in *P. ritae* (Fig. 8.129), whereas *P. extraneus* has two distinct medial mandibular teeth (Fig. 8.65). This species is endemic to Fiji (Fig. 8.190).

Pseudofoenus fallax (Schletterer) comb. nov.

Comments

This species was recently redescribed by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus ferrugineus (Crosskey) comb. nov.

(Figs 8.68-8.71, 8.163, 8.191)

Hyptiogaster ferruginea Crosskey, 1953a: 365

Eufoenus ferruginea Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Mackay, Queensland, 1907, R.E. Turner" (BMNH, No. 3 c. 323).

Paratypes. 1♂, Mackay, Queensland, 1910, R.E. Turner (BMNH); 1♀, Mackay, Queensland, 1891, G. Turner (BMNH).

Other specimens examined. **Queensland:** 4♀, 6♂, Cooper Creek, 21km N Daintree River, 29-31.xii.1972, B. Cantrell (UQBA, WARI).

Female

Length. 9 mm.

Colour. Body generally red except flagellomeres, dorsal surface of legs and metasoma dark brown.

Head. Wider than long when viewed dorsally; face rugulose medially, smooth laterally, pubescence short; frons rugulose, pubescence short, denser near antennal scrobes; frontal carina weak (Fig. 8.68); vertex smooth, with scattered punctures, with scattered short setae; gena smooth, pubescence short; occipital carina broad, smooth; malar space 0.04 x height eye; clypeus 1.43 (1.30-1.70) x as wide as high, smooth; distance from lateral ocellus to eye margin 0.60 (0.50-0.67) x distance between lateral ocellus and occipital carina; scape 2.5 (2.2-2.8) x length pedicel; first flagellomere 1.12 (1.06-1.26) x as long as scape, 1.9 (1.6-2.1) x as long as second flagellomere; mandible with two prominent medial teeth.

Mesosoma. Propleuron rugulose medially, strigate laterally, ventro-lateral carina absent, pubescence short; lateral pronotum smooth; medial and lateral lobes of mesoscutum coarsely rugose-punctate, with scattered short setae, medial line absent; scutellum coarsely rugose-punctate; axillae and metanotum rugose; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, with short pubescence; propodeum rugose, with strong lateral median carina and strong median longitudinal carina; propodeal spiracle elongate, fringed with long setae; hind coxa rugulose dorsally except coxal depression smooth, imbricate laterally, pubescence long laterally; hind trochanter imbricate, with weak groove apically on inner lateral surface (Fig. 8.69), with scattered short setae; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent stout setae; hind femur 4.1 (3.8-4.3) x as long as wide, 0.84 (0.80-0.86) x length hind tibia; hind tibia with ventro-apical pecten of very short robust spines; hind tarsal segments 1-3 with ventro-apical pecten of short robust spines, segment 1, 2.83 (2.67-3.00) x length segment 2; segment 2, 1.39 (1.33-1.50) x length segment 3; segment 3, 1.45 (1.30-1.50) x length segment 4; segment 4, 0.48 (0.45-0.50) x length segment 5 (Fig. 8.163); hind tarsal claw 0.65 (0.60-0.67) x length segment 5 (Fig. 8.163); hind wing with 3 hamuli .

Metasoma. 2.52 (2.40-2.60) x length of mesosoma; T1 smooth except for slight rugosity laterally, longitudinal median ridge absent (Fig. 8.70).

Male

Similar to female except: length 8 mm (7-9 mm); metasoma more slender; digitus 0.8 x length basiparamere; basiparameres smooth.

Comments

Pseudofoenus ferrugineus comb. nov. has a weak groove apically on the hind trochanter (Fig. 8.69) similar to that found in *P. australis* comb. nov. It is superficially similar to *P. masneri* sp. nov., but the latter is a smaller wasp, lacks the groove on the hind trochanter, and has a longer metasoma relative to the mesosoma. This species has only been collected from two localities in tropical Queensland (Fig. 8.191).

Pseudofoenus floricolus (Turner) comb. nov.

(Figs 8.72-8.76, 8.164, 8.191)

Hyptiogaster floricola Turner, 1918a: 412. - Hedicke, 1939: 48; Crosskey, 1953a: 381.

Eufoenus floricolus Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Kalamunda, Western Australia, 9-28.ii.1914, R.E. Turner". "On blossoms of *Eucalyptus calophylla* R.Br." (BMNH, No. 3 a. 152).

Paratypes. **Western Australia:** 20♀, 4♂, same data as holotype (BMNH).

Other specimens examined. **Australian Capital Territory:** 1♂, Cotter, 22.xi.1951, H.M. Cane (BMNH). **New South Wales:** 1♂, 112km N Tibooburra, 3.xi.1949, E.F. Riek (BMNH); 1♂, Cobar, 23.xi.1949, E.F. Riek (ANIC); 2♀, 1♂, 23km SEbyS Byrock, 30.50S 146.33E, 20.x.1975, J.C. Cardale (ANIC). **Northern Territory:** 5♀, 1♂, Darwin, 1942, R.C.L. Perkins (BMNH); 2♀, 1♂, N. Australia, 1942, R.C.L. Perkins (BMNH); 1♀, Katherine, 11.xi.1952, A.V. Hill (ANIC); 9♀, 2♂, 18km N Alice Springs, 625m, 28.x.1962, E.S. Ross & D.Q. Cavagnaro (CASC); 1♂, 11km S Ti-Tree Well, 500m, 28.x.1962, E.S. Ross & D.Q. Cavagnaro (CASC); 1♂, Macdonald Downs, 400m, 30.x.1962, E.S. Ross & D.Q. Cavagnaro (CASC); 2♂, 25km E Alice Springs, 22-27.ix.1972, H.E. Evans & R.W. Matthews (ANIC, MCZC); 1♂, Ayers Rock, 25.ix.1972, Evans & Matthews (MCZC); 1♀, 9km E Tennant Creek, 10.xi.1974, E.M. Exley & R.I. Storey (UQBA). **Queensland:** 1♀, Stanthorpe, 17.i.1930, no collector (UQBA); 1♀, 4♂, Collinsville, 15.ix.1950, E.F. Riek (ANIC); 1♀, Longreach, 24.x.1968, E.M. Exley (UQBA); 1♂, Paluma Range, 870m, 17.xi.1971, C.G. Roshe (BMNH); 2♀, Bald Mountain area, via Emu Vale, 27-31.i.1972, S.R. Monteith (ANIC); 1♀, Barnborough Downs via Winton, 15.xii.1973, R. Patterson (ANIC); 1♀, Rubyvale, 30.x.1977, E.M. Exley (UQBA); 1♀, Cape Hillsborough NP, 45km N Mackay, 15.x.1979, H.E. & M.A. Evans & A. Hook (UQBA); 3♀, Isaacs R., 100km NE Clermont, 20.x.1979, H.E. & M.A. Evans & A. Hook (UQBA); 1♀, Amby, 22-27.xi.1979, H.E. & M.A. Evans & A. Hook (UQBA); 1♀, Paluma, 12.v.1980, I.D. Naumann & J.C. Cardale (ANIC); 1♀, Davies Ck., 18km EbyS Mareeba, 18.v.1980, I.D. Naumann & J.C. Cardale (ANIC); 2♀, Luster Creek, 8km WbyN Mt Molloy, 21-22.v.1980, I.D. Naumann & J.C. Cardale (ANIC); 1♀, Bald Mountain area, 9.x.1980, M.A. Schneider (UQBA); 2♂, 7km SE Eidsvold, 11.x.1984, I.D. Naumann & J.C. Cardale (ANIC); 1♀, Mt. Kiangarow, Bunya Mountains NP, 4-6.xii.1985, D. Bickel & G. Cassis (ANIC); 1♂, Russet Park, Kuranda, 16.xi.1987, T.W. Davies (CASC); 1♂, Mt Moffat NP, 12.xii.1987, D.K. Yeates (UQBA); 1♀, Thylungra, 26.05S 143.26E, 4.iv.1994, G.V. Maynard & G. Davis (ANIC). **South Australia:** 1♀, Cannuwaukaninna Dune, 16km W Etadunna Homestead, 6.iii.1972, E.G. Matthews (SAMA); 1♀, 1♂, Brachina Gorge, 4-10.xi.1987, I. Naumann & J. Cardale (ANIC); 3♀, Waite Campus, Uni. of Adelaide, Glen Osmond, 27.ii-3.iii.1989, P. Dangerfield (WARI); 1♂, 5km W Auburn, 6.xii.1990, J.T. Jennings (WARI); 1♂, Roseworthy Campus, Uni. of Adelaide, Roseworthy, 31.xi.1990-6.i 1991, J.T. Jennings (WARI). **Western Australia:** 2♀, Hovea, 23.i.1934, K.R. Norris, (ANIC); 1♂, 16km SE Perth, 27.xii.1966, E.M. Exley (UQBA); 1♂, Gascoyne Exp. Sta., Carnarvon, 3-7.x.1969, H.E. Evans & R.W. Matthews (MCZC); 1♀, Kimberley R.S., 16km N Kununurra, 12-15.ix.1972, R.W. Matthews (ANIC); 1♀, 1♂, Newman, 22-25.xii.1975, E.M. Exley (ANIC); 1♀, Kalgoorlie, 1.ii.1973, E.M. Exley (UQBA); 1♀, 2♂, Darlington, iv.1976, G.H. Lowe (WAMA); 1♂, Moir's Rock, NNW Salmon Gums, 32.39S 121.25E, 3.i.1987, G. & A. Daniels (UQBA).

Female

Length. 5.5 mm (4-7 mm).

Colour. Body generally dark brown, head black and some specimens with black on mesoscutum, posterior margins of metasomal segments light brown, this giving a banded appearance, apex of femora, base and apex of tibiae and apex of first tarsal segments yellow.

Head. Wider than long when viewed dorsally (Fig. 8.72); face punctulate, slightly rugulose medially, pubescence short; frons punctulate, slightly rugulose medially, smooth near median ocellus, with scattered short setae, denser near antennal scrobes; frontal carina absent; vertex smooth, with a few small shallow punctures medially, with scattered short setae; gena smooth, pubescence short; occipital carina smooth; malar space 0.055 (0.047-0.060) x height eye; clypeus 1.59 (1.35-1.80) x as wide as high, punctulate; epistomal suture between clypeus and face absent (Fig. 8.73), although often evidenced by very faint line; distance from lateral ocellus to eye margin 0.64 (0.54-0.78) x distance between lateral ocellus and occipital carina; scape 2.42 (2.33-2.60) x length pedicel; first flagellomere 1.00 (0.96-1.20) x as long as scape.

1.74 (1.56-1.92) x as long as second flagellomere; mandible with two prominent medial teeth, basal tooth triangular (Fig. 8.73).

Mesosoma. Propleuron rugulose dorsally, punctulate laterally, ventro-lateral carina present, pubescence long; lateral pronotum punctulate; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence, dorsal part smooth medially, rugulose, almost strigate laterally, ventral part rugose, almost strigate; propodeum coarsely rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, margins glabrous; hind coxa strigate dorsally, imbricate laterally, pubescence long; hind trochanter without groove, imbricate, with scattered short setae (Fig. 8.74); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent stout setae; hind femur 3.94 (3.46-4.25) x as long as wide, 0.80 (0.74-0.85) x length hind tibia; hind tibia with weak ventro-apical pecten of short spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.73 (2.53-2.86) x length segment 2; segment 2, 1.31 (1.10-1.45) x length segment 3; segment 3, 1.46 (1.25-1.71) x length segment 4; segment 4, 0.51 (0.50-0.53) x length segment 5 (Fig. 8.164); hind tarsal claw 0.67 (0.56-0.80) x length segment 5 (Fig. 8.164); hind wing with 2-3 hamuli (3/3 hamuli except for one specimen 3/2).

Metasoma. 2.12 (1.96-2.29) x length of mesosoma; T1 smooth except for a few very small shallow punctures posteriorly, longitudinal median ridge absent (Fig. 8.75).

Male

Similar to female except: length 6.6 mm (6-8 mm); metasoma narrower towards apex, 2.70 (2.46-3.10) x length mesosoma; digitus about 0.8 x length basiparamere; basiparameres smooth (Fig. 8.76).

Variation

Some specimens of both sexes are generally darker. This colour variation may be an artefact of age and/or whether or not they were collected into alcohol. The epistomal suture between the clypeus and the face varies from being apparently absent to being represented by a faint line.

Comments

Pseudofoenus floricolus is readily separated from other *Pseudofoenus* species by the absence of the epistomal suture between the clypeus and the face (inter-antennal area) (Fig. 8.73). This species has been collected from the flowers of various Myrtaceae including *Eucalyptus calophylla* Lindley (BMNH), *E. odontocarpa* F. Muell. (UQBA) and *Melaleuca lineariifolia* Smith (UQBA), and from plants of *Wahlenbergia* sp. (Campanulaceae) (ANIC). It has a widespread distribution, having been collected from all states and territories of Australia, but is apparently absent from Victoria and Tasmania (Fig. 8.191).

Pseudofoenus inaequalis (Turner) comb. nov.

(Figs 8.77-8.79, 8.165, 8.192)

Hyptiogaster inaequalis Turner, 1918a: 410. - Hedicke, 1939: 49; Crosskey, 1953a: 371; Parrott, 1955: 68.

Eufoenus inaequalis Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Yallingup, Western Australia, xi.1913, R.E. Turner" (BMNH, No. 3 a. 153). Left antennal flagellomeres 2-14 and right 3-14 missing.

Other specimens examined. **Western Australia:** 2♀, 1♂, same data as holotype (BMNH); 5♀, Yallingup, 1945, [L. Glauert] (WAMA).

Female

Length. 10.4 mm (9-12 mm).

Colour. Body generally orange red, with variable amounts of black around ocelli, and on frons, propleuron, mesoscutum and tegulae, and with variable amounts of dark brown on trochanters.

Head. Wider than long when viewed dorsally (Fig. 8.77); face imbricate, pubescence short; frons imbricate, slightly rugulose medially, with scattered short setae, denser near antennal scrobes; frontal carina distinct; vertex imbricate, with a few shallow punctures between lateral ocelli and eyes, with scattered short setae; gena imbricate, pubescence short; occipital carina smooth; malar space 0.07 (0.07-0.08) x height eye; clypeus 1.72 (1.50-1.90) x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.67 (0.59-0.76) x distance between lateral ocellus and occipital carina; scape 2.82 (2.43-3.00) x length pedicel; first flagellomere 1.45 (1.41-1.47) x as long as scape, 1.81 (1.57-2.00) x as long as second flagellomere; mandible with two prominent medial teeth.

Mesosoma. Propleuron imbricate, ventro-lateral carina absent, with long setae dorsally, short setae laterally; lateral pronotum imbricate; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part coarsely rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence, dorsal part rugulose, ventral part rugose; propodeum coarsely rugose-punctate, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with short setae; hind coxa rugulose dorsally to strigate in coxal depression, imbricate laterally pubescence long laterally; hind trochanter without groove, imbricate, with short scattered setae (Fig. 8.78); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent stout setae; hind femur 3.09 (3.04-3.20) x as long as wide, 0.78 (0.73-0.82) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.95 (2.78-3.13) x length segment 2; segment 2, 1.31 (1.13-1.50) x length segment 3; segment 3, 1.35 (1.20-1.60) x length segment 4; segment 4, 0.3 x length segment 5 (Fig. 8.165); hind tarsal claw 0.91 (0.88-1.00) x length segment 5 (Fig. 8.165); hind wing with 3 hamuli.

Metasoma. 2.08 (1.87-2.25) x length of mesosoma; T1 punctate-imbricate, with smooth, slightly raised longitudinal median ridge (Fig. 8.79).

Male

Similar to female except: head black except for small red patch near eyes, and clypeus red brown, antennae dark brown, black on mesoscutum more extensive, black on axillae, mesepisternum, coxae and dorsal T1 and T2; hind tarsal segment 1 2.4 x length segment 2, segment 2 1.4 x length segment 3, segment 3 1.5 x length segment 4, segment 4 0.43 x length segment 5; hind tarsal claw 0.5 length hind tarsal segment 5; genitalia missing.

Comments

Pseudofoenus inaequalis is superficially similar in appearance to *P. feckneri* sp. nov., but the latter has different sculpturing patterns on the face, frons and vertex, the occipital carina is sculptured, and the ratio of the length of flagellomere 1 to the length of the scape is much larger.

Parrott (1955) indicated that *E. inaequalis* is 'positively' parasitic on the larvae of *Cladocerapis persooniae* Rayment (Colletidae). This was based on observations by T. Rayment and six specimens collected from Jamberoo, Illawarra Range, NSW. Rayment indicated there were "many hundreds of these parasites flying to and fro". However, these specimens have not been located, so this host relationship cannot be confirmed. It is unlikely, however, that the wasps were of this species given that all known specimens are from Yallingup, Western Australia (Fig. 8.192). It is more likely that the species in question was *P. feckneri* sp. nov. which has been collected from the general area of Jamberoo (see comments above under *P. feckneri* sp. nov.).

Pseudofoenus iqbali sp. nov.

(Figs 8.80-8.82, 8.166, 8.192)

Material Examined

Holotype. ♀, "Black Mountain, Australian Capital Territory, 26.iii.1985, J. James" (ANIC).

Paratypes. **Australian Capital Territory:** 2♂, Corin Dam, 56km W Canberra, 25-31.xii.1969, H. Evans & R.W. Matthews (MCZC); 1♀, Black Mountain, i.1982, I.D. Naumann, J.C. Cardale & M.E. Matthews (ANIC); 1♂, Black Mountain, xii.1982, I.D. Naumann & J.C. Cardale (ANIC); 1♂, Black Mountain, 25-30.i.1984, L. Masner (AEIC); 3♀, 2♂, Black Mountain, 18-23.ii.1985, W.W. Middlekauff (CASC); 13♀, same data as holotype (ANIC, WARI). **New South Wales:** 1♂, Sunny Corner State Forest, 25km EbyS Bathurst, 19.iv.1981, J.C. Cardale (ANIC).

Female

Length. 5 mm.

Colour. Body generally brown, face, frons, vertex, gena, scutellum and axillae black, with variable amounts of black on clypeus and mesoscutum, posterior margins of metasomal segments white, giving a banded appearance.

Head. Wider than long when viewed dorsally; face punctulate-imbricate, pubescence short; frons punctulate-imbricate, with shallow median longitudinal groove, with scattered short setae; frontal carina absent; vertex rugulose medially to punctulate-imbricate laterally, with scattered short setae; gena punctulate-imbricate with scattered long setae; occipital carina smooth; malar space 0.19 (0.18-0.20) x height eye; clypeus 2.08 (1.95-2.30) x as wide as high, punctulate-imbricate; distance from lateral ocellus to eye margin 0.81 (0.68-0.90) x distance between lateral ocellus and occipital carina; scape 2.60 (2.44-2.70) x length pedicel; first flagellomere 0.86 (0.78-0.91) x as long as scape, 1.26 (1.17-1.40) x as long as second flagellomere; mandible with two prominent medial teeth, basal tooth triangular.

Mesosoma. Propleuron rugulose medially, punctulate-imbricate laterally, ventro-lateral carina present, pubescence long laterally; dorsal part of lateral pronotum imbricate, with one or two shallow punctures, ventral part rugulose; medial lobe of mesoscutum rugulose-punctate (almost strigate anteriorly), with scattered short setae, medial line absent; lateral lobes of mesoscutum rugulose-punctate anteriorly to smooth with a few shallow punctures posteriorly, with scattered short setae; scutellum, axillae and metanotum smooth, with a few shallow punctures; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugulose, with median transverse carina; mesepimeron narrow, carinate; metapleuron rugulose, with long pubescence; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, margins glabrous; hind coxa imbricate, strigate in coxal depression, pubescence long laterally; hind trochanter without groove, imbricate, with a few long setae (Fig. 8.80); hind femur imbricate, with scattered short setae and scattered emergent setae; hind tibia punctate-imbricate, with scattered long setae, pubescence short on inner lateral surface; hind femur 3.42 (3.14-3.67) x as long as wide, 0.76 (0.73-0.80) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-2 slightly asymmetrical (Fig. 8.166), segments 1-3 with ventro-apical pecten of short robust spines, segment 1, 2.5 (2.3-2.7) x length segment 2; segment 2, 1.36 (1.30-1.44) x length segment 3; segment 3, 1.25 x length segment 4; segment 4, 0.7 x length segment 5 (Fig. 8.166); hind tarsal claw 0.7 x length segment 5 (Fig. 8.166); hind wing with 3 hamuli.

Metasoma. 2.01 (1.92-2.11) x length of mesosoma; T1 imbricate, longitudinal median ridge absent (Fig. 8.81).

Male

Similar to female except: length 5.5 mm (5.0-6.0 mm); metasoma somewhat narrower towards apex; digitus 0.9 x length basiparamere; basiparameres smooth (Fig. 8.82).

Comments

The female of this species is similar in appearance to that of *P. beverlyae* sp. nov. but the two differ in size and sculpturing patterns (see comments above under *P. beverlyae*). It is also somewhat similar to *P. macdonaldi* sp. nov., but the latter is a smaller species (3 mm in length) and the sculpturing pattern on the head is generally punctulate-imbricate whereas it is generally imbricate in *P. iqbali*. This species has been collected from southern New South

Wales and the Australian Capital Territory (Fig. 8.192), and is named after Muhammad Iqbal, post-doctoral fellow, Department of Applied and Molecular Ecology, Waite Campus, The University of Adelaide.

Pseudofoenus karimuiensis sp. nov.

(Figs 8.83-8.84, 8.167, 8.190)

Material Examined

Holotype. ♀, "Karimui, S Goroka, Papua New Guinea, 1000m, 8.vi.1961, J.L. & M. Gressitt" (BPBM). Tip of metasoma in gelatine capsule; left hind tarsal segment 5 and claw, right hind tarsal segments 3-5 and claw missing.

Female

Length. 7 mm.

Colour. Body generally dark brown, fore legs light brown; wings dark brown.

Head. Wider than long when viewed dorsally (Fig. 8.83); face imbricate, pubescence short; frons rugulose medially, smooth near eyes and median ocellus, with scattered short setae; frontal carina absent; vertex smooth medially, weakly imbricate towards gena, with scattered short setae; gena weakly imbricate, pubescence short; occipital carina smooth; malar space 0.06 x height eye; clypeus 1.20 x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.5 x distance between lateral ocellus and occipital carina; scape 1.9 x length pedicel; first flagellomere 1.4 x as long as scape, 2.9 x as long as second flagellomere; mandible with two prominent, widely separated medial teeth.

Mesosoma. Propleuron rugulose, ventro-lateral carina not visible, pubescence short; lateral pronotum imbricate; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, denser ventrally, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence, dorsal part rugose, ventral part rugose, with smooth centrally; propodeum rugose; propodeal spiracle not visible; hind coxa finely strigate dorsally.

imbricate laterally, pubescence long laterally; hind trochanter without groove, imbricate, pubescence short; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with stout emergent setae; hind femur 4.5 x as long as wide, 0.96 x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.67 x length segment 2; segment 2, 1.22 x length segment 3; segment 3, 1.0 x length segment 4 (Fig. 8.167); segment 5 and hind claws missing; hamuli not visible.

Metasoma. 2.43 x length of mesosoma; T1 imbricate, longitudinal median ridge absent (Fig. 8.84).

Male

Unknown.

Comments

P. karimuiensis, together with *P. schmidti* sp. nov., are the first hyptiogastrine wasps to be described from New Guinea. Also, a further two undescribed species of *Pseudofoenus* from Papua New Guinea exist in the BPBM and MCZC collections. This species is superficially similar in appearance to *P. nalbarraensis* sp. nov., but the latter has a frontal carina, a much narrower clypeus and differs in sculpturing patterns, for example, on the propodeum and T1. It is known only from the type locality Karimui, Papua New Guinea (Fig. 8.190), and it is named after this location.

Pseudofoenus kelleri sp. nov.

(Figs 8.85-8.88, 8.168, 8.193)

Material Examined

Holotype. ♀, "28km WSW Leinster (27.55S 120.41E), W. Aust., 11 Aug. 1983, T.F. Houston & R.P. McMillan" (WAMA).

Paratypes. **Western Australia:** 5♂, same data as holotype (WAMA).

Female

Length. 6 mm.

Colour. Body generally black, with variable amounts of yellow on propleuron, lateral pronotum, tegulae, mesepimeron, metapleuron and point of attachment of metasoma, legs largely dark brown but with variable amounts of yellow on femora, tibiae and tarsi, posterior margins of metasomal segments white, giving a banded appearance.

Head. Wider than long when viewed dorsally (Fig. 8.85); face, frons, vertex, gena and clypeus imbricate, with a few scattered shallow punctures, and with a few scattered long setae; frons with shallow median groove near median ocellus; frontal carina absent; occipital carina smooth; malar space 0.15 x height eye; clypeus 2.0 x as wide as high, imbricate, with a few shallow punctures; distance from lateral ocellus to eye margin 1.05 x distance between lateral ocellus and occipital carina; scape 2.73 x length pedicel; first flagellomere 0.77 x as long as scape, 1.44 x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.86).

Mesosoma. Propleuron rugulose dorsally, imbricate, with a few scattered shallow punctures ventrally, and with a few scattered long setae, ventro-lateral carina weak; lateral pronotum imbricate in dorsal part, ventral part imbricate, with a few scattered shallow punctures, and with a few scattered long setae; medial and lateral lobes of mesoscutum, scutellum, axillae and metanotum imbricate, with a few scattered shallow punctures, with a few scattered long setae; weak medial line present on mesoscutum; mesepisternum with short pubescence dorsally, very long ventrally, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose tending to smooth ventrally, without median transverse carina; mesepimeron narrow, carinate; metapleuron with short pubescence, longer ventrally, dorsal part imbricate, ventral part rugose; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, not fringed with setae; hind coxa imbricate, pubescence long laterally; hind trochanter without groove, imbricate, with a few scattered shallow punctures, with a few scattered long setae (Fig. 8.87); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent setae; hind femur 2.64 x as long as wide, 0.68 x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-2 asymmetrical (Fig. 8.168), segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.16 x length segment 2; segment 2, 1.73 x length segment 3; segment 3, 1.22 x length segment 4; segment 4, 0.5 x length segment 5; hind tarsal claw 0.61 x length segment 5 (Fig. 8.168); hind wing with 3 hamuli.

Metasoma. 2.0 x length of mesosoma; T1 smooth medially to imbricate laterally, longitudinal median ridge absent (Fig. 8.88).

Male

Similar to female except: length 6.8 mm (6-8 mm); flagellomeres 1 and 2 about equal in length; digitus 0.9 x length basiparamere; basiparameres smooth.

Comments

Pseudofoenus kelleri is similar in appearance to *P. coorowensis* sp. nov. and *P. crosskeyi* sp. nov. (see comments under *P. coorowensis*). The type series was collected from near Leinster, Western Australia (Fig. 8.193), from flowers of *Baeckea stowardii* S. Moore (Myrtaceae) This species is named for Dr Michael Keller, Senior Lecturer in Entomology, Department of Applied and Molecular Ecology, Waite Campus, The University of Adelaide.

Pseudofoenus kurmondi (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus loxleyi (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus macdonaldi sp. nov.

(Figs 8.89-8.92, 8.169, 8.193)

Material Examined

Holotype. ♀, "Eidsvold, Queensland, 25.22S 151.07E, 11.x.1984, I.D. Naumann & J.C. Cardale" (ANIC).

Paratypes. **New South Wales:** 1♀, 1♂, Fowlers Gap Res. Stn., 29-xi-2.xii.1981, I.D. Naumann (ANIC). **Queensland:** 10♀, 16♂, same data as holotype (ANIC, WARI). **South Australia:** 1♀, 10km WNW Penong, 31.53S 132.54E, I.D. Naumann & J.C. Cardale (ANIC). **Western Australia:** 2♀, ca 4km NE Fraser Range HS, 17.xi.1978, T.F. Houston *et al.* (WAMA).

Female

Length. 3.0 mm (2.5-3.5 mm).

Colour. Body generally brown black, with antennae, lateral pronotum, metanotum and legs brown, posterior margins of metasomal segments white, giving a banded appearance.

Head. Wider than long when viewed dorsally (Fig. 8.89); face imbricate, with a few shallow punctures, with scattered short setae; frons imbricate, with weak shallow median longitudinal groove, almost glabrous, with a few scattered short setae; frontal carina absent; vertex imbricate, almost glabrous, with a few scattered short setae; gena imbricate, with scattered long setae; occipital carina smooth; malar space 0.18 (0.16-0.19) x height eye; clypeus 2.27 (2.08-2.56) x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.85 (0.76-1.00) x distance between lateral ocellus and occipital carina; scape 1.99 (1.78-2.13) x length pedicel; first flagellomere 0.77 (0.76-0.81) x as long as scape, 1.70 (1.63-1.86) x as long as second flagellomere; mandible broad, with two prominent medial teeth.

Mesosoma. Propleuron rugulose, ventro-lateral carina present, with scattered long setae; lateral pronotum imbricate; medial and lateral lobes of mesoscutum imbricate, with a few shallow punctures, with scattered short setae, medial line absent; scutellum, axillae and metanotum imbricate; mesepisternum rugulose in dorsal part, imbricate near anterior margin, pubescence short, separated from ventral part by carinate depression, ventral part rugose, with weak median transverse carina, with scattered long setae; mesepimeron broad, carinate; metapleuron with long pubescence ventrally, dorsal part imbricate, ventral part rugose; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with a few long setae; hind coxa imbricate, smooth in coxal depression, pubescence long laterally; hind trochanter without groove, imbricate, with scattered long setae (Fig. 8.90); hind femur imbricate, with scattered long setae; hind tibia imbricate, with a few scattered punctures, with scattered long setae, inner surface with short pubescence; hind femur 3.30 (3.13-3.40) x as long as wide, 0.82 (0.74-0.94) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-2 somewhat asymmetrical (Fig. 8.169), and with ventro-apical pecten of short robust spines, segment 1, 2.80 (2.70-2.89) x length segment 2; segment 2, 1.33 (1.29-1.43) x length segment 3; segment 3, 1.27 (1.17-1.40) x length segment 4; segment 4, 0.6 x length segment 5; hind tarsal claw 0.63 (0.56-0.67) x length segment 5 (Fig. 8.169); hind wing with 3-4 hamuli (90% of specimens with 3 and 10% with number variable between each wing).

Metasoma. 2.23 (2.04-2.38) x length of mesosoma; T1 imbricate, longitudinal median ridge absent (Fig. 8.91).

Male

Similar to female except: metasoma narrower towards apex; hind tarsal segments 1-2 symmetrical; digitus 0.95 x length basiparamere; basiparameres smooth (Fig. 8.92).

Comments

Pseudofoenus macdonaldi is the smallest of all hyptiogastrine wasps (3.0 mm), and is somewhat similar to *P. iqbali* sp. nov., but the two species can be separated by both size and sculpturing patterns that are given in the key. It has been collected from three widely separated localities in Queensland, New South Wales and South Australia (Fig. 8.193), and is named after John Macdonald, Scientific Collections Unit, NSW Agriculture.

Pseudofoenus malkini sp. nov.

(Figs 8.93-8.96, 8.170, 8.194)

Material Examined

Holotype. ♀, "Sir Graham Moore Island, Western Australia, 20.x.1945, R. Malkin" (USNM).

Paratypes. **Western Australia:** 1♀, 1♂, same data as holotype (ANIC, USNM).

Female

Length. 4 mm.

Colour. Body pale orange.

Head. Wider than long when viewed dorsally (Fig. 8.93); face imbricate, almost glabrous, with a few scattered short setae; frons imbricate, almost glabrous, with a few scattered short setae, denser near antennal scrobes; frontal carina present; vertex imbricate, almost glabrous, with a few scattered short setae; gena imbricate, with scattered short setae; occipital carina smooth, broad (Fig. 8.93); malar space 0.079 (0.075-0.082) x height eye; clypeus 1.8 x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.66 (0.64-0.68) x distance between lateral ocellus and occipital carina; scape 2.5 x length pedicel; first flagellomere 0.92 x as long as scape, 1.53 x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.94).

Mesosoma. Propleuron imbricate, ventro-lateral carina absent, with a few scattered short setae; lateral pronotum imbricate; medial and lateral lobes of mesoscutum punctate-imbricate, with a few scattered short setae, medial line absent; scutellum, axillae and metanotum punctate-imbricate; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part imbricate, with median transverse carina; mesepimeron broad, carinate; metapleuron rugulose-imbricate, pubescence, short; propodeum rugulose, short median longitudinal carina posteriorly; propodeal spiracle elongate, margins glabrous; hind coxa imbricate, almost glabrous, with a few scattered short setae; hind trochanter without groove, imbricate, with a few scattered long setae; hind femur imbricate, with a few scattered short setae; hind tibia imbricate, pubescence short; hind femur 2.90 (2.67-3.13) x as long as wide, 0.70 (0.69-0.71) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 1.94 (1.88-2.00) x length segment 2; segment 2, 1.5 x length segment 3; segment 3, 1.0 x length segment 4; segment 4, 1.0 x length segment 5 (Fig. 8.170); hind tarsal claw 0.7 x length segment 5 (Fig. 8.170); hind wing with 3 hamuli.

Metasoma. 2.2 x length of mesosoma; T1 imbricate, longitudinal median ridge absent.

Male

Similar to female except: length 5 mm; hind tarsal segment 1 with numerous stout setae (Fig. 8.96); digitus not visible; basiparameres smooth.

Comments

The male of *P. malkini* differs in only minor detail from the female. It is slightly longer, and hind tarsal segment 1 has numerous stout sensory setae (Fig. 8.96), which are lacking on the female (Fig. 8.95). These setae are not known from other *Pseudofoenus* spp. and their function is unknown. It is named after the collector, B. Malkin, and has been collected only from Sir Graham Moore Island, northern Western Australia (Fig. 8.194).

Pseudofoenus marionae (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus masneri sp. nov.

(Figs 8.97-8.100, 8.171, 8.194)

Material Examined

Holotype. ♀, Port Douglas, Queensland, 23.ii.1984, L. Masner (ANIC).

Paratypes. **Queensland:** 7♀, 2♂, same data as holotype (AEIC, ANIC).

Female

Length. 7.5 mm (6-8 mm).

Colour. Body generally golden brown, with antennal flagellomeres and dorsal surfaces of head, mesosoma and metasoma generally slightly darker brown.

Head. Wider than long when viewed dorsally (Fig. 8.97); face punctulate, pubescence short; frons rugulose medially, punctulate near eyes, pubescence short; frontal carina weak; vertex smooth, with scattered short setae; gena smooth, pubescence short; occipital carina broad, smooth; malar space 0.03 (0.025-0.035) x height eye; clypeus 1.64 (1.50-1.85) x as wide as high, punctulate, with weak medial carina anteriorly; distance from lateral ocellus to eye margin 0.57 (0.54-0.58) x distance between lateral ocellus and occipital carina; scape 2.50 (2.14-2.80) x length pedicel; first flagellomere 1.20 (1.07-1.27) x as long as scape, 1.80 (1.50-2.11) x as long as second flagellomere; mandible with two prominent medial teeth.

Mesosoma. Propleuron imbricate, ventro-lateral carina present, pubescence short; lateral pronotum almost smooth, weakly rugulose; medial and lateral lobes of mesoscutum coarsely rugose-punctate, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose-punctate; mesepisternum with short pubescence, denser ventrally, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence. dorsal part smooth, ventral part rugose; propodeum areolate, with lateral carina medially, with median longitudinal carina posteriorly, reaching about one third of height of propodeum; propodeal spiracle elongate, fringed with long setae; hind coxa smooth dorsally, weakly strigate in coxal depression, imbricate laterally, pubescence long laterally, glabrous dorsally; hind trochanter without groove, imbricate, with scattered short setae (Fig. 8.98); hind femur imbricate, pubescence short; hind tibia imbricate, with a few shallow punctures, pubescence short; hind femur 4.00 (3.73-4.25) x as long as wide, 0.78 (0.74-0.80) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.90 (2.60 0 3.30) x length segment 2; segment 2, 1.32 (1.14-1.60) x length segment 3; segment 3, 1.65 (1.50-1.75) x length segment

4; segment 4, 0.48 (0.43-0.57) x length segment 5 (Fig. 8.171); hind tarsal claw 0.7 (0.50-0.9) x length segment 5 (Fig. 8.171); hind wing with 3 hamuli.

Metasoma. 3.00 (2.75-3.30) x length of mesosoma; T1 smooth, with a few scattered setae, longitudinal median ridge absent (Fig. 8.99).

Male

Similar to female except: length 8.5 mm (8-9 mm); digitus 0.9 x length basiparamere; basiparameres smooth (Fig. 8.100).

Comments

Pseudofoenus masneri sp. nov. is superficially similar in appearance to *P. ferrugineus* comb. nov. but the latter is larger and has a weak groove apically on the hind trochanter. *Pseudofoenus masneri* sp. nov. lacks such a groove (Fig. 8.98). This species is named after Lubomir Masner, Agriculture Canada, Ottawa, who collected the type series. It has only been collected from Port Douglas, Queensland (Fig. 8.194).

Pseudofoenus nalbarraensis sp. nov.

(Figs 8.101-8.104, 8.172, 8.195)

Material Examined

Holotype. ♀, "75km W Nalbarra HS, 28.39S 117.36E, Western Australia, 29-30.viii.1981, T.F. Houston" (WAMA). Tarsal segments 4-5 and claw missing from left hind leg.

Paratypes. **Western Australia:** 3♂, same data as holotype (WAMA).

Female

Length. 9.5 mm.

Colour. Body generally red brown, head black except for small red patch near eyes, black on dorsal propleuron, mesoscutum, axillae, ventral mesopleuron and metanotum, dorsal hind trochanters, and dorsal surface of metanotal segments except T1 and T2.

Head. Wider than long when viewed dorsally (Fig. 8.101); face smooth, pubescence short; frons punctate except for a few radial striations near ocelli, with scattered short setae, denser near antennal scrobes; frontal carina absent; vertex punctate behind ocelli and towards eye margins, weakly rugulose towards occipital carina, pubescence short; gena weakly imbricate, pubescence long; occipital carina smooth; malar space 0.06 x height eye; clypeus 2.86 x as wide as high, smooth; distance from lateral ocellus to eye margin 0.83 x distance between lateral ocellus and occipital carina; scape 2.5 x length pedicel; first flagellomere 1.1 x as long as scape, 1.7 x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.102).

Mesosoma. Propleuron rugulose, ventro-lateral carina present, pubescence long; lateral pronotum smooth in dorsal part, ventral part weakly imbricate and with scattered very small punctures; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum almost smooth, weakly rugulose; mesepisternum with long pubescence ventrally, dorsal part weakly imbricate, with scattered very small punctures, separated from ventral part by carinate depression, ventral part rugulose, with median transverse carina; mesepimeron broad, carinate; metapleuron with long pubescence ventrally, dorsal part weakly rugulose, ventral part rugose; propodeum areolate, posterior margin carinate, with short median longitudinal carina posteriorly; propodeal spiracle elongate, almost glabrous, fringed with a few short setae; hind coxa strigate dorsally, rugulose laterally, pubescence long laterally; hind trochanter without groove, imbricate, pubescence short (Fig. 8.103); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered stout emergent setae; hind femur 4.9 x as long as wide, 1.14 x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of very short robust spines, segment 1, 2.0 x length segment 2; segment 2, 1.2 x length segment 3; segment 3, 1.6 x length segment 4; segment 4, 0.45 x length segment 5 (Fig. 8.172); hind tarsal claw 0.8 x length segment 5 (Fig. 8.172); hind wing with 4 hamuli.

Metasoma. 2.05 x length of mesosoma; T1 punctate-imbricate, longitudinal median ridge absent (Fig. 8.104).

Male

Similar to female except: length 10 mm; variable amounts of black around tegulae and on mid and hind coxae and mid trochanters; hind tarsal segment 1, 1.8 x length segment 2; segment 2, 1.3 x length segment 3; segment 3, 1.2 x length segment 4; segment 4, 0.7 x length segment 5; hind tarsal claw 0.55 x length segment 5; digitus 0.9 x length basiparamere; basiparameres smooth.

Comments

This species is similar in appearance to *E. karimuiensis* sp. nov. The two can be readily separated by the shape of the clypeus (broader in the latter species) and the propodeum having areolate sculpturing in *P. nalbarraensis*, whereas in *P. karimuiensis* sp. nov. it is rugose. Also, the latter species has only been collected from Papua New Guinea. All specimens of *P. nalbarraensis* were collected whilst hovering over ground nests of *Neopasiphe* (Colletidae) bees. This species is named after the type locality, Nalbarra Homestead, Western Australia (Fig. 8.195).

Pseudofoenus nitidiusculus (Turner) comb. nov.

(Figs 8.105-8.108, 8.173, 8.196)

Hyptiogaster nitidiuscula Turner, 1918a: 411. - Hedicke, 1939: 49; Crosskey, 1953a: 371.

Eufoenus nitidiusculus Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Yallingup, Western Australia, 1-12.vii.1913, R.E. Turner" (BMNH, No. 3 a. 143). Antennae missing.

Other specimens examined. **Western Australia:** 6♀, 1♂, same data as holotype (BMNH).

Female

Length. 9.6 mm (9-10 mm).

Colour. Body generally red brown, with variable amounts of black on last few metasomal tergites.

Head. Wider than long when viewed dorsally (Fig. 8.105); face imbricate, pubescence short; frons punctate-imbricate, with scattered short setae, denser near antennal scrobes; frontal carina strong; vertex punctate-imbricate, with scattered short setae; gena imbricate, pubescence short; occipital carina smooth, broad; malar space 0.05 (0.04-0.06) x height eye; clypeus 2.04 (1.94-2.27) x as wide as high, imbricate, with a short median carina anteriorly; distance from lateral ocellus to eye margin 0.74 (0.69-0.85) x distance between lateral ocellus and occipital carina; scape 3.0 (2.7-3.4) x length pedicel; first flagellomere 0.94 (0.88-1.00) x as long as scape, 1.6 (1.5-1.7) x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.106).

Mesosoma. Propleuron rugulose-imbricate dorsally, punctate-imbricate laterally, ventro-lateral carina weak, pubescence long; lateral pronotum punctate-imbricate; medial and lateral lobes of mesoscutum punctate-imbricate, with scattered short setae; scutellum, and axillae punctate-imbricate; metanotum rugulose; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with rugose, pubescence short; propodeum areolate, posterior margin carinate, with short median longitudinal carina posteriorly; propodeal spiracle elongate, glabrous; hind coxa imbricate laterally, strigate dorsally, pubescence long laterally; hind trochanter without groove, imbricate, with a few scattered short setae (Fig. 8.107); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered stout emergent setae; hind femur 3.15 (2.77-3.53) x as long as wide, 0.67 (0.64-0.68) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, most pronounced on segment 1, segment 1, 2.4 (2.2-2.9) x length segment 2; segment 2, 1.4 (1.3-1.5) x length segment 3; segment 3, 1.3 (1.2-1.4) x length segment 4; segment 4, 0.5 x length segment 5 (Fig. 8.173); hind tarsal claw 0.65 (0.60-0.70) x length segment 5 (Fig. 8.173); hind wing with 3 hamuli.

Metasoma. 2.34 (2.15-2.55) x length of mesosoma; T1 imbricate, with a few shallow punctures laterally, longitudinal median ridge absent (Fig. 8.108).

Male

Similar to female except: digitus about 0.9 x length basiparamere; basiparameres smooth.

Comments

Pseudofoenus nitidiusculus is superficially similar in appearance to *P. inaequalis* comb. nov., and has been collected from Yallingup, Western Australia (Fig. 8.196), where both species are sympatric. They are readily separated by a number of characters including the sculpturing of the mesoscutum. The former has punctate-imbricate sculpturing whereas the sculpturing in the latter is rugose. Also, *P. inaequalis* comb. nov. has a longitudinal median ridge on T1 which is absent in *P. nitidiusculus* comb. nov. (Fig. 8.108).

Pseudofoenus patellatus (Westwood) comb. nov.

(Figs 8.109-8.114, 8.174, 8.196)

Foenus patellatus Westwood, 1851: 221.

Gasteruption patellatum Schletterer, 1885: 311. - Schletterer, 1889: 458; Kieffer, 1912: 338; Hedicke, 1939: 40.

Gasteruption plicatum Schletterer, 1889: 466.

Hyptiogaster plicata Kieffer, 1903: 94.

Eufoenus plicatus Szépligeti, 1903: 365. - Crosskey, 1962: 398. **Syn. nov.**

Hyptiogaster plicata Kieffer, 1904: 16. - Kieffer, 1912: 199; Hedicke, 1939: 49; Crosskey, 1953a: 376.

Hyptiogaster michrochela Kieffer, 1911: 181. - Kieffer, 1912: 202; Hedicke, 1939: 49; synonymy by Crosskey, 1953a: 369.

Hyptiogaster patellata Crosskey, 1953a: 369. - Parrott, 1955: 65; Crosskey, 1956: 124.

Eufoenus patellatus Crosskey, 1962: 398.

Material Examined

Holotype. patellatus: ♂, "Adelaide, South Australia" (OXUM). *michrochela*: ♂, "Adelaide, South Australia" (BMNH, No. 3 a. 161). *plicatus*: ♂, "Sydney, New South Wales" (ZMHB). Right antenna and tip of metasoma damaged

Other specimens examined. **Australian Capital Territory:** 4♀, 3♂, Black Mountain, 18-23.ii.1985, W.W. Middlekauff (CASC); 1♂, Canberra, 27.i.no year, no collector (AEIC). **New South Wales:** 2♀, 2?, Dobroyd, 4.xii.1923, Nicholson (AMSA); 1♂, Leets Vale, 16.x.1925, Mackerras (ANIC); 2♀, Dobroyd Pt., North Harbour, Sydney, 14.xii.1925, T.G. Campbell (AMSA); 1♂, Mt. Victoria, 1.i.1931, A.N. Burns (MVMA); 1?, Collubri, Nyngan, ii.1933, J. Armstrong (AMSA); 1♀, (?)Gagone Creek, 29.iv.1944, no collector (AMSA); 1♀, 65km N Sydney, 12.xii.1946, E.F. Riek (ANIC); 2♂, Caldwell, 28.xii.1931, V. Robb (MVMA); 1♀, 5km S Merrygoen, 18.i.1961, M.J.D. White (ANIC); 1♀, Wilsons Valley, Snowy Mountains, 16.ii.1963, D.K. McAlpine (AMSA); 1♀, Wilton, 27.i.1964, no collector (ANIC); 1♂, 32km E Euston, 15.xii.1967, T.F. Houston (SAMA); 1♀, Batemans Bay, 23.xii.1969, H. Evans & R.W. Matthews (MCZC); 1♀, Boonoo Boonoo River, 7.xi.1976, G. Thelschinger (ANIC); 1♀, Red Rock NP, 20-21.i.1980, H.E. & M.A. Evans & A. Hook (UQBA); 16♀, 15♂, Fowlers Gap Res. Stn., 31.05S 141.42E, 29.xi-2.xii.1981, I.D. Naumann & J.C. Cardale (ANIC, WARI); 1♀, 5♂, Fowlers Gap Res. Stn., 31.05S 141.42E, 8-9.xii.1982, I.D. Naumann (ANIC); 1♀, Horseshoe Creek nr Kyogie, 4.xi.1987, D.J. Scambler (AMSA); 1♂, Onarug NP, 4.ii.1989, G.R. Brown & M.A. Terras (NSWA); 1♀, 1♂, Illawarra, no date, H. Peterson (USNM); 1♀, Mittagong, no date, Lea (SAMA). **Northern Territory:** 1♀, 27km N by W Alice Springs, 8.xi.1979, I.D. Naumann (ANIC). **Queensland:** 2♀, 5♂, Eidsvold, x.1929-iv.1930, T.L. Bancroft (ANIC); 1♀, 1♂, Stanthorpe, 11.ii.1930, no collector (UQBA); 1♀, Carnarvon Range, ii.1944, N. Geary (AMSA); 1♀, Cunnamulla, 21.x.1944, N. Geary (AMSA); 1♂, Sunnybank, 1.xii.1951, E.F. Riek (ANIC); 2♀, 2♂, Caloundra, 17.xii.1955, J. Kerr (MVMA); 1♂, Brisbane, 25.ii.1956, J. Kerr (MVMA); 1♀, Esk, 14.xii.1958 J.K.[Kerr] (MVMA); 1♂, Highvale, 3.i.1960, R. Straatman (ANIC); 1♀, North Peak, Mt. Walsh NP, 600m, 9.xii.1971, H. Fracau (ANIC);

5♀, 3♂, Bluff Range, Biggenden, various dates, xii.1971, H. Fracau (ANIC); 1♂, Mt Walsh, Biggenden, 650m, 3.i.1972, H. Fracau (ANIC); 1♀, Bluff Range, Biggenden, 9-20.xii.1972, H. Fracau (ANIC); 1♂, Rockpool Gorge, Bluff Range, Biggenden, 4.x.1976, H. Fracau (ANIC); 1♀, Hastings Ck., 15km S Biggenden, 5.xi.1976, H. Fracau (ANIC); 1♀, Mt. Walsh, Biggenden, 16.i.1977, H. Fracau (ANIC); 1♀, Isaacs River, 100km NE Clermont, 20.x.1979, H.E. & M.A. Evans & A. Hook (UQBA); 1♂, Carnarvon Gorge NP, 22-25.x.1979, H.E. & M.A. Evans & A. Hook (UQBA); 2♀, 2♂, Blunder Cr., Brisbane, 12 xi.1979, H.E. & M.A. Evans & A. Hook (UQBA); 1♀, 17km N Murgon, 8.xi.1981, E.M. Exley & J. King (UQBA); 5♀, 1♂, Taroom District, Boggomoss, 25.27S 150.03E, 11-14.xi.1996, C.J. Burwell & S. Evans (QMBA); 1♀, Rockhampton, no other data (MAMU); 1♀, 1♂, Eidsvold, no date, T.L. Bancroft (ANIC); 1♀, no date or collector [colln. Gribodo] (MCSN); 1♂, Port Denison, no date or collector (MAMU). **South Australia:** 1♀, Naracoorte, 30.xi.1985, B. Frost (WARI); 1♀, Kolay Dam, Paney Stn., Gawler Ranges, 32.33S 135.36E, 7-11.xii.1989, J. Forrest (SAMA); 1♂, Balhanna, no date, E. Guest (SAMA). **Victoria:** 1♀, Healesville, 25.ii.1914, R. Kelly (MVMA); 1♀, Buchan, 26.i.1937, A.N. Burns (MVMA); 1♀, Ringwood, 15.iii.1937, A.N. Burns (MVMA); 1♀, Castlemaine, 19.i.1948, B.G. (MVMA); 1♀, Healesville, 28.xii.1953, A.N. Burns (MVMA); 1♀, Yaapeet, 18-22.ii.1970, H.E. Evans & R.W. Matthews (MCZC); 3♀, Wyperfield NP, 40km N Rainbow, 18-23.ii.1970, H.E. Evans & R.W. Matthews (MCZC); 5♀, 1♂, 8-24km S Rainbow, 21-22.ii.1970, H.E. Evans & R.W. Matthews (MCZC); 1♀, Melbourne, no date, H. Edwards (MCZC); 1♂, Bright, no date, R.W. Davies (QMBA); 1♀, Rutherglen, no date, Hill (MVMA). **Western Australia:** 1♂, 10km N Katanning, 22.xii.1977, R.P. McMillan (WAMA); 1♂, 7.5km WSW Lake Cronin, 32.23S 119.46E, 19-26.ix.1978, T.F. Houston *et al.* (WAMA); 1♀, 9km NNE Buningonia Spring, 31.26S 123.33E, 18-25.xi.1978, T.F. Houston *et al.* (WAMA); 1♀, Wilga, 19.i.1980, K. Carnaby (AMSA); 1♀, 50km E Mullewa, 4.ix.1981, G.A. Holloway (AMSA); 1♀, Kalbarri, 6.ix.1981, L. Kelsey (ANIC); 2♀, Burma Road Reserve, 30km E Walkaway, ix.1987, R.P. McMillan (WAMA). **Other:** 1♀, Australia, no date or collector [colln. Gribodo] (MCSN); 1♂, no data label (AMSA); 2♂, no data label (QPIM).

Female

Length. 14 mm (11-18 mm).

Colour. Body generally red brown, with variable amounts of black on clypeus, vertex, propleuron, lateral pronotum, mesoscutum, scutellum, axillae, metanotum, mesepisternum, metapleuron, propodeum, dorsal surface of tergites, coxae, trochanters, femora, and tibiae, hind tarsi predominantly white except base of segment 1 and segments 3-5 with dark brown.

Head. Wider than long when viewed dorsally (Fig. 8.109); face imbricate, pubescence short; frons imbricate, some specimens rugulose-imbricate medially and radial striations near ocelli, pubescence short, denser near antennal scrobes; frontal carina strong; vertex with shallow lateral groove behind ocelli, imbricate, some specimens with radial striations near ocelli and rugulose-imbricate behind ocelli, pubescence short; gena imbricate, pubescence short; occipital carina broad, smooth; malar space 0.04 x height eye; clypeus 1.75 (1.50-2.00) x as wide as high, imbricate, with short medial carina anteriorly, pubescence short; distance from lateral ocellus to eye margin 0.40 (0.33-0.44) x distance between lateral ocellus and occipital carina; scape 2.65 (2.22-3.12) x length pedicel; first flagellomere 1.37 (1.29-1.46) x as long as scape, 1.74 (1.52-2.06) x as long as second flagellomere; mandible with two prominent medial teeth (sometimes slightly worn, indicated by dull surface), basal tooth triangular (also sometimes slightly worn) (Fig. 8.110).

Mesosoma. Propleuron imbricate, ventro-lateral carina present, pubescence long; lateral pronotum imbricate, pubescence short; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short dense pubescence, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, with short dense pubescence; propodeum rugose, short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with short setae; hind coxa striate dorsally, imbricate laterally, pubescence long laterally; hind trochanter with or without groove, imbricate, with scattered short setae; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered emergent stouter setae; hind femur 4.2

(3.8-4.5) x as long as wide, 0.75 (0.72-0.82) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.4 (2.1-2.9) x length segment 2; segment 2, 1.4 (1.2-1.6) x length segment 3; segment 3, 1.5 (1.25-1.70) x length segment 4; segment 4, 0.55 (0.47-0.67) x length segment 5 (Fig. 8.174); hind tarsal claw 0.73 (0.56-0.83) x length segment 5 (Fig. 8.174); hind wing with 3 hamuli.

Metasoma. 2.6 (2.4-2.7) x length of mesosoma; T1 imbricate with a few punctures laterally, longitudinal median ridge absent, some specimens smooth medially (Fig. 8.113).

Male

Similar to female except: hind trochanter with or without a slight groove on lateral inner surface (Figs 8.111-112); digitus about 0.9 x length basiparamere; basiparameres smooth (Fig. 8.114).

Variation

See comments below.

Comments

Foenus patellatus was first described by Westwood (1851). It was later transferred to *Gasteruption* (Schletterer 1885), then to *Hyptiogaster* (Crosskey 1962) and later to *Eufoenus* (Crosskey 1962). *Hyptiogaster michrochela* was described by Kieffer (1911), but was synonymised with *E. patellatus* by Crosskey (1953a). *Gasteruption plicatum* was first described by Schletterer (1889), transferred to *Hyptiogaster* (Kieffer 1903) and then to *Eufoenus* (Szépligeti 1903). Crosskey (1962) did not inspect the holotype of *H. plicata* but relied on a description provided by Dr Bischoff. His description indicated that the frontal carina was absent, but in fact there is a pronounced carina.

Upon inspection of the holotypes of *patellatus*, *microchela* and *plicatus*, all three are similar, differing only in minor sculpturing patterns on the frons and vertex, and in the degree of pubescence on the head. The holotypes of *patellatus* and *microchela* have no radial striations near the ocelli, the frons and vertex behind ocelli are rugulose-imbricate, and the head is not very pubescent. The holotype of *plicatus* has radial striations near the ocelli, is somewhat rugulose-imbricate on the frons and vertex behind the ocelli, and the head is generally more pubescent.

Also, variation exists among specimens collected at the same time and locality. Of five females and three males collected at Bluff Range, NSW in December 1971 (ANIC), three females and two males have radial striations near the ocelli and the frons and vertex behind the ocelli are rugulose-imbricate. The remaining specimens lack the striations and the frons and vertex behind the ocelli are rugulose-imbricate. Of all the non-type material, 13% females and 5% of males have a rugulose-imbricate frons and medial vertex and radial striations near the ocelli. The above variations are considered to be intraspecific and so *plicatus* is hereby synonymised with *patellatus*.

Males of *P. patellatus* comb. nov. generally lack a groove on the hind trochanter, or if present, it may be either indistinct and more latero-ventral, or distinct and latero-dorsal.

Given the presence of short and hidden ovipositor, this species is transferred to *Pseudofoenus*. This species is readily recognised by the predominantly white hind tarsal segments. It is somewhat similar to *P. australis* comb. nov. in that both species show similar variation in the groove on the hind trochanter. It can be readily separated from *P. australis* comb. nov. which has red brown hind tarsal segments.

This species has a wide distribution across the southern two-thirds of the Australian mainland, but has not been collected from Tasmania (Fig. 8.196). Little is known of the biology of this species, although adults have been collected on flowers of *Angophora* sp. (Myrtaceae) in New South Wales and *Hakea* sp. (Proteaceae) and *Atalaya hemiglauca* (F. Muell.) F. Muell. ex Benth. (Sapindaceae) in Western Australia.

Pseudofoenus pilosus (Kieffer) comb. nov.

(Figs 8.115-8.118, 8.175, 8.197)

Hyptiogaster pilosa Kieffer, 1911b: 180. - Kieffer, 1912: 200; Hedicke, 1939: 49; Crosskey, 1953a: 376; Crosskey, 1956: 122.

Eufoenus pilosus Crosskey, 1962: 398.

Material Examined

Holotype. ♂, "Kuranda, Queensland, xi.1913, F.P. Dodd" (BMNH, No. 3 a. 158).

Other specimens examined. **Queensland:** 1♀, Toowoomba, 1.i.1942, I. Common (UQBA); 1♀, 48km S Cunnamulla, 24.x.1957, E.F. Riek (ANIC); 1♀, nr Beerburrum, 29.xi.1966, T.F. Houston (SAMA); 5♀, 8♂, Russet Park, Kuranda, 8&12.xi.1987, T.W. Davies (CASC); 1♀, Cairns district, no date, F.P. Dodd (SAMA). **New South Wales:** 1♂, Yass, 16.i.1931, H.E. English (ANIC); 1♀, Kangaroo Valley, 22.iii.1961, E.F. Riek (ANIC). **South Australia:** 1♂, nr River Torrens, Fulham, 27.iii.1965, T.F.H. [Houston] (SAMA); 1♀, Madigan Gulf, Lake Eyre Nth., 28.x.1966, G.F. Gross (SAMA); 1♀, Flinders Chase NP, Kangaroo Island, 24.xii.1989-6.i.1990, R. Wharton (TAMU). **Western Australia:** 1♀, Byford, Swan River, Oct, L.J. Newman (WADA); 1♀, Newman, 22.xii.1975, E. Exley & R. Storey (UQBA); 2♀, 1♂, Newmanns Rocks, 50km W Balladonia, 32.06S 123.10E, 30.xii.1986, G. & A. Daniels (UQBA)

Female

Length. 6.8 mm (4-8 mm).

Colour. Body generally red brown, with variable amounts of black on propleuron, mesoscutum and axillae, dorsal T1, face, frons and vertex dark brown. Some specimens are generally much darker (see below).

Head. Wider than long when viewed dorsally; epistomal suture deep and well-defined laterally, absent medially (Fig. 8.115); face rugulose medially, smooth laterally, pubescence long; frons rugulose-punctate medially to punctate laterally, with scattered long setae, denser near antennal scrobes; frontal carina absent; vertex rugulose-punctate and smooth near eyes and lateral ocelli or smooth with scattered punctures, with scattered long setae; gena punctulate, smooth near eyes, with scattered long setae, or without punctures; occipital carina broad, smooth; malar space 0.11 (0.08-0.15) x height eye; clypeus 1.64 (1.50-1.75) x as wide as high, punctulate or smooth, pubescence long; distance from lateral ocellus to eye margin 0.83

(0.75-0.94) x distance between lateral ocellus and occipital carina; scape, pedicel and flagellomeres 1 and 2 with long setae; scape 2.84 (2.34-3.50) x length pedicel; first flagellomere 1.00 (0.71-1.29) x as long as scape, 1,91 (1.80-2.00) x as long as second flagellomere; mandible with two prominent medial teeth (sometimes worn, indicated by dull surface), anterior surface pitted, basal tooth triangular (also sometimes worn) (Fig. 8.116).

Mesosoma. Propleuron imbricate dorsally, rugulose laterally, ventro-lateral carina present, pubescence long laterally; lateral pronotum rugulose; medial and lateral lobes of mesoscutum coarsely rugose-punctate anteriorly to punctate posteriorly or smooth with a few scattered punctures, with scattered long setae, medial line present; scutellum and axillae coarsely punctate or smooth with a few shallow punctures; metanotum coarsely punctate; mesepisternum with long pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part coarsely rugose, without median transverse carina; mesepimeron broad, weakly carinate; metapleuron rugose, pubescence long; propodeum coarsely rugose, without median longitudinal carina posteriorly; propodeal spiracle elongate, margins glabrous; hind coxa strigate, pubescence long laterally; hind trochanter without groove, imbricate, with scattered long setae; hind femur imbricate, with a few shallow punctures, these associated with long setae, with scattered short setae; hind tibia punctate-imbricate, pubescence short, with scattered emergent setae; hind femur 3.75 (3.17-3.53) x as long as wide, 0.83 (0.82-0.88) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines, with long setae; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 2.77 (2.44-3.00) x length segment 2; segment 2, 1.36 (1.13-1.50) x length segment 3; segment 3, 1.40 (1.20-1.60) x length segment 4; segment 4, 0.46 (0.36-0.50) x length segment 5 (Fig. 8.175); hind tarsal claw 0.64 (0.60-0.71) x length segment 5 (Fig. 8.175); hind wing with 3-4 hamuli (43% of specimens with 3/3, 43% with 4/4 and 14% with number variable between each wing).

Metasoma. 2.0 (2.0-2.1) x length of mesosoma; T1 weakly imbricate, longitudinal median ridge absent (Fig. 8.117); segments 2 to apex with long outstanding setae.

Male

Similar to female except: digitus 0.95 x length basiparamere; basiparameres smooth (Fig. 8.118).

Variation

Specimens from Kuranda (CASC) and Cairns (SAMA), Queensland and Swan River, Western Australia (WADA) are much darker in colour and have variable amounts of black on the lateral pronotum, mesepisternum, metapleuron, coxae, trochanters and femora.

Specimens from Kangaroo Valley, New South Wales (ANIC), Newman, Western Australia (UQIC) and Kangaroo Island, South Australia (TAMU) are much smaller (4 mm), the mesoscutum is generally smooth except for a few scattered punctures, and the scutellum and axillae are smooth. The Kangaroo Island specimen also has a smoother vertex and clypeus.

Comments

Pseudofoenus pilosus comb. nov. is readily separated from all other species by its pilose surface, particularly on the metasoma. Given the considerable intraspecific variation in the specimens currently assigned to this species, there is a distinct possibility they represent a species complex. Until further material is accomodated, a conservative approach has been taken here and all pilose specimens placed in *P. pilosus*. This species has been collected widely from mainland Australia except for central and northern Australia (Fig. 8.197).

Pseudofoenus reticulatus (Crosskey) comb. nov.

(Figs 8.119-8.121, 8.176, 8.197)

Hyptiogaster reticulata Crosskey, 1956: 240.

Eufoenus reticulatus Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Cotter River, Australian Capital Territory, 6.ii.1947, E.F. Riek" (ANIC).

Paratype: **Australian Capital Territory:** 1♂, Canberra, 25.xi.1947, E.F. Riek (ANIC). [Note: Labelled *Eufoenus rieki* in Crosskey's handwriting.]

Female

Length. 5 mm.

Colour. Body generally red brown, with variable amounts of dark brown on clypeus, face, frons, propleuron, mesoscutum and metanotum, brown black on propodeum and dorsal T1.

Head. Wider than long when viewed dorsally; face imbricate, with scattered shallow punctures, these associated with long setae; epistomal suture absent (Fig. 8.119); frons with shallow medial groove, imbricate, with scattered shallow punctures, these associated with long setae; frontal carina absent; vertex imbricate, with scattered shallow punctures, these associated with long setae; gena imbricate, with scattered shallow punctures, these associated with long setae; occipital carina smooth; malar space 0.14 x height eye; clypeus 2.33 x as wide as high, imbricate, with scattered shallow punctures, these associated with long setae; distance from lateral ocellus to eye margin 1.0 x distance between lateral ocellus and occipital carina; scape 2.45 x length pedicel; first flagellomere 0.75 x as long as scape, 1.82 x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.119).

Mesosoma. Propleuron imbricate, ventro-lateral carina absent, pubescence long; lateral pronotum imbricate, with scattered shallow punctures, these associated with long setae; medial and lateral lobes of mesoscutum imbricate, with scattered shallow punctures, these associated with long setae, medial line absent; scutellum, axillae and metanotum imbricate, with scattered shallow punctures, these associated with long setae; mesepisternum with long pubescence, very long ventrally, dorsal part imbricate, separated from ventral part by carinate depression, ventral part rugulose-punctate, without median transverse carina; mesepimeron narrow, carinate; metapleuron with long pubescence, dorsal part imbricate, ventral part rugulose; propodeum rugose-imbricate, posterior margin carinate, short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with a few long setae; hind coxa imbricate, pubescence very long laterally; hind trochanter without groove, imbricate, with scattered long setae: hind femur imbricate, with scattered long setae; hind tibia punctate-imbricate, pubescence short, with scattered emergent setae; hind femur 3.0 x as long as wide, 0.73 x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segment 1 with ventro-apical pecten of short robust spines, segments 2-4 with several long stout ventro-apical setae; segment 1, 2.9 x length segment 2; segment 2, 1.3 x length segment 3; segment 3, 1.0 x length segment 4; segment 4, 0.9 x length segment 5 (Fig. 8.176); hind tarsal claw 1.0 x length segment 5 (Fig. 8.176); hind wing with 3 hamuli.

Metasoma. 1.75 x length of mesosoma; T1 imbricate, with a few scattered shallow punctures, these associated with long setae; longitudinal median ridge absent (Fig. 8.120).

Male

Similar to female except: 6 mm long; colour generally a darker brown, posterior margins of metasomal segment white, giving a banded appearance; metasoma 2.3 x length of mesosoma; digitus 0.9 x length basiparamere; basiparameres smooth (Fig. 8.121).

Comments

The male specimen in ANIC with a printed label 'Canberra, 25.xi.1947, E.F. Riek', '*Hyptiogaster rieki* Crosskey' in Crosskey's handwriting, and with a later paratype label, is clearly the paratype of *E. reticulatus* (Crosskey) (see below under *P. rieki* comb. nov. for further discussion). *Pseudofoenus reticulatus* comb. nov. is a small species (length 5 mm), that can be distinguished from all other species by the characters given in the key. This species has only been collected in the Australian Capital Territory (Fig. 8.197).

Pseudofoenus rieki (Crosskey) comb. nov.

(Figs 8.122-127, 8.177, 8.198)

Hyptiogaster rieki Crosskey, 1956: 122.

Eufoenus rieki Crosskey, 1962: 398.

Material Examined

Holotype. ♀, "Sunnybank, Queensland, 1.xii.1951, E.F. Riek" (ANIC). Metasoma right antenna and left antennal flagellomeres 6-14 missing.

Paratypes: **Queensland:** 15♀, 17♂, Sunnybank, Queensland, 1.xii.1951, E.F. Riek (ANIC) (6♀ and 6♂ with metasoma missing); 1♀, Brook Creek, Burnside, Northern Aust.[Qld], 2.v.1929, T.G. Campbell (ANIC).

Other specimens examined: **South Australia:** 3♀, no locality, date or collector (MAMU).

Female

Length. 13 mm (11-14 mm).

Colour. Body generally red brown, with variable amounts of black on medial frons and notauli, darker brown on lateral pronotum and mesepimeron, and dorsal surface of middle femora and hind trochanters.

Head. Wider than long when viewed dorsally (Fig. 8.122); face imbricate, with scattered short setae; frons imbricate, slightly rugose near median ocellus, shallow groove behind posterior ocelli, with scattered short setae; frontal carina strong (Fig. 8.122); vertex imbricate, pubescence short; gena imbricate, pubescence short; occipital carina smooth; malar space 0.07 x height eye; clypeus 1.25 x as wide as high, imbricate with a few scattered punctures, with long setae near anterior margin; distance from lateral ocellus to eye margin 0.6 x distance between lateral ocellus and occipital carina; scape 2.6 (1.7-2.3) x length pedicel; first flagellomere 1.5 (1.4-1.6) x as long as scape, 2.2 (1.7-2.3) x as long as second flagellomere; mandible with two medial teeth (Fig. 8.123).

Mesosoma. Propleuron imbricate, ventro-lateral carina absent, pubescence short; lateral pronotum imbricate; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose, with scattered short setae; mesepisternum with short pubescence, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, with short pubescence; propodeum rugose, short median longitudinal carina posteriorly; propodeal spiracle elongate, margins glabrous; hind coxa strigulate dorsally, imbricate laterally, pubescence short dorsally, long laterally; hind trochanter without groove, imbricate, pubescence short (Figs 8.124-125); hind femur imbricate, pubescence short; hind tibia imbricate with scattered punctures, pubescence short, but with stouter emergent setae associated with punctures; hind femur 3.5 (3.3-3.6) x as long as wide, 0.8 (0.74-0.82) x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 1.8 (1.5-1.9) x length segment 2; segment 2, 1.4 (1.3-1.5) x length segment 3; segment 3, 1.3 (1.2-1.3) x length segment 4; segment 4, 0.5 (0.38-0.56) x length segment 5 (Fig. 8.177); hind tarsal claw 0.9 (0.6-1.1) x length segment 5 (Fig. 8.177), sometimes worn; hind wing with 2-3 hamuli (one specimen with 2 hamuli on left wing)

Metasoma. 2.36 (2.15-2.57) x length of mesosoma; T1 weakly imbricate medially, punctate-imbricate laterally (each puncture associated with a stout seta), longitudinal median ridge absent (Fig. 8.126).

Male

Similar to female except: mean length 14 mm (13-15 mm); hind claws smaller, 0.63 (0.50-0.76) x length hind tarsal segment 5; digitus 0.9 x length basiparamere; basiparameres smooth (Fig. 8.127).

Comments

Pseudofoenus rieki comb. nov. is one of two known hyptiogastrine species in which the male has a 14-segmented antenna, the other being *P. extraneus* comb. nov. *Pseudofoenus rieki* has a strong frontal carina and a large hind tarsal claw, 0.9 (0.64-1.10) x the length of hind tarsal segment 5 (Fig. 8.177), whereas *P. extraneus* comb. nov. lacks a frontal carina and has a smaller hind tarsal claw, 0.65 x the length of hind tarsal segment 5 (Fig. 8.162). Also, the former species is Australian in distribution (Fig. 8.198), whereas the latter is endemic to Fiji.

The male specimen in ANIC with a printed label 'Canberra, 25.xi.1947, E.F. Riek', '*Hyptiogaster rieki* Crosskey' in Crosskey's handwriting, and with a paratype label, is in fact the paratype of *E. reticulatus* (Crosskey). It varies in many ways to *E. rieki*. For example, it is much smaller (7 mm in length), and the face, frons, vertex, and mesoscutum are imbricate with scattered punctures. Also, this specimen is not listed among the paratypes in the original description (Crosskey 1956), and therefore has no status as a paratype. This is clearly an error in labelling and the paratype has been treated under *P. reticulatus* comb. nov. (see above). This species has been collected from several localities in Queensland and from South Australia (exact locality unknown) (Fig. 8.198).

Pseudofoenus ritae (Cheesman) comb. nov.

(Figs 8.128-8.131, 8.178, 8.190)

Hyptiogaster ritae Cheesman, 1936: 176. - Hedicke, 1939: 49; Crosskey, 1953a: 380.

Eufoenus ritae Crosskey, 1962: 398.

Material Examined

Holotype. ♂, "Aneityum, Vanuatu, x.1930, L.E. Cheesman" (BMNH, No. 3 a. 157).

Paratypes: **Vanuatu:** 1♀, 2♂, Aneityum, x.1930, L.E. Cheesman (BMNH); 1♀, 1♂, same data (ANIC); 2♀, 2♂, Ounoua, Malekula, 2.iv.1929, L.E. Cheesman (BMNH); 1♀, Tanna, x.1930, L.E. Cheesman (BMNH).

Other specimens examined. **Vanuatu:** 1♀, Espiritu Santo, 16.iv.1943, W. Bauer (MCZC). **New Caledonia:** 1♂, Col d'Amieu, 15-17.x.1978, J.S. Dugdale (NZAC).

Female

Length. 8.0 mm (7.5-8.5 mm).

Colour. Body red brown.

Head. Wider than long when viewed dorsally (Fig. 8.128); face imbricate, pubescence short; epistomal suture absent medially (Fig. 8.129); frons strigate medially to rugose-punctate laterally, pubescence short; frontal carina absent; vertex rugose, with short pubescence; gena short, pubescence short; occipital carina smooth, broad (Fig. 8.128); malar space 0.1 x height eye; clypeus 1.3 x as wide as high, imbricate; distance from lateral ocellus to eye margin 0.9 x distance between lateral ocellus and occipital carina; scape 2.5 x length pedicel; first flagellomere 1.2 x as long as scape, 2.0 (1.95-2.05) x as long as second flagellomere; mandible narrow, with single weak medial tooth (Fig. 8.129).

Mesosoma. Propleuron strigate medially to rugulose laterally, ventro-lateral carina absent, pubescence short; lateral pronotum rugulose, pubescence short; medial and lateral lobes of mesoscutum coarsely rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum coarsely rugose, with scattered short setae; mesepisternum with short pubescence, dorsal part rugulose, separated from ventral part by carinate depression, ventral part rugulose, with weak median transverse carina; mesepimeron broad, carinate; metapleuron coarsely rugose, pubescence short; propodeum coarsely rugose, short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa striate dorsally, imbricate laterally, pubescence short; hind trochanter without groove, imbricate, pubescence short; femur and tibia imbricate, pubescence short, a few scattered emergent setae; hind femur 4.8 x as long as wide, 0.8 x length hind tibia; hind tibia 6.0 x as long as wide, with ventro-apical pecten of short robust spines; hind tarsal segment 1 with ventro-apical pecten of short robust spines, segment 1, 2.6 x length segment 2; segment 2, 1.1 x length segment 3; segment 3, 1.7 x length segment 4; segment 4, 0.4 x length segment 5 (Fig. 8.178); hind tarsal claw 0.6 x length segment 5 (Fig. 8.178); hind wing with 3 hamuli.

Metasoma. 2.5 x length of mesosoma; T1 smooth, with scattered short setae, longitudinal median ridge absent (Fig. 8.130)

Male

Similar to female; digitus 0.8 x length basiparamere; basiparameres smooth (Fig. 8.131).

Comments

Pseudofoenus ritae and *P. extraneus* are somewhat similar in appearance, and both are endemic to islands in the south-west Pacific, the former to New Caledonia and Vanuatu, and the latter to Fiji (Fig. 8.190). The two species can be separated by the sculpturing pattern on the head. In *P. ritae*, the face is imbricate whereas in *P. extraneus* it is strigate.

Pseudofoenus schmidti sp. nov.

(Figs 8.132-8.134, 8.179, 8.190)

Material Examined

Holotype. ♀, "Merauke, 8.30S 140.22E, Irian Jaya, Indonesia, 3.iv.1988, R. Hensen" (RMNH).

Paratypes. **Indonesia: Irian Jaya:** 2♀, same data as holotype (RMNH).

Female

Length. 8 mm.

Colour. Body generally brown, with variable amounts of dark brown on face, frons, vertex, flagellomeres, mesoscutum, axillae, mesepisternum, legs and metasoma, posterior margins of metasomal segments lighter, this giving a banded appearance, hind tibia white basally.

Head. Wider than long when viewed dorsally (Fig. 8.132); face punctulate, pubescence short; frons rugulose-punctate medially, punctulate laterally, pubescence short; frontal carina absent; vertex smooth, weakly rugulose and with a shallow groove behind lateral ocelli, not reaching past ocelli, pubescence short; gena smooth, pubescence short; occipital carina smooth, broad; malar space 0.04 x height eye; clypeus 1.82 (1.80-1.85) x as wide as high, smooth; distance from lateral ocellus to eye margin 0.55 (0.50-0.58) x distance between lateral ocellus and occipital carina; scape 2.1 x length pedicel; first flagellomere 1.15 (1.13-1.20) x as long as scape, 1.73 (1.70-1.80) x as long as second flagellomere; mandible with two prominent medial teeth (Fig. 8.133).

Mesosoma. Propleuron imbricate, ventro-lateral carina present, pubescence short, denser laterally; lateral pronotum smooth; medial and lateral lobes of mesoscutum coarsely punctate, with scattered very short setae, medial line present; scutellum, axillae and metanotum coarsely punctate; mesepisternum with short pubescence, denser in ventral part, dorsal part rugose, separated from ventral part by carinate depression, ventral part coarsely rugose, with median transverse carina; mesepimeron broad, carinate; metapleuron with short pubescence, dorsal part smooth, ventral part areolate; propodeum areolate, with lateral medial carina and with median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa smooth dorsally except for a few shallow punctures and slightly strigate in coxal depression, imbricate laterally, pubescence long laterally; hind trochanter without groove, smooth, with scattered short setae; hind femur imbricate, pubescence short; hind tibia imbricate, pubescence short, with scattered emergent stout setae; hind femur 3.74 (3.47-3.94) x as long as wide, 0.79 (0.77-0.81) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 3.00 (2.89-3.11) x length segment 2; segment 2, 1.40 (1.30-1.50) x length segment 3; segment 3, 1.3 x length segment 4; segment 4, 0.5 x length segment 5 (Fig. 8.179); hind tarsal claw 0.5 x length segment 5 (Fig. 8.179); hind wing with 3-4 hamuli (two specimens with 3/3 and one with 3/4).

Metasoma. 2.59 (2.44-2.73) x length of mesosoma; T1 smooth, with a few shallow punctures, longitudinal median ridge absent (Fig. 8.134).

Male

Unknown.

Comments

Pseudofoenus schmidti sp. nov. is characterised by the absence of a frontal carina, the broad and smooth occipital carina, and the very small malar space. This species is named after Prof. Otto Schmidt, Head, Department of Applied and Molecular Ecology, Waite Campus, The University of Adelaide. It is the first species described from Indonesia, although the holotype locality is relatively close to northern Australia (Fig. 8.190).

Pseudofoenus spinitarsis (Westwood) comb. nov.

(Frontispiece, Figs 8.135-8.139, 8.180, 198)

Foenus spinitarsis Westwood, 1851: 221.

Gasteruption spinitarsis Schletterer, 1885: 313, 323. - Schletterer, 1889: 432; Dalla Torre, 1902: 1072; Kieffer, 1912: 234, 286; Hedicke, 1939: 31.

Hemifoenus brevithorax Kieffer, 1911: 182. - Kieffer, 1912: 192; Turner, 1918a: 410, 412; Brues, 1922: 13; Hedicke, 1939: 50.

Hyptiogaster interrupta Crosskey, 1953a: 375. - Crosskey, 1956: 126 (?var. of *H. spinitarsis*).

Hyptiogaster brevithorax Crosskey, 1956: 374.

Hyptiogaster spinitarsis Crosskey, 1956: 125.

Eufoenus spinitarsis Crosskey, 1962: 398 (syn. *H. brevithorax*).

Eufoenus interruptus Crosskey, 1962: 398 (syn. *E. spinitarsis*).

Material Examined

Holotype. spinitarsis: ♂, "Gold Coast, Africa" (OXUM) [holotype locality is, however, Australian (Crosskey 1956)]. *brevithorax:* ♀, "Melbourne, Victoria, 1907, R.E. Turner" (BMNH, No 3 a. 141). *interruptus:* ♀, "Mt. Wellington, Tasmania, i.1913, R.E. Turner" (BMNH, No. 3 c. 324).

Other specimens examined. **Australian Capital Territory:** 1♀, Canberra, xi-xii.1953, F.M. Hull (CNCI); 1♂, Blundells, 6.i.1961, E.F. Riek (ANIC); 1♀, Blundells, 31.i.1970, E.F. Riek (ANIC); 2♀, Corrin Dam, 55km W Canberra, 9.iii.1970, H. Evans & R.W. Matthews (MCZC); 1♀, Black Mountain, 18-23.ii.1985, W.W. Middlekauff (CASC); 2♀, 1♂, Peters Camp, 31.i.1986, Z. Liepa (ANIC). **New South Wales:** 1♀, Dobroyd, 14.x.1923, Nicholson (AMSA); 2♀, Barrington Tops, 1925, no collector (MAMU); 1♀, Lane Cove, 3.ix.1944 (AMSA); 1♀, Tubrabucca, 29.xii.1946, A.N. Burns (QMBA); 1♀, ?Bendora, 2.iii.1948, E.F. Riek (ANIC); 1♀, 2♂, Nimmitabel, 18.i.1961, E.F. Riek (ANIC); 1♀, Batlow, 18.ii.1962, R. Crosier (ANIC); 1♀, Sawpit Creek, Snowy Mountains, 14.ii.1963, D.K. McAlpine (AMSA); 1♀, Alpine Creek, Snowy Mountains Hwy., 2.ii.1965,

Z. Liepa (ANIC); 1♀, Kandos Weir, 29.xii.1977, G. Daniels (AMSA); 1♀, Bondi S.F., 24.i.1980, D.S. Kent (AMSA); 1♀, 1km SW Mt Banda Banda, Mt Boss S.F., 28.i.1985, G. Williams (AMSA); 1♂, Sawpit Creek, Kosciusko NP, 21.i.1987, G, J, & A. Holloway (AMSA). **Northern Territory:** 1♀, 56km SbyE Alice Springs, 24.11S 134.01E, 3.xii.1978, J.C. Cardale (ANIC); Areyonga, 600m, 10.x.no year, no collector (AEIC). **Queensland:** 1♀, Bunya Mountains NP, 4-6.vii.1985, D. Bickel & G. Cassis (AMSA); 1♀, Baldy Mt. Rd, 2.4km from S end, 17.20S 145.25E, 1.xii.1997, C.J. Burwell (QMBA). **South Australia:** 1♀, Gawler, 21.xii.1990, J.T. Jennings (WARI); 4♀, S. Aust., no other data (MAMU). **Tasmania:** 1♀, Hobart, 4.iii.1917, C.E. Coles (SAMA); 1♀, 5km W Buckland, 20.i.1948, Key, Carne & Kerr (ANIC); 1♀, Derwent Bridge, 26.i.1948, Key & Carne (ANIC); 1♂, St Helens, 41.15S 148.10E, 14.i.1983, I.D. Naumann & J.C. Cardale (ANIC); 1♀, Ewarts Creek, 41.58S 145.28E, 16.i-2.ii.1983, I.D. Naumann & J.C. Cardale (ANIC); 1♀, 5km EbyS Harford, 41.15S 146.36E, 19.i.1983, I.D. Naumann & J.C. Cardale (ANIC). **Victoria:** 1♀, Rutherglen, 1906, [C.] French (ANIC); 1♀, 6.5km N ?Briggolong, 13.xii.1949, T.G. Campbell (ANIC); 1♀, 7♂, Fernshaw, 4.i.1955, A.N. Burns (MVMA); 3♀, 1♂, Fernshaw, 26.i.1955, A. N. Burns (MVMA); 4♀, Fernshaw, 26.i.1955, Neboiss (MVMA); 1♀, Warburton, 16.xii.1958, A.N. Burns (MVMA); 2♀, Growler Creek, Lind NP, 26.ii.1980, I.D. Naumann & J.C. Cardale (ANIC); 1♀, Melbourne, no collector or date (MVMA); 1♀, Warburton district, no collector or date (MVMA).

Female

Length. 9 mm (7-11 mm).

Colour. Body generally red brown, with variable amounts of black on mesoscutum, propleuron and dorsal T1, pedicel and flagellomeres dark brown, with variable amounts of dark brown on tarsi and metasomal tergites.

Head. Wider than long when viewed dorsally (Fig. 8.135); face and frons punctate-imbricate, almost glabrous except for a few scattered short setae; frons with shallow median longitudinal groove near median ocellus; frontal carina absent; vertex with a shallow lateral groove behind ocelli, not reaching eyes, punctate-rugulose from behind ocelli to occipital carina, punctate-imbricate laterally, almost glabrous except for a few scattered short setae; gena punctate-imbricate, pubescence short; occipital carina smooth; malar space 0.22 (0.19-0.26) x height eye; clypeus 2.13 (1.95-2.40) x as wide as high, punctate-imbricate, almost glabrous except for a few scattered short setae and a fringe of long setae on anterior margin; distance from lateral ocellus to eye margin 0.75 (0.70-0.83) x distance between lateral ocellus and occipital carina; scape 3.0 (2.4-3.4) x length pedicel; first flagellomere 1.0 (0.8-1.2) x as long as scape, 1.8 (1.4-2.0) x as long as second flagellomere; mandible with two medial teeth (sometimes worn, this indicated by dull surface) (Fig. 8.136).

Mesosoma. Propleuron rugulose dorsally, punctate-imbricate laterally, ventro-lateral carina absent, with scattered long setae; lateral pronotum imbricate in dorsal part, ventral part punctate-imbricate; medial and lateral lobes of mesoscutum with scattered punctures, smooth except for underlying rugosity anteriorly, almost glabrous except for a few scattered short setae, medial line absent; scutellum, axillae and metanotum smooth and with scattered punctures; mesepisternum with short pubescence dorsally, longer ventrally, dorsal part rugulose-imbricate, separated from ventral part by carinate depression, ventral part rugose, with median transverse carina; mesepimeron narrow, carinate; metapleuron rugulose-imbricate, with short pubescence; propodeum strigate, with median lateral carina and median longitudinal carina; propodeal spiracle elongate, fringed with long setae anteriorly, glabrous posteriorly; hind coxa rugulose imbricate except strigate in coxal depression, pubescence long laterally; hind trochanter without groove, imbricate, with scattered short setae (Fig. 8.137); hind femur and tibia imbricate except for a few scattered punctures, with scattered short setae, longer ventrally; hind femur 3.0 (2.9-3.2) x as long as wide, 0.78 (0.73-0.83) x length hind tibia; hind tibia without ventro-apical pecten of short robust spines; mid tarsal segments 1-2 with stout latero-apical spine; hind tarsal segments 1-2 asymmetrical, with ventro-apical pecten of short robust spines, segments 1-2 with stout latero-apical spine (Fig. 8.180), segment 1, 1.7 (1.55-2.00) x length segment 2; segment 2, 1.95 (1.54-2.44) x length segment 3; segment 3, 1.5 (1.3-1.7) x length segment 4; segment 4, 0.6 (0.55-0.64) x length segment 5 (Fig. 8.180); hind tarsal claw 0.7 (0.63-0.83) x length segment 5 (Fig. 8.180); hind wing with 3-5 hamuli (25% of specimens with 3/3, 46% with 4/4, 4% with 5/5 and 25% with number variable between each wing).

Metasoma. 1.92 (1.60-2.20) x length of mesosoma; T1 punctate-imbricate, longitudinal median ridge absent (Fig. 8.138).

Male

Similar to female except: posterior margin of metasomal tergites white; mid tarsal segments 1-2 without stout latero-apical spine; hind tarsal segments 1-2 asymmetrical, without stout latero-apical spine, segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 1.84 (1.65-1.95) x length segment 2; segment 2, 1.40 (1.36-1.46) x length segment 3; digitus about 0.9 x length basiparamere; basiparameres smooth (Fig. 8.139).

Variation

There is some colour variation within this species, although this is minimal among specimens collected at the same site. One specimen from Gawler, South Australia (WARI) is generally much darker, with the frons, face and vertex black. One specimen from the Bunya Mountains National Park, Queensland (AMSA) lacks the black markings on the mesoscutum, propleuron and dorsal T1 and is generally a darker brown.

Comments

The females of *P. spinitarsis* comb. nov. are easily separated from most other *Pseudofoenus* by the asymmetrical hind tarsal segments 1 and 2, each tipped with a stout apical spine (Fig. 8.180). This species is similar in appearance to *P. darwini* comb. nov. and *P. crosskeyi* sp. nov. (see under *P. darwini* for comments). Males of this species are similar to the females, but lack the stout latero-apical spines on segments 1-2 of both the mid and hind tarsi. Little is known of the biology of this species, although one specimen has been collected from flowers of *Angophora* sp. (Myrtaceae) (AMSA). It has been collected from many localities in south-eastern Australia and Tasmania and from two localities in central Australia (Fig. 8.198).

Pseudofoenus swani (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

Pseudofoenus taylori sp. nov.

(Figs 8.140-8.143, 8.181, 8.198)

Material Examined

Holotype. ♀, "W. Aust., 16 km SW of Tangadee Homestead (24.25S, 118.56E), 22 August 1984, T.F. Houston & B.P. Hanich, 589-5" "on flowers of *Ptilotus*" (WAMA).

Paratypes. **Western Australia:** 2♀, Nilemah Station, 80km S Denham, 8-9.x.1969, H. Evans & R.W. Matthews (MCZC); 1♀, Youanmi, 13.x.1974, A.M. & M.J. Douglas (WAMA); 2♂, 40km N Yuna, 5.ix.1981, G.A. Holloway (AMSA); 1♂, 37km NE Laverton, 28.21S 122.37E, 10-12.ix.1982, B. Hanich & T.F. Houston (WAMA); 1♂, 32km N Charlies Knob, 25.03S 124.59E, 6.viii.1983, T.F. Houston & R.P. McMillan (WAMA); 1♀, 1♂, 25km SW of Tangadee Homestead (24.25S, 118.56E), 22 August 1984, T.F. Houston & B.P. Hanich (WAMA, WARI); 2♂, same data as holotype (WAMA, WARI); 1♂, 15.7km NNW Wannoo, 26.49S 114.37E, 24.viii.1984, T.F. Houston & B.P. Hanich (WAMA); 1♀, 13km S Wannoo, 26.49S 114.37E, 24-28.viii.1984, T.F. Houston & B.P. Hanich (WAMA).

Other specimens examined. **Northern Territory:** 1♀, 33km WNW Alice Springs, 23.36S 133.34E, 30.ix.1978, J.C. Cardale (ANIC); 1♀, 9km NbyE Alice Springs, 23.38S 133.53E, 1.x.1978, J.C. Cardale (ANIC).

Female

Length. 13.3 mm (13-14 mm).

Colour. Body generally red, head black except for small red spot on vertex near eyes, last few metasomal segments black, with variable amounts of black on propleuron, mesoscutum, scutellum, tegulae, and basally on hind tibiae, antennae brown black, stout emergent setae on hind tibia and hind tarsal segment 1 golden brown.

Head. Wider than long when viewed dorsally (Fig. 8.140); face imbricate, pubescence short; frons rugose medially, punctate-imbricate laterally, pubescence short; frontal carina strong, reaching median ocellus; vertex imbricate except rugose immediately behind lateral ocelli, pubescence short; gena imbricate, pubescence short; occipital carina broad, smooth; malar space 0.05 x height eye; clypeus 1.43 (1.37-1.47) x as wide as high, imbricate, pubescence short; distance from lateral ocellus to eye margin 0.41 (0.38-0.44) x distance between lateral ocellus and occipital carina; scape 3.2 (2.8-3.7) x length pedicel; first flagellomere 1.38 (1.31-1.46) x as long as scape, 1.88 (1.84-2.00) x as long as second flagellomere; mandible with two prominent medial teeth, basal tooth triangular.

Mesosoma. Propleuron punctate-imbricate, ventro-lateral carina absent, pubescence short; lateral pronotum rugulose in dorsal part, ventral part rugose; medial and lateral lobes of mesoscutum rugose, with scattered short setae, medial line present; scutellum, axillae and metanotum rugose; mesepisternum with short pubescence, dorsal part rugose (almost strigate), separated from ventral part by carinate depression, ventral part rugose with median transverse carina; mesepimeron broad, carinate; metapleuron rugose, pubescence short; propodeum rugose, short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with short setae anteriorly; hind coxa punctate-imbricate, strigate in coxal depression, pubescence short; hind trochanter with weak groove on inner lateral surface, imbricate, with a few scattered short setae (Fig. 8.141); hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short, with scattered stout emergent setae, these associated with punctures; hind femur 4.40 (4.14-4.60) x as long as wide, 0.79 (0.74-0.83)x length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segments 1-2 somewhat flattened, segment 1 with stout emergent setae, segment 1, 1.76 (1.58-1.91) x length segment 2; segment 2, 1.79 (1.71-1.92) x length segment 3; segment 3, 1.77 (1.71-1.88) x length segment 4; segment 4, 0.50 (0.44-0.57) x length segment 5 (Fig. 8.181); hind tarsal claw 0.62 (0.56-0.71) x length segment 5 (Fig. 8.181); hind wing with 3 hamuli, distance between basal and middle hamuli greater than distance between second and apical hamuli.

Metasoma. 2.70 (2.41-2.82) x length of mesosoma; T1 punctate-imbricate, longitudinal median ridge absent (Fig. 8.142).

Male

Similar to female except: digitus 0.9 x length basiparamere; basiparameres smooth.

Variation

Two specimens from Alice Springs (ANIC) have variable amounts of black on mesepisternum and metapleuron, and less black coloration on the metasoma segments and hind tibiae. These specimens are also less pubescence on the head.

Comments

This is a large species (13-14 mm)) with a strong frontal carina and the metasoma without a longitudinal ridge. It is similar to *P. masneri* sp. nov. and *P. ferrugineus* comb. nov., but can be readily distinguished from these and other species by those characters given in the key.

Pseudofoenus taylori sp. nov. has been collected from flowers of *Ptilotus* sp. (Amaranthaceae) (WAMA, WARI), *Dicrastylis flexuosus* (Price) C. Gardner (Verbenaceae) (WAMA, WARI), *Baeckea* sp. (Myrtaceae) (WAMA) and *Micromyrtus hymenonema* (F. Muell.) C. Gardner (Myrtaceae) (WAMA). It has also been collected flying over the nesting area of the bee *Ctenocolletes nicholsoni* (Cockerell) (Stenotritidae) (WAMA) (Houston 1987). This species has been collected from a number of localities in Western Australia (Fig. 8.198). Two specimens have also been collected from near Alice Springs, although given the variation in colour and pubescence, they have been excluded from the type series. Further collecting may show them to be a separate species.

This species is named after Dr Gary Taylor, Department of Applied and Molecular Ecology, Waite Campus, The University of Adelaide.

Pseudofoenus whiani (Jennings and Austin) comb. nov.

Comments

This species was recently described by Jennings and Austin (1997b - see Appendix A5) and is hereby transferred to *Pseudofoenus s. l.*

8.4.2.2.4. Species *incertae sedis*

Eufoenus flavinervis (Kieffer)

Hyptiogaster flavinervis Kieffer, 1907: 272. - Kieffer, 1912: 199; Hedicke, 1939: 48; Crosskey, 1953a: 383.

?*Eufoenus flavinervis* Crosskey, 1962: 398.

Holotype. ♂, New South Wales. Location of holotype unknown.

Comments

On the basis of the original description (Kieffer 1907), Crosskey (1962) tentatively placed this species in *Eufoenus*. Given that the location of the type specimen is unknown and no other specimens have to date been found that match the original description, the status of this species must remain doubtful.

Eufoenus melanopleurus (Crosskey)

(Figs 8.144-146, 8.182)

Hyptiogaster melanopleura Crosskey, 1956: 121.

Eufoenus melanopleurus Crosskey, 1962: 398.

Material Examined

Holotype. ♂, "50 miles west of Wilcannia, New South Wales, 23.xi.1949, E.F. Riek" (ANIC). Metasoma missing.

Male

Length. 8.5 mm (Crosskey 1956).

Colour. Body generally yellow orange, with variable amounts of dark brown on head, pleura and around tegulae, lighter brown on fore and mid trochanters, mid and hind coxae, and tips of mandibles.

Head. Wider than long when viewed dorsally (Fig. 8.144); face punctulate, pubescence short; frons punctulate, pubescence short, denser near antennal scrobes; frontal carina present; vertex smooth, with scattered punctures, a shallow lateral groove behind lateral ocelli, not reaching past ocelli, with scattered short setae; gena bulges somewhat behind eyes (Fig. 8.144); gena smooth, with scattered punctures, with scattered short setae; occipital carina weakly carinate; malar space 0.07 x height eye; clypeus 2.33 x as wide as high, smooth, with a few punctures medially, rugulose laterally, with short medial carina anteriorly; distance from lateral ocellus to eye margin 0.8 x distance between lateral ocellus and occipital carina; scape 2.4 x length pedicel; first flagellomere 1.25 x as long as scape, 1.7 x as long as second flagellomere; mandible with two prominent medial teeth, most apical tooth somewhat bulbous, basal tooth not visible (Fig. 8.145).

Mesosoma. Propleuron rugulose medially, punctulate-imbricate laterally, ventro-lateral carina present, pubescence long; lateral pronotum weakly imbricate with a few shallow punctures; medial and lateral lobes of mesoscutum rugose with scattered short setae, medial line absent; scutellum, axillae and metanotum rugose; mesepisternum with long pubescence, dorsal part smooth separated from ventral part by carinate depression, ventral part smooth, with a few small scattered punctures, with median transverse carina; mesepimeron broad, carinate; metapleuron with long pubescence, dorsal part rugose dorsally to smooth ventrally, ventral part rugose; propodeum rugose, with short median longitudinal carina posteriorly; propodeal spiracle elongate, fringed with long setae; hind coxa medially punctate-imbricate at base to strigulate apically, pubescence long laterally; hind trochanter with weak transverse groove dorsally and on inner lateral surface (Fig. 8.146), imbricate, with short scattered setae; hind femur imbricate, pubescence short; hind tibia punctate-imbricate, pubescence short and with scattered stouter emergent setae; hind femur 3.75 x as long as wide, 0.9 x length hind tibia;

hind tibia without ventro-apical pecten of short robust spines; hind tarsal segments 1-4 with ventro-apical pecten of short robust spines, segment 1, 3.0 x length segment 2; segment 2, 0.9 x length segment 3; segment 3, 1.4 x length segment 4; segment 4, 0.45 x length segment 5 (Fig. 8.182); hind tarsal claw 1.0 x length segment 5 (Fig. 8.182); hind wing with 3 hamuli.

Metasoma. Missing.

Female

Unknown.

Comments

This species is known only from the holotype male. It differs from all other *Pseudofoenus* in the gena being bulbous behind the eyes (Fig. 8.144). The presence of an indistinct groove on the hind trochanter (Fig. 8.146), which Crosskey (1956, 1962) overlooked, suggests that this species might belong to *Hyptiogaster*, although this is not conclusive. However, given that no females have been associated with the male, the placement of this species is doubtful. It is known only from the holotype locality.

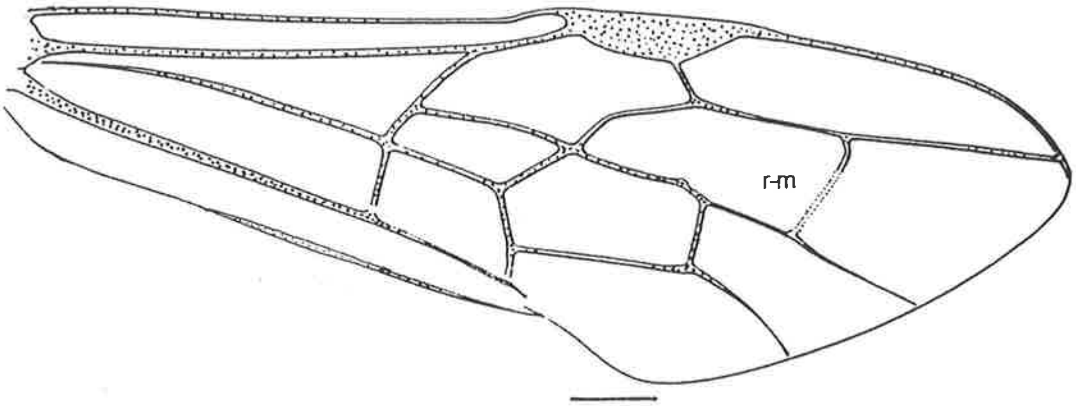
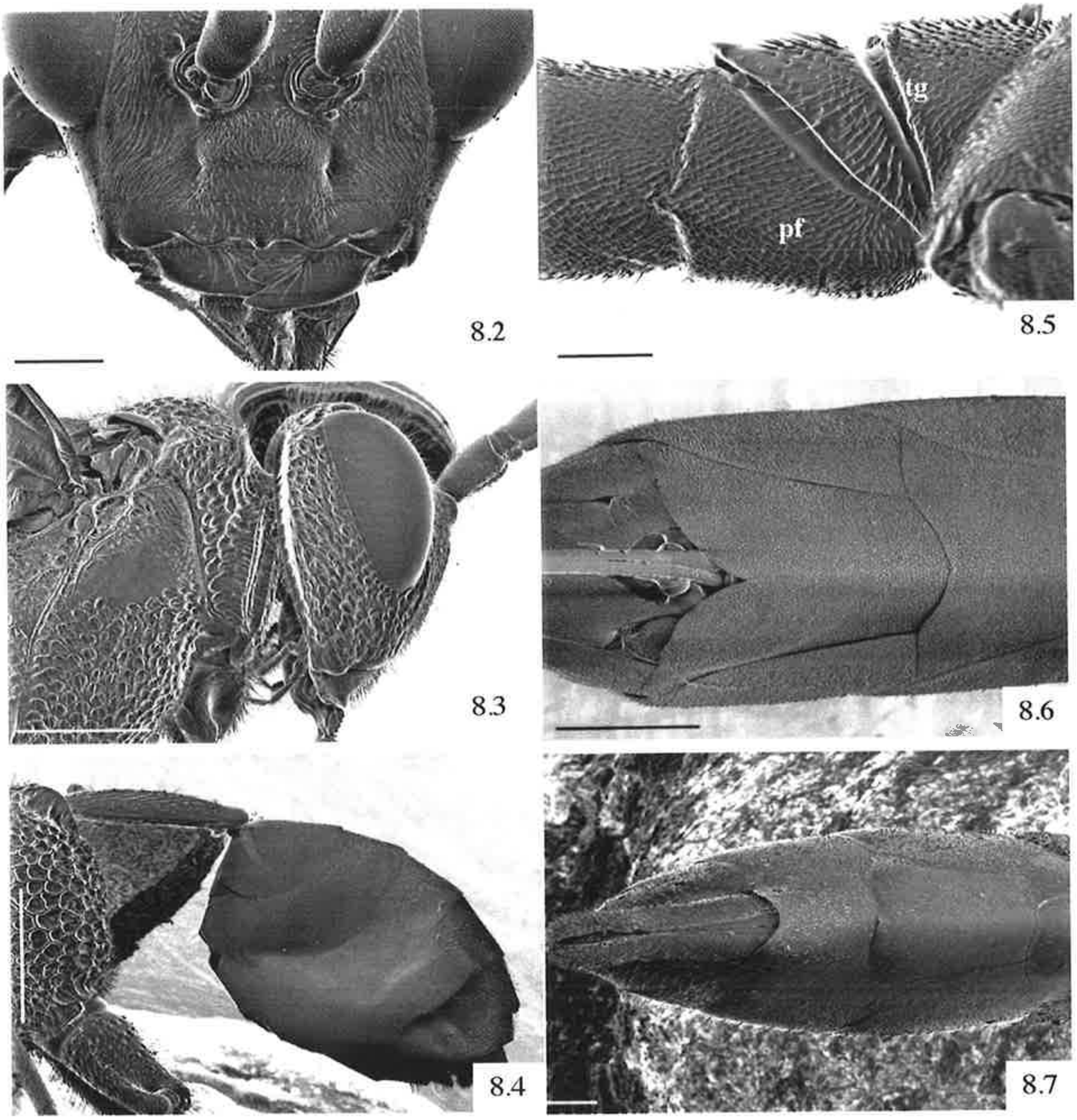
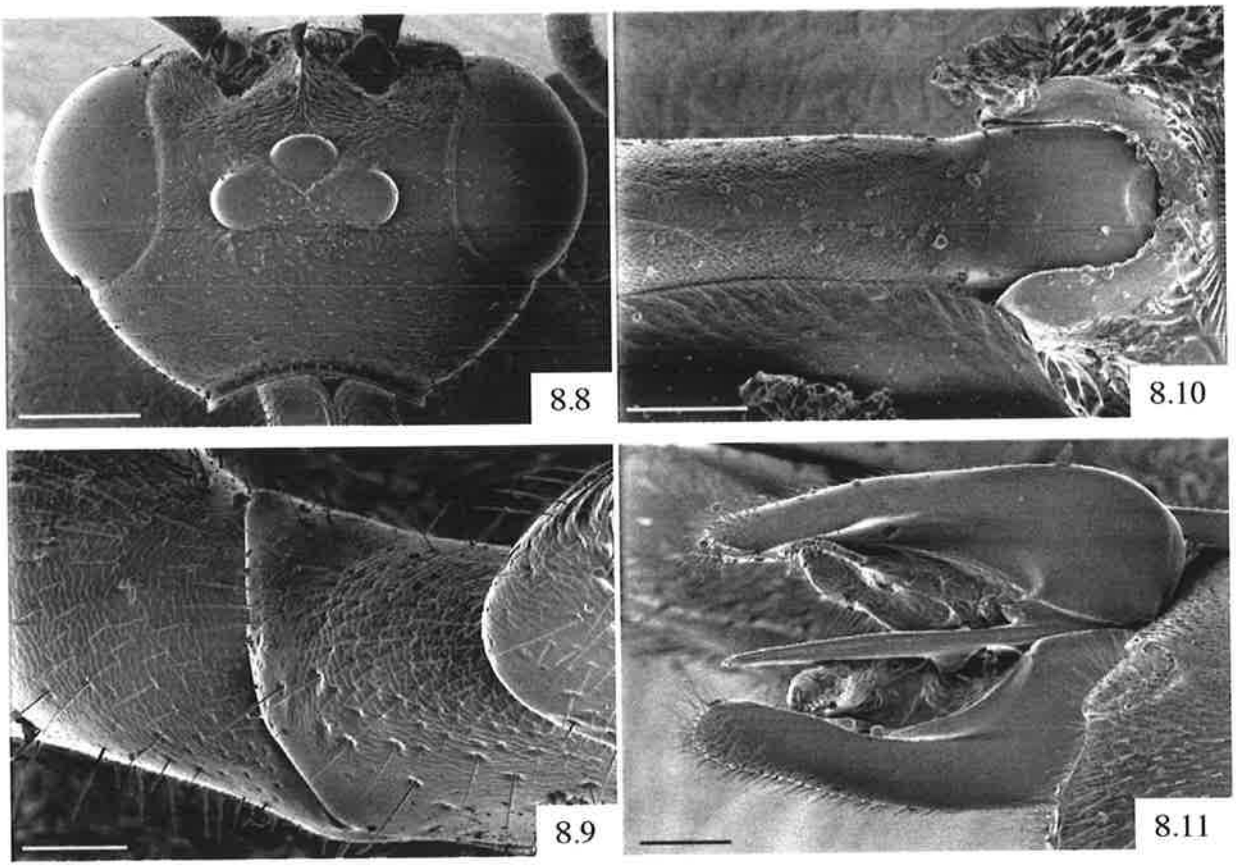


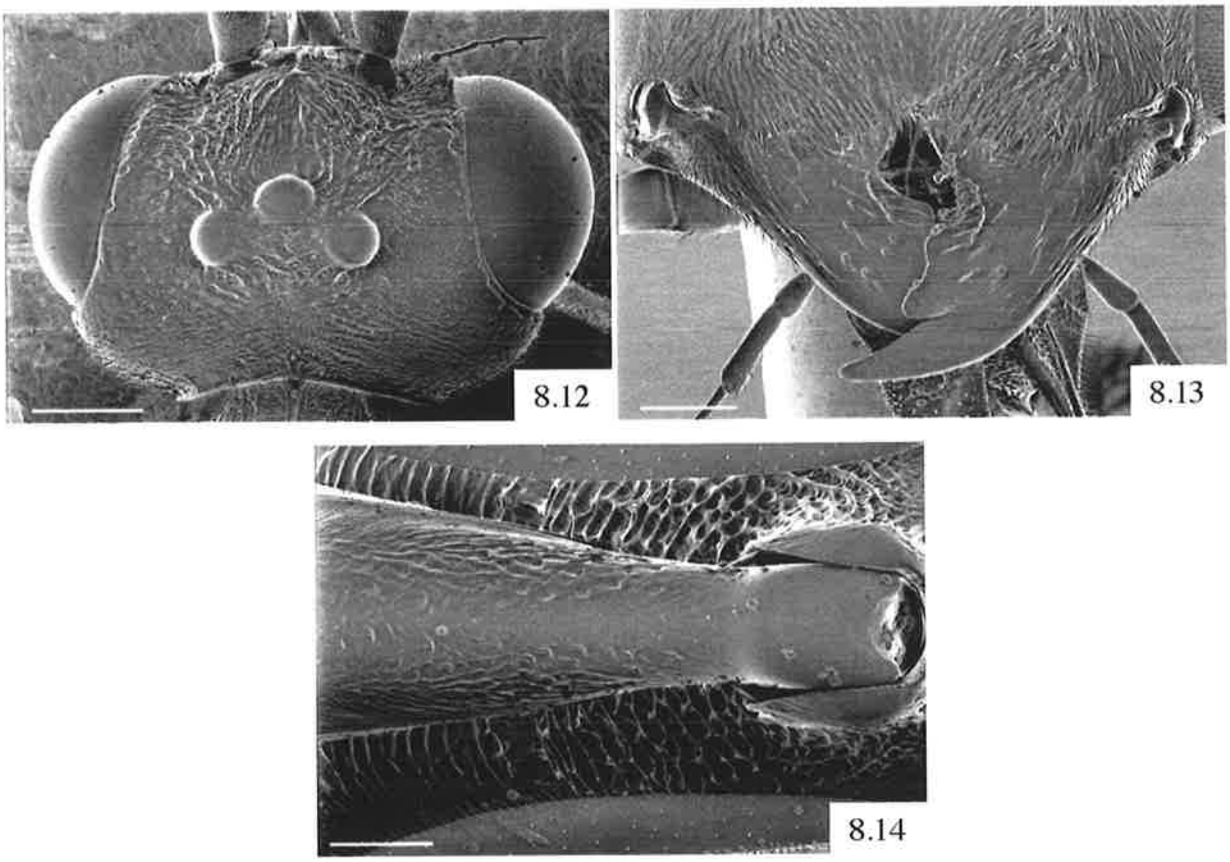
Figure 8.1. Fore wing of *Pristaulacus rufus* (Westwood) showing vein r-m. Scale line: 0.5 mm.



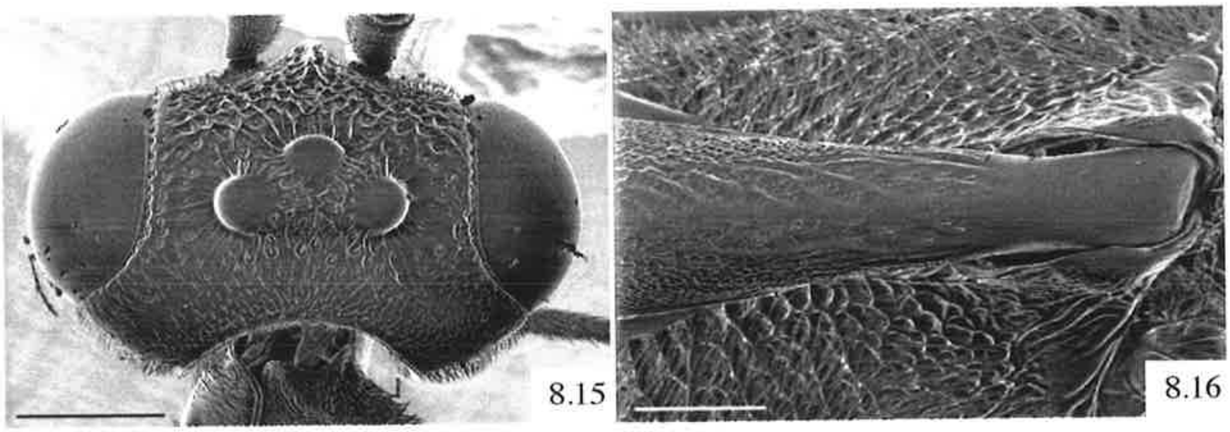
Figuress 8.2-8.7. **8.2.** anterior view of head of *Pristaulacus rufus* (Westwood), ♀; **8.3.** lateral view of head and mesosoma of *Evania* sp., ♂; **8.4.** lateral view of metasoma of *Evania* sp., ♂; **8.5.** lateral view of hind trochanter and prefemur of *Gasteruption* sp. 1, ♀ (tg = trochanteral groove, pf = prefemur); **8.6.** ventral view of subgenital sternite of *Gasteruption* sp. 1, ♀; **8.7.** ventral view of subgenital sternite of *P. darwini* comb. nov., ♀. Scale lines: *8.2*, *8.6-8.7*, 500 µm, *8.3-8.4*, 1 mm, *8.5*, 100 µm.



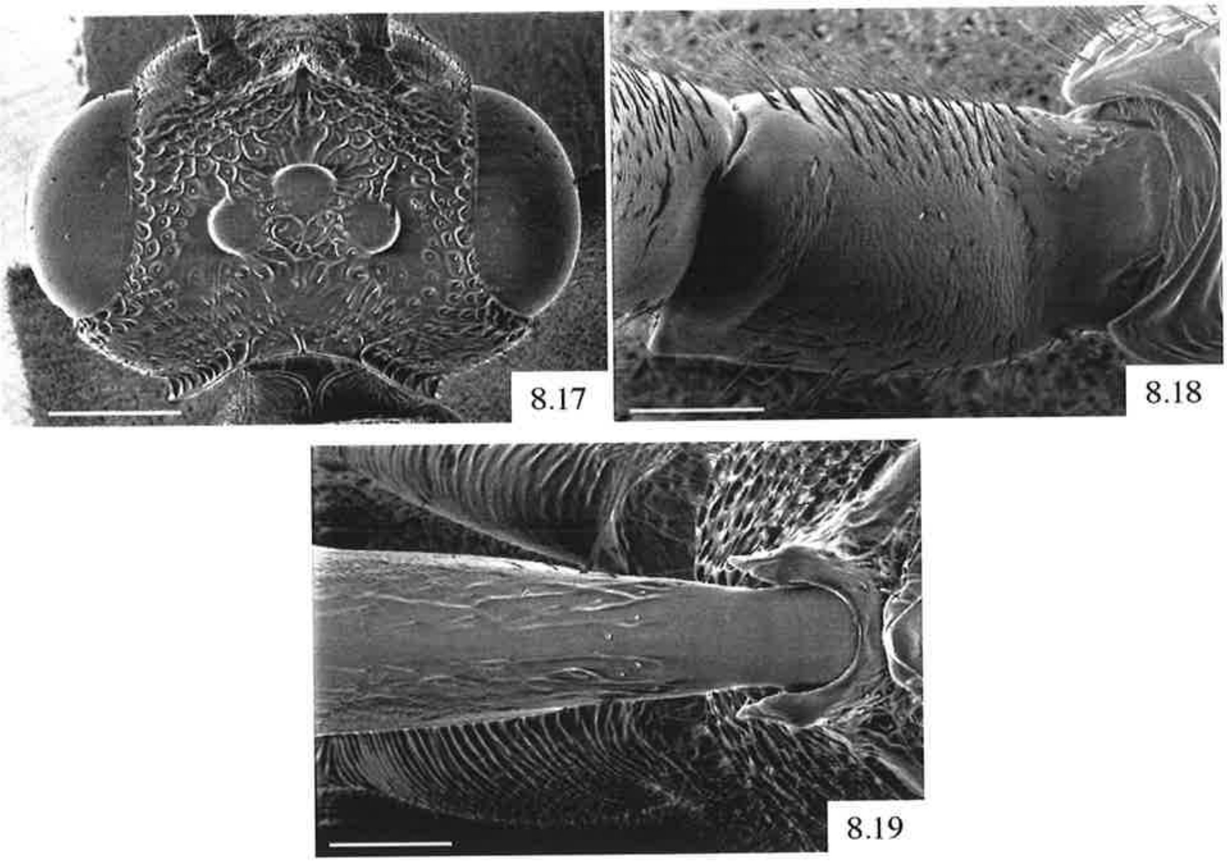
Figuress 8.8-8.11. *Pseudofoenus morganensis* sp. nov. **8.8.** dorsal view of head, holotype ♀; **8.9.** dorso-lateral view of hind trochanter, holotype ♀; **8.10.** dorsal view of T1, holotype ♀; **8.11.** dorsal view of genitalia, paratype ♂. Scale lines: *8.8*, 500 µm, *8.9*, 100 µm, *8.10-11*, 200 µm.



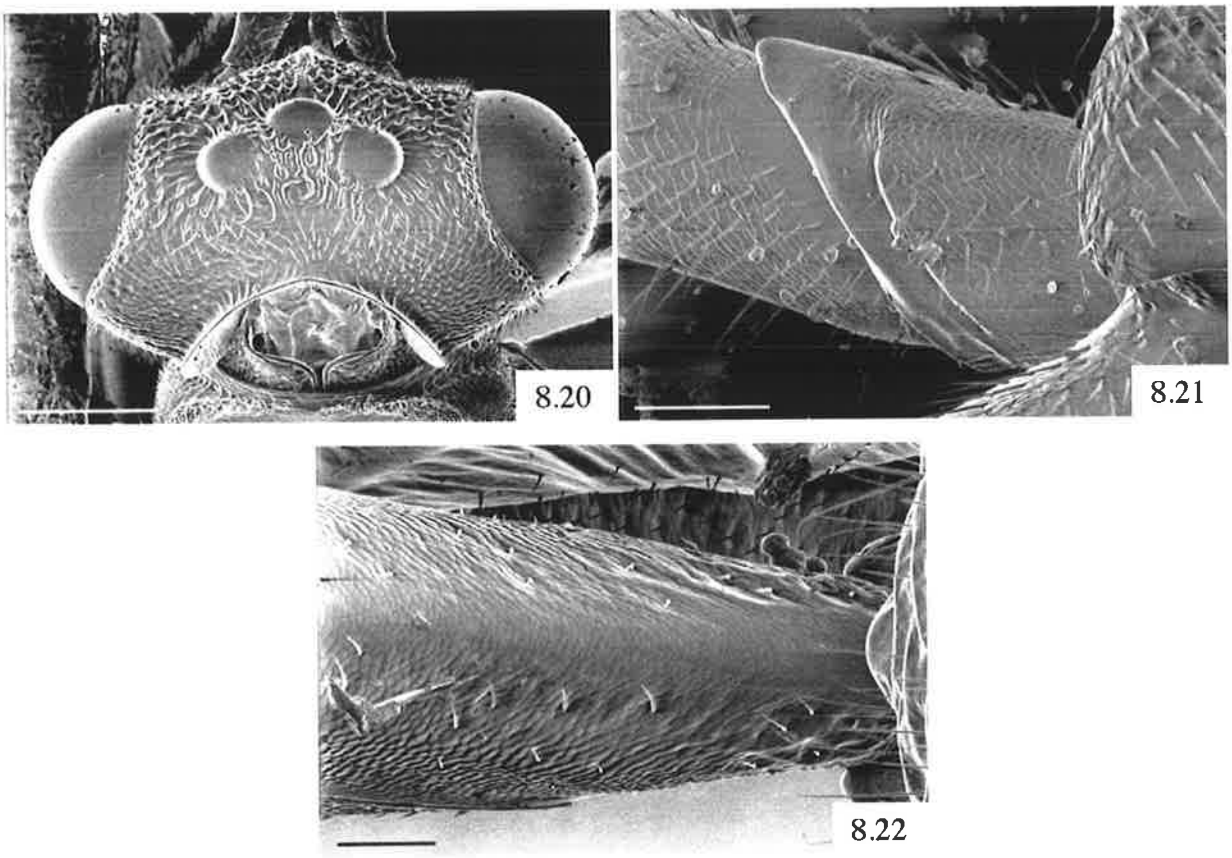
Figures 8.12-8.14. *Pseudofoenus cardalae* sp. nov., paratype ♀. **8.12.** dorsal view of head; **8.13.** anterior view of mouthparts; **8.14.** dorsal view of T1. Scale lines: *8.12,* 500 µm, *8.13-14,* 200 µm.



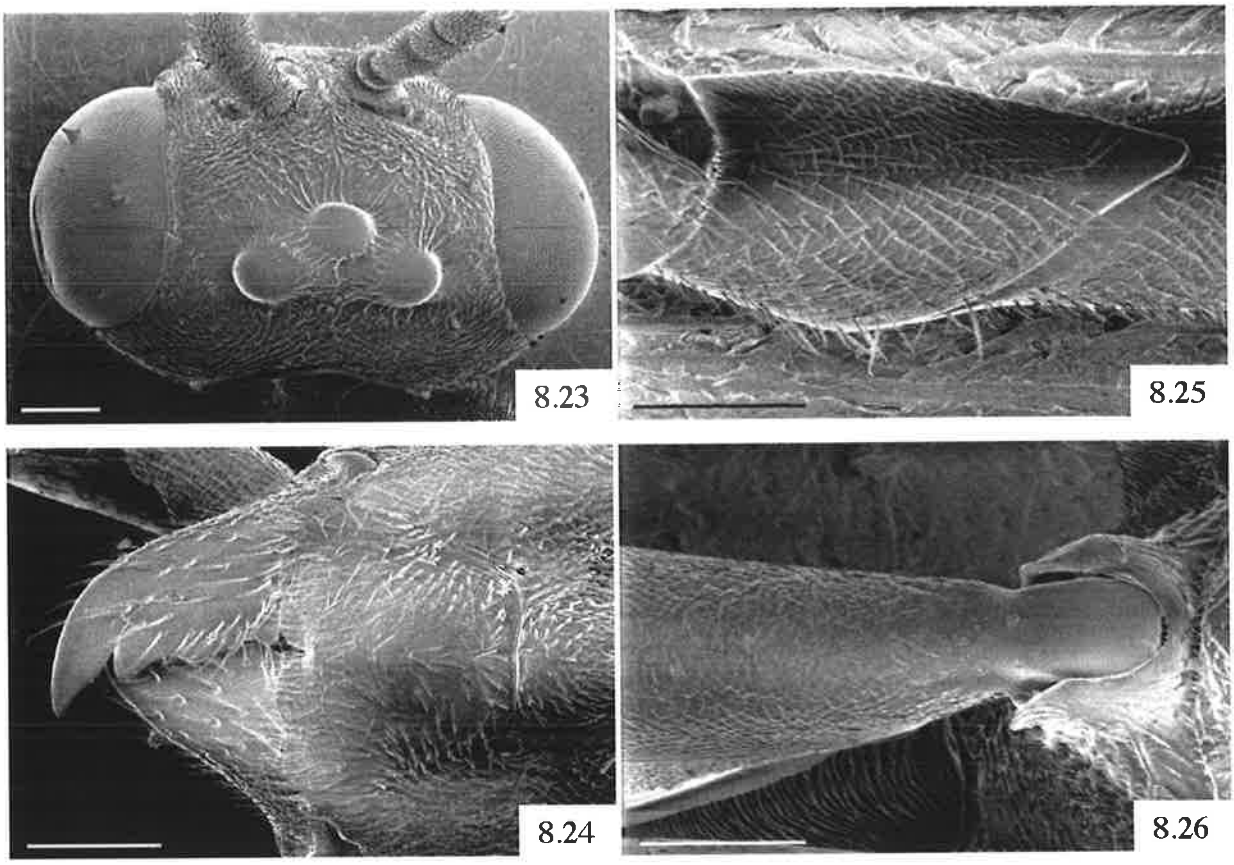
Figures 8.15-8.16. 8.15. dorsal view of head of *P. douglasi* sp. nov., paratype ♀; **8.16.** dorsal view of T1 of *P. douglasi* sp. nov., paratype ♀; Scale lines: *8.15*, 500 μm, *8.16*, 200 μm.



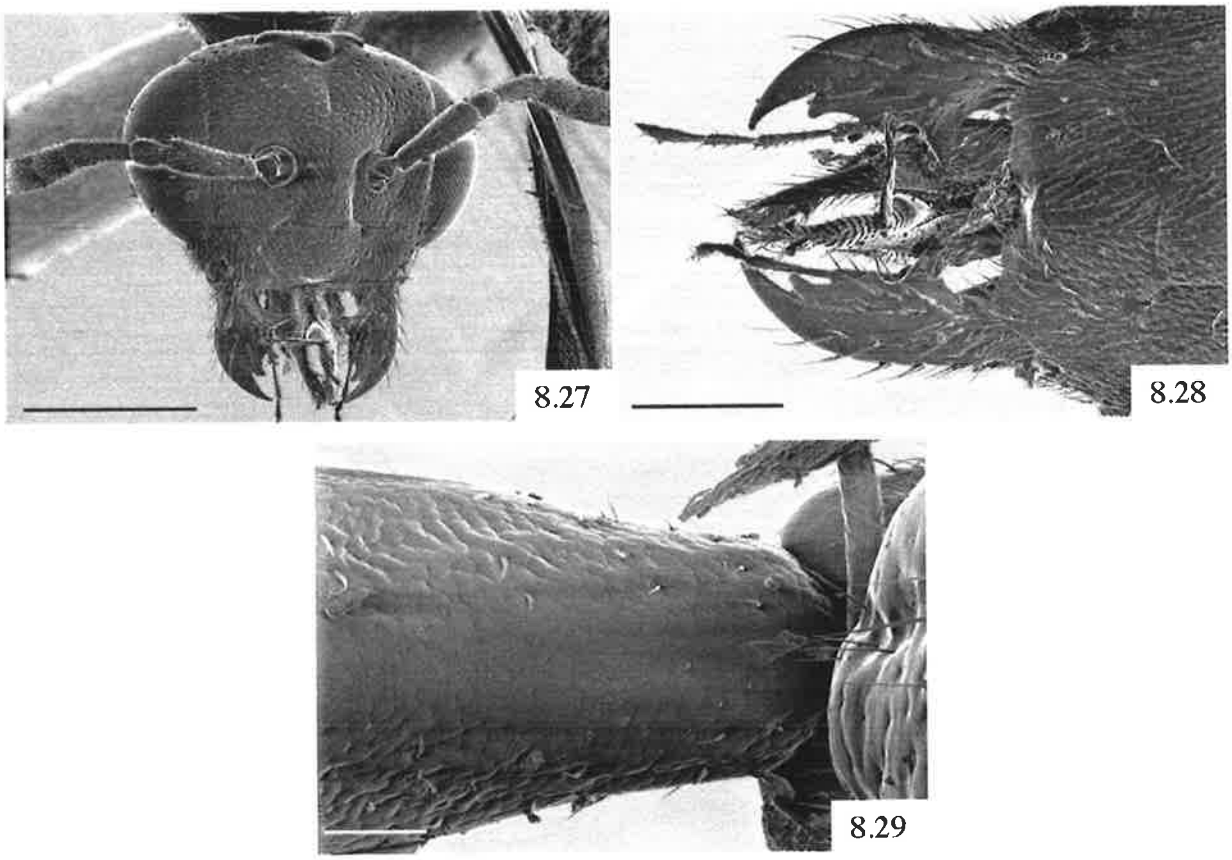
Figures 8.17-8.19. *Pseudofoenus ericae* sp. nov., paratype ♀. **8.17.** dorsal view of head; **8.18.** dorso-lateral view of hind trochanter; **8.19.** dorsal view of T. Scale lines: *8.17*, 500 μm, *8.18*, 100 μm, *8.19*, 200 μm.



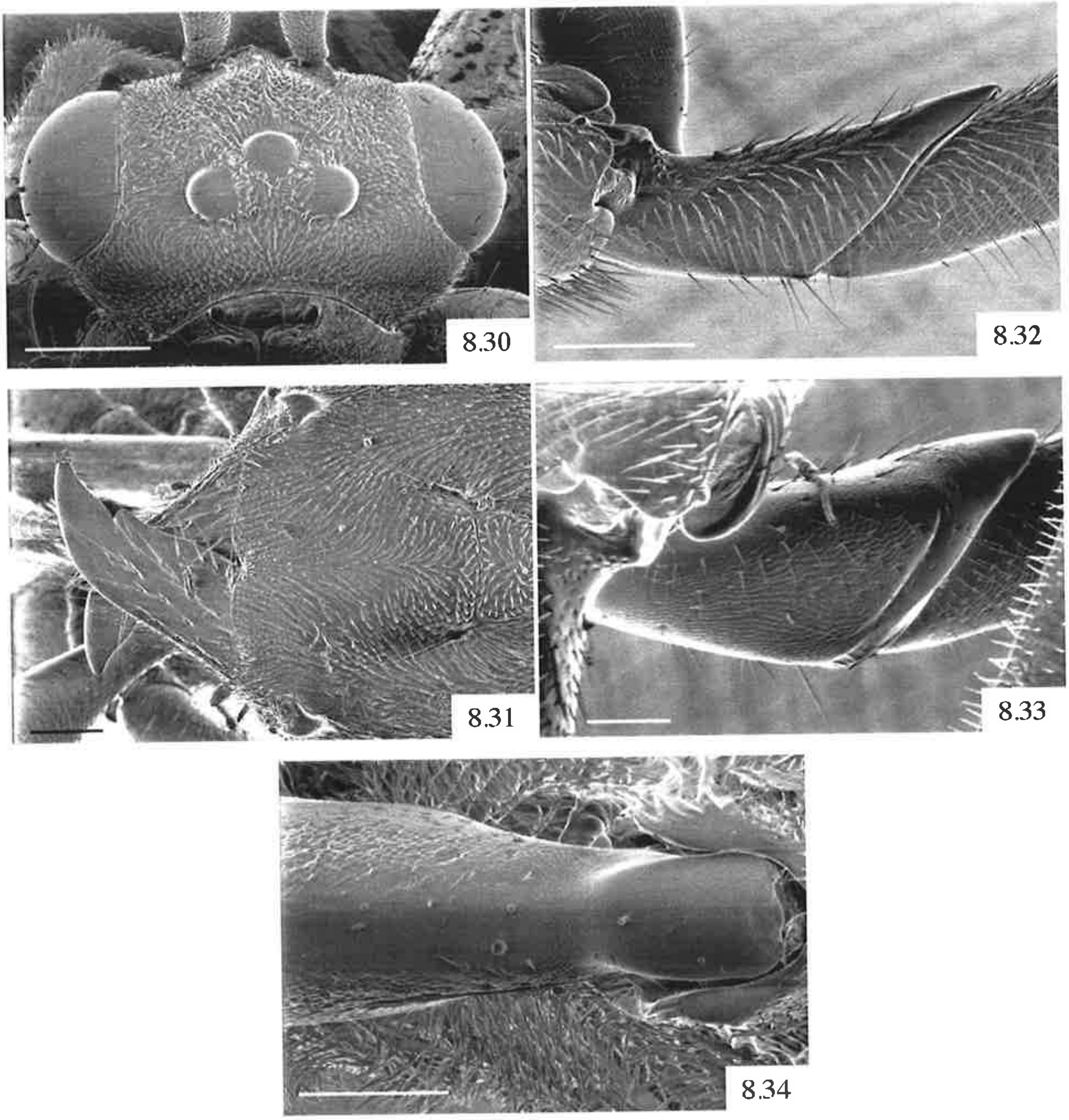
Figures 8.20-8.22. *Pseudofoenus feckneri* sp. nov. **8.20.** dorsal view of head, paratype ♀ ; **8.21.** dorso-lateral view of hind trochanter, paratype ♂; **8.22.** dorsal view of T, paratype ♀. Scale lines: *8.20*, 500 µm, *8.21-22*, 100 µm.



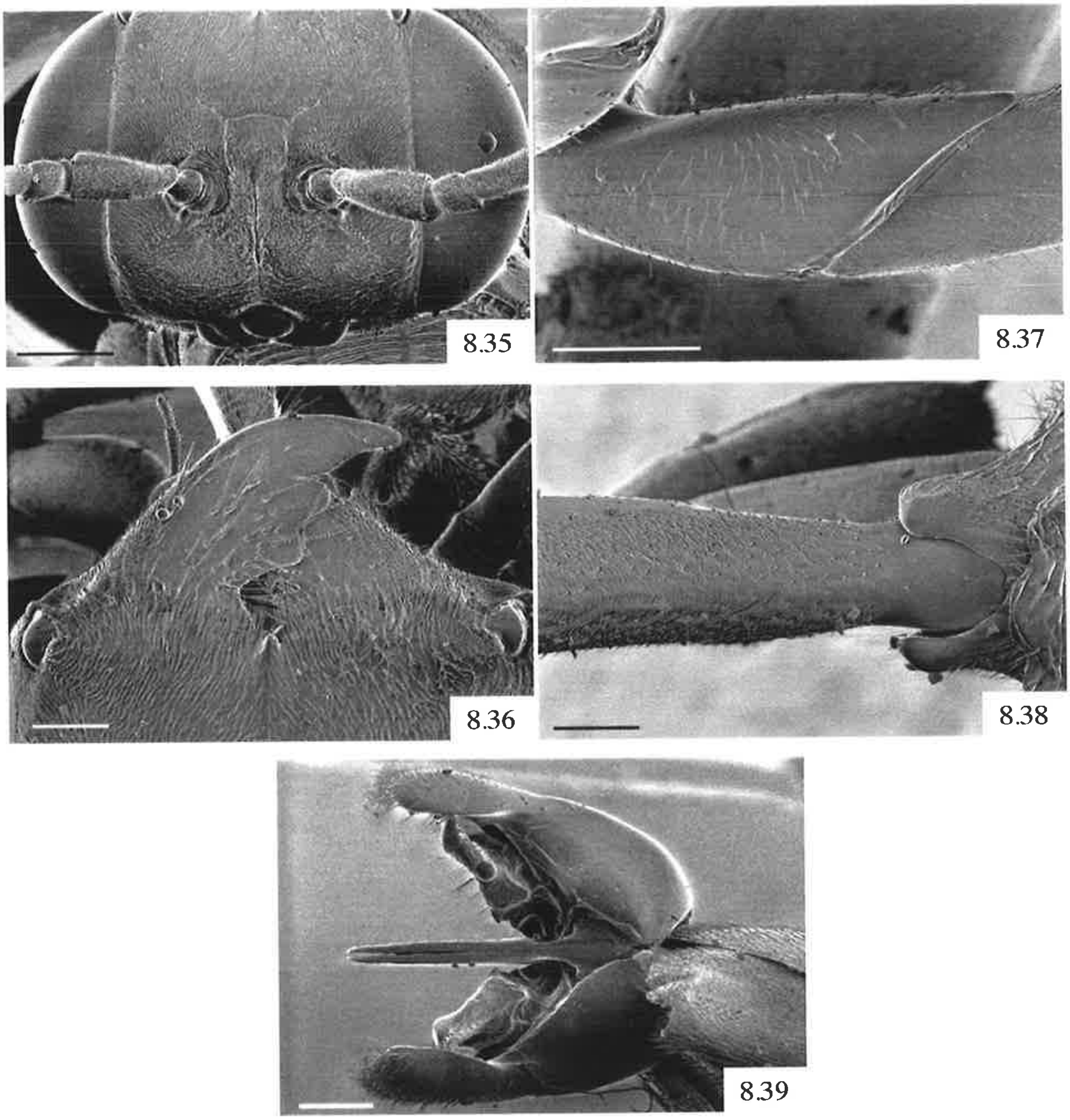
Figures 8.23-8.26. *Pseudofoenus microcephalus* (Crosskey) comb. nov., holotype ♀. **8.23.** dorsal view of head; **8.24.** anterior view of clypeus and mandibles; **8.25.** dorsal view of hind trochanter; **8.26.** dorsal view of T1. Scale lines: *8.23-25*, *8.22*, 200 µm, *8. 26*, 100 µm.



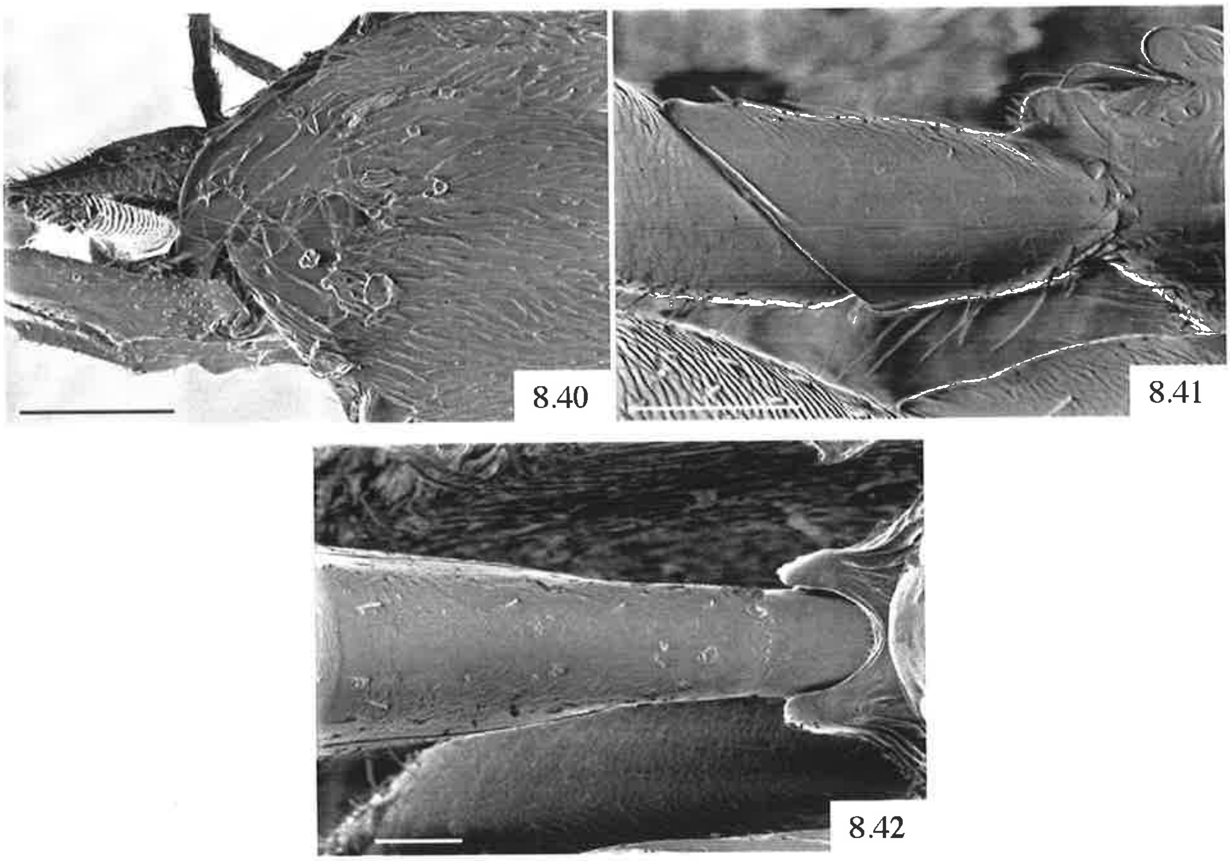
Figures 8.27-8.29. *Pseudofoenus minimus* (Turner) comb. nov. **8.27.** anterior view of head, ♀; **8.28.** anterior view of clypeus and mandibles, ♀; **8.29.** dorsal view of T1, ♂. Scale lines: *8.27*, 500 µm, *8.28*, 200 µm, *8.29*, 50 µm.



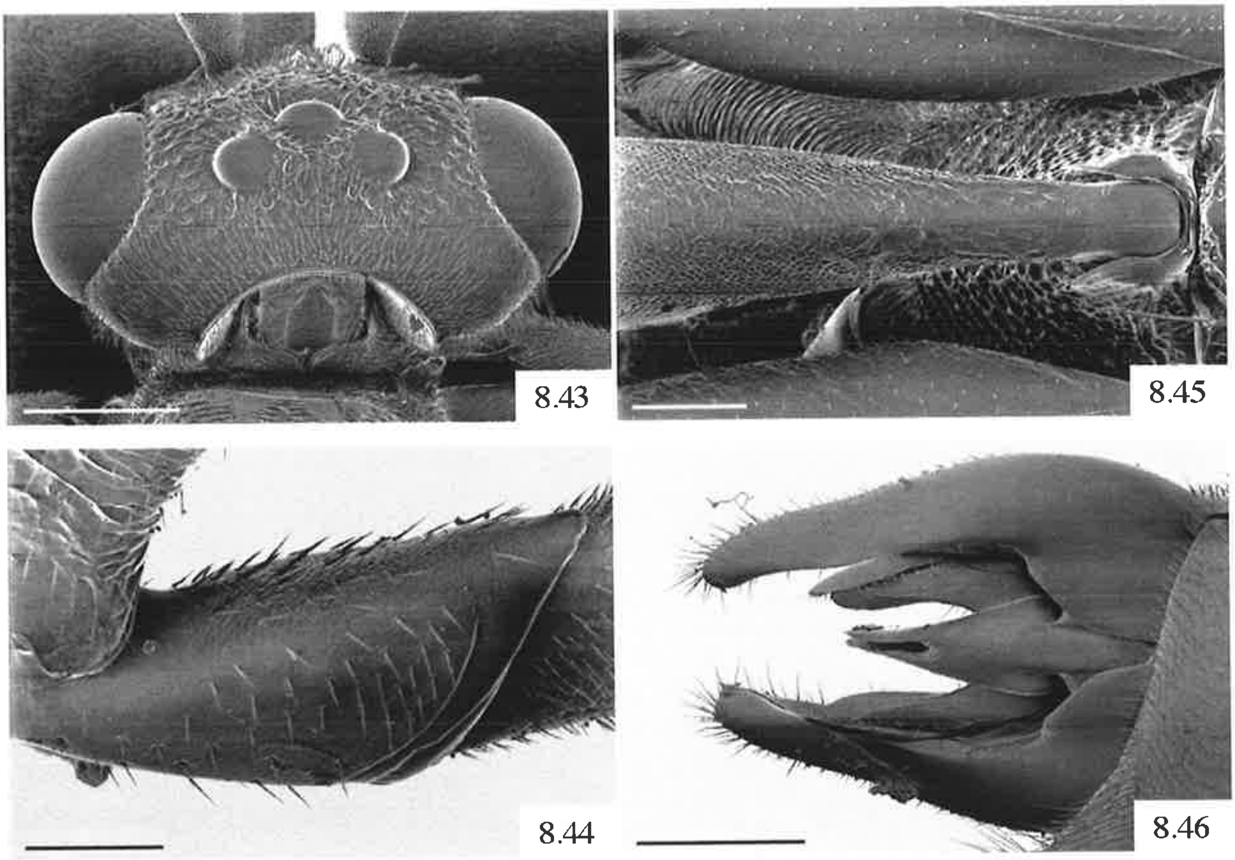
Figures 8.30-8.34. *Pseudofoenus antennalis* (Schletterer) comb. nov. **8.30.** dorsal view of head, ♂; **8.31.** anterior view of clypeus and mandibles, ♀; **8.32.** outer lateral view of hind trochanter, ♂; **8.33.** inner lateral view of hind trochanter, ♂; **8.34.** dorsal view of T1, ♂. Scale lines: *8.30,* 500 µm, *8.31-32, 8.34,* 200 µm, *8.33,* 100 µm.



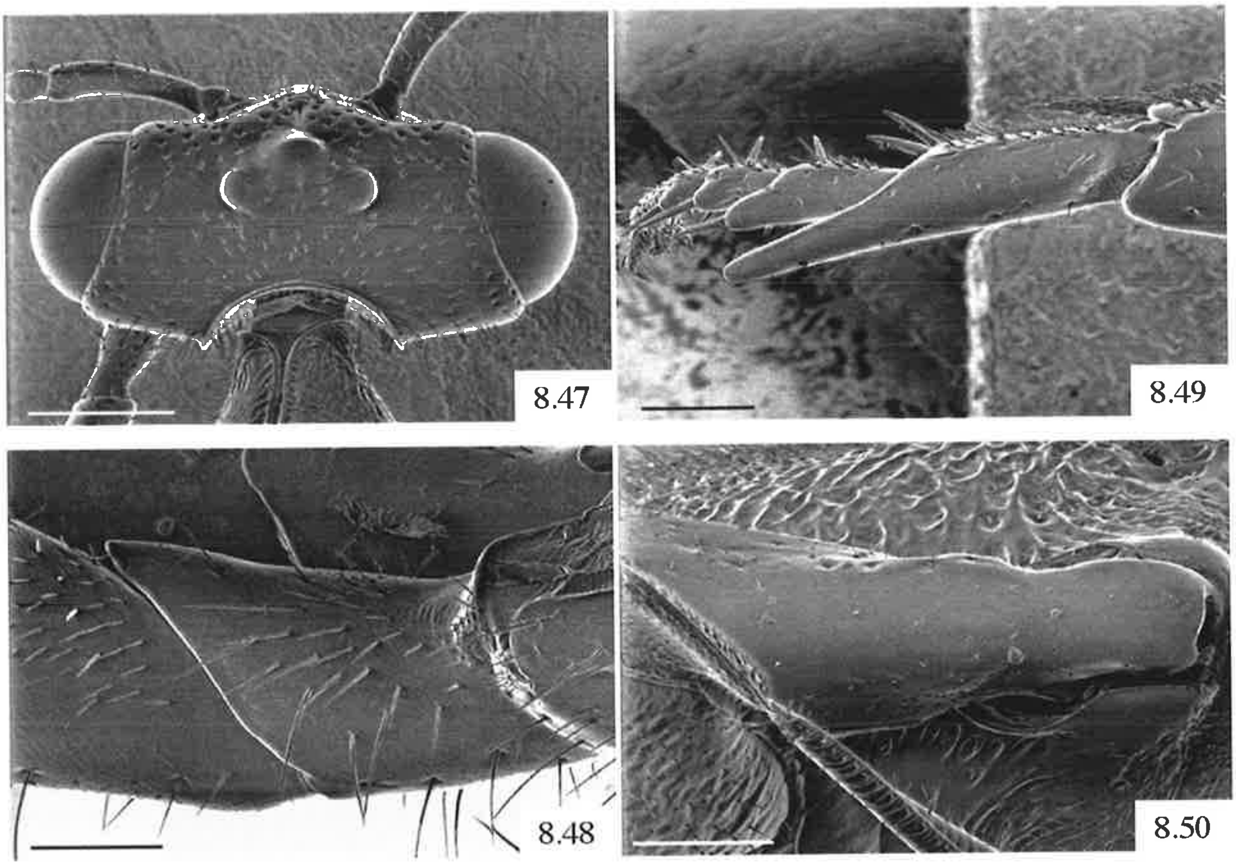
Figures 8.35-8.39. *Pseudofoenus australis* (Westwood) comb. nov. **8.35.** dorso-anterior view of head, ♀; **8.36.** anterior view of clypeus and mandibles, ♀; **8.37.** lateral view of hind trochanter, ♂; **8.38.** dorsal view of T1, ♀; **8.39.** dorsal view of genitalia, ♂. Scale lines: *8.35*, 500 µm, *8.36-39*, 200 µm.



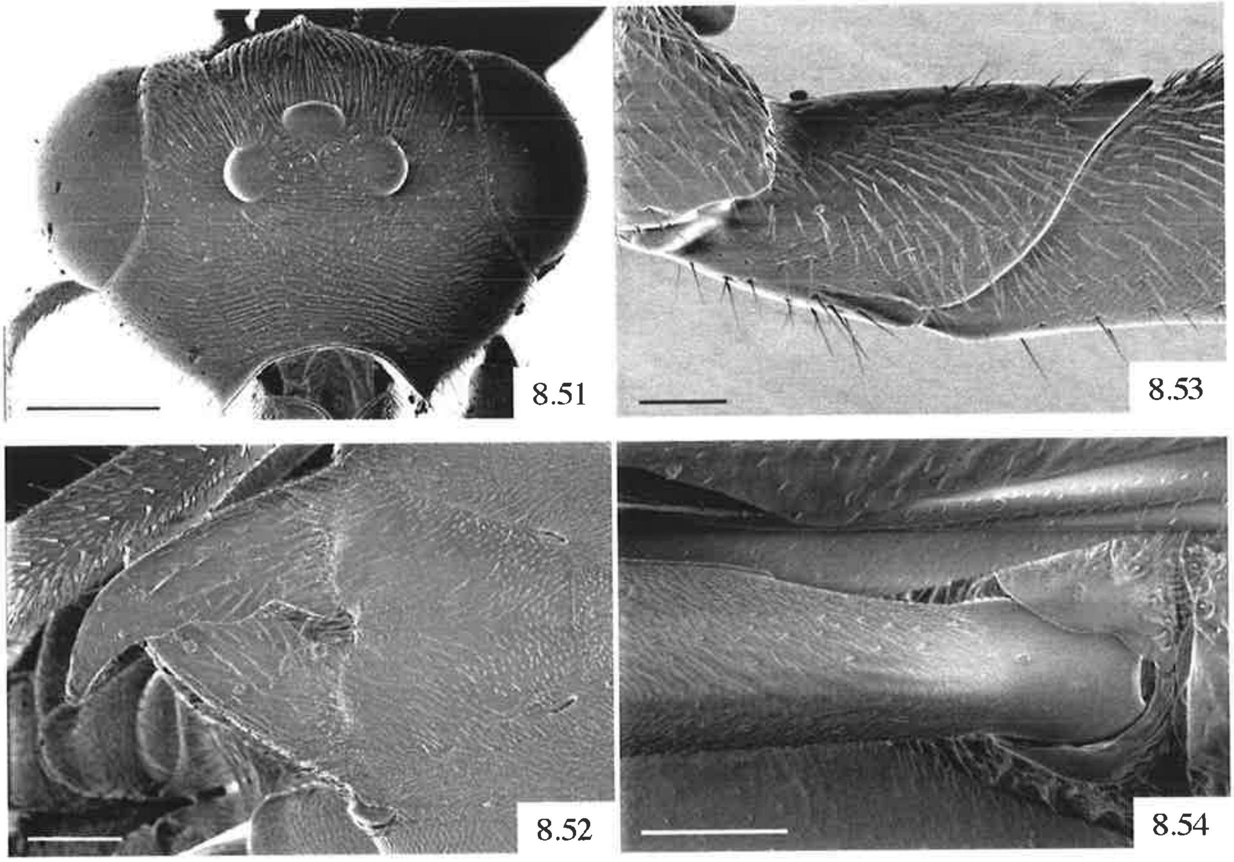
Figures 8.40-8.42. *Pseudofoenus beverlyae* sp. nov., paratype ♀. **8.40.** anterior view of clypeus and mandibles; **8.41.** outer lateral view of hind trochanter; **8.42.** dorsal view of T1. Scale lines: *8.40,* 200 µm, *8.41-42,* 100 µm.



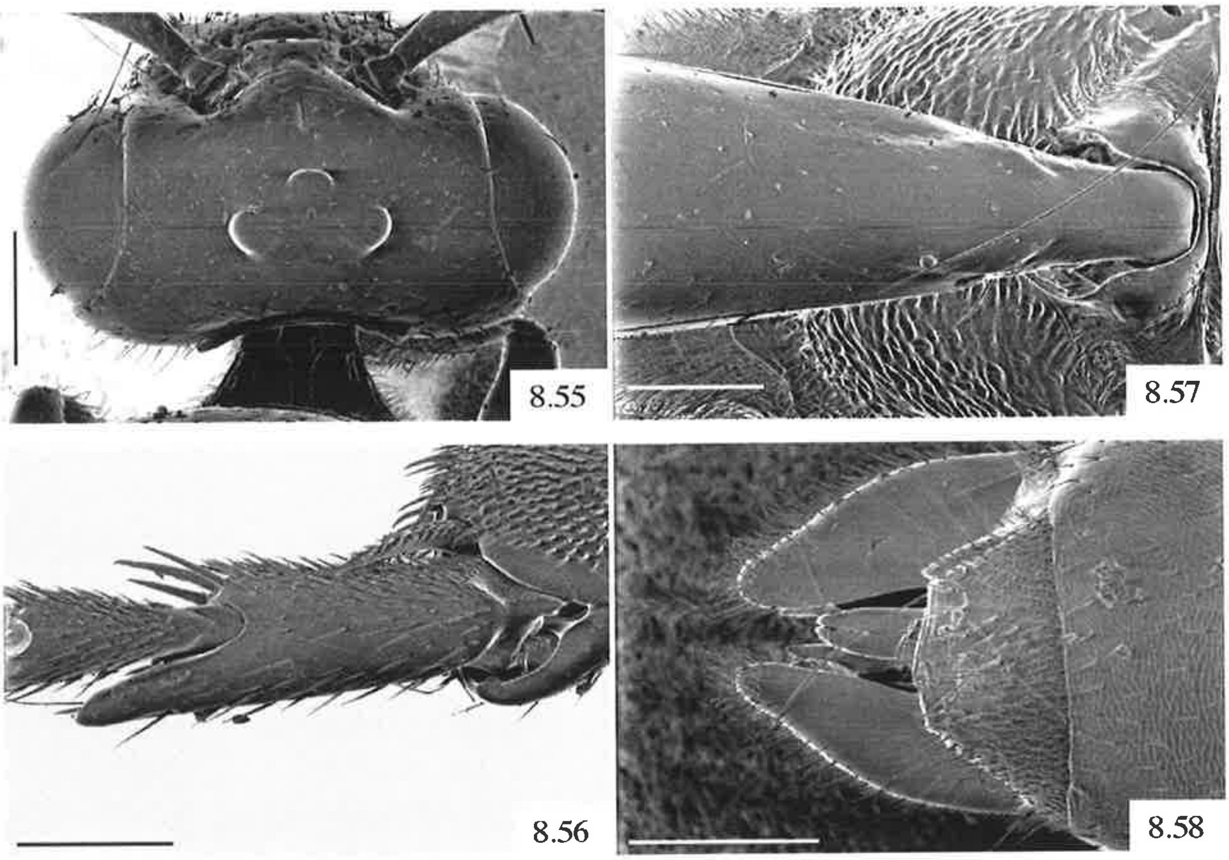
Figures 8.43-8.46. *Pseudofoenus collessi* sp. nov,. paratypes. **8.43.** dorsal view of head, ♀; **8.44.** inner lateral view of hind trochanter, ♀; **8.45.** dorsal view of T1, ♀; **8.46.** dorsal view of genitalia, ♂. Scale lines: *8.43*, 500 µm, *8.44*, 100 µm, *8.45-46*, 200 µm.



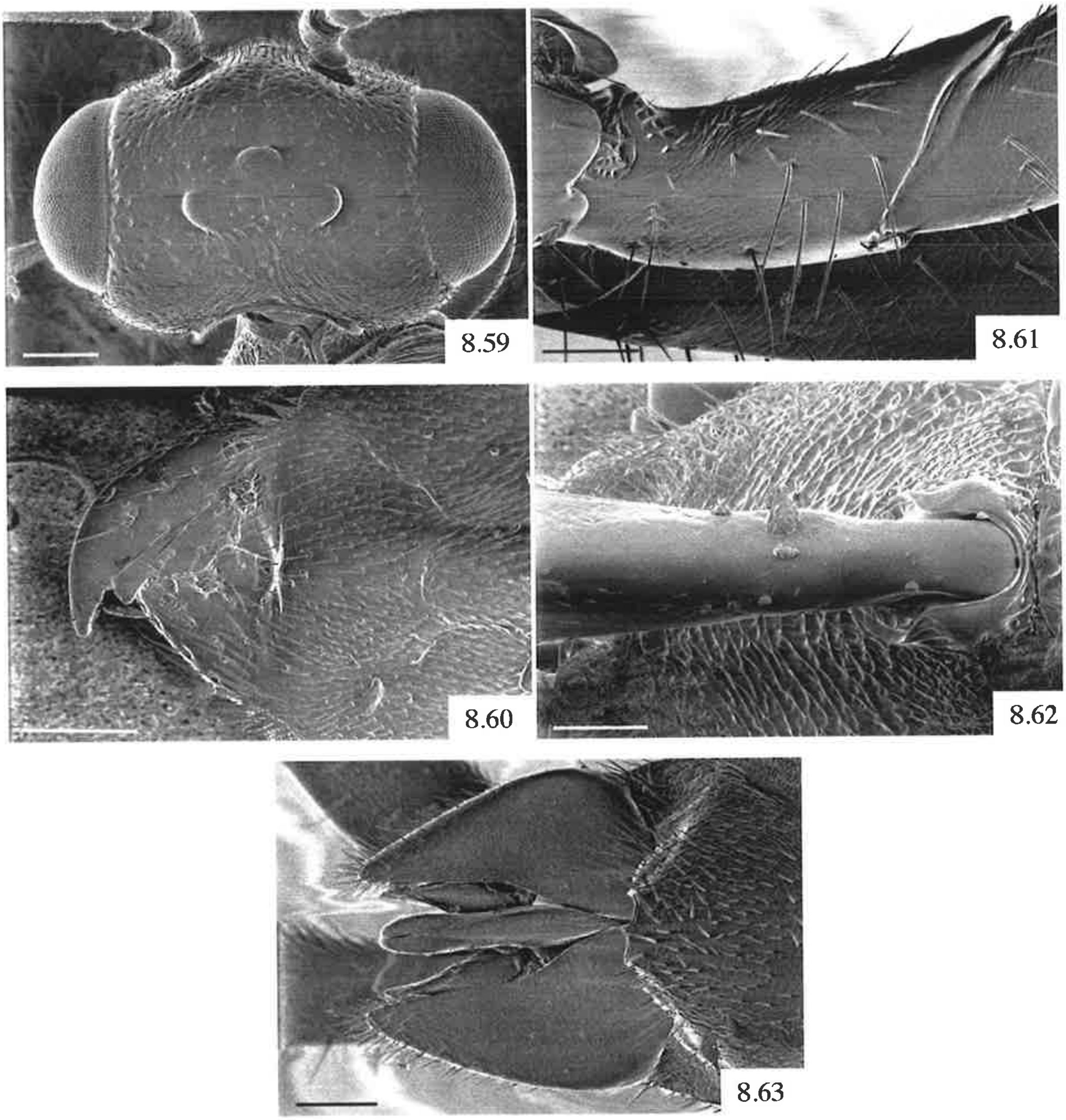
Figures 8.47-8.50. *Pseudofoenus coorowensis* sp. nov. **8.47.** dorsal view of head, ♀; **8.48.** lateral view of hind trochanter, ♂; **8.49.** lateral view of hind tarsal segments 1-3, ♀; **8.50.** dorsal view of T1, ♀. Scale lines: *8.47,* 500 µm, *8.48,* 100 µm, *8.49-50,* 200 µm.



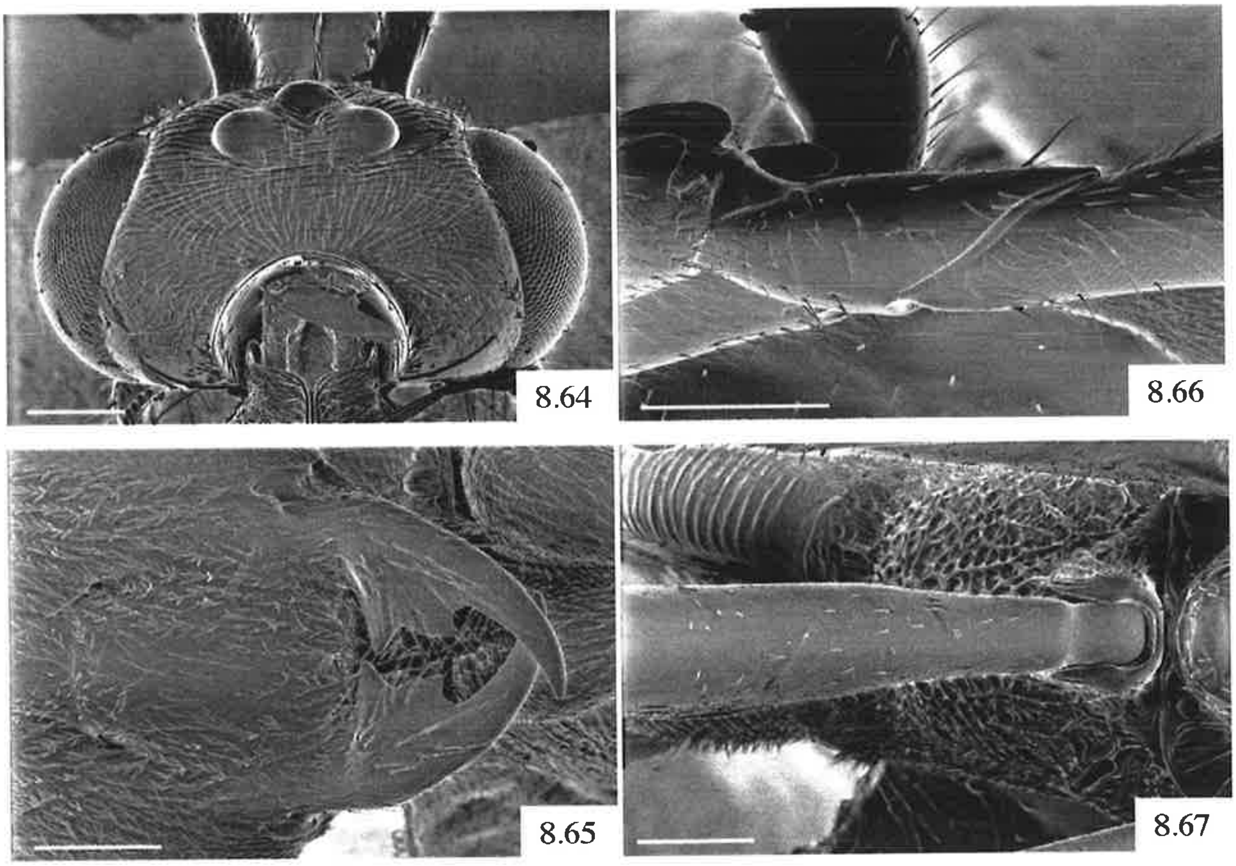
Figures 8.51-8.54. *Pseudofoenus crassitarsis* (Kieffer) comb. nov., ♀. **8.51.** dorsal view of head; **8.52.** anterior view of clypeus and mandibles; **8.53.** lateral view of hind trochanter; **8.54.** dorsal view of T1. Scale lines: *8.51*, 500 µm, *8.52, 54*, 200 µm, *8.53*, 100 µm.



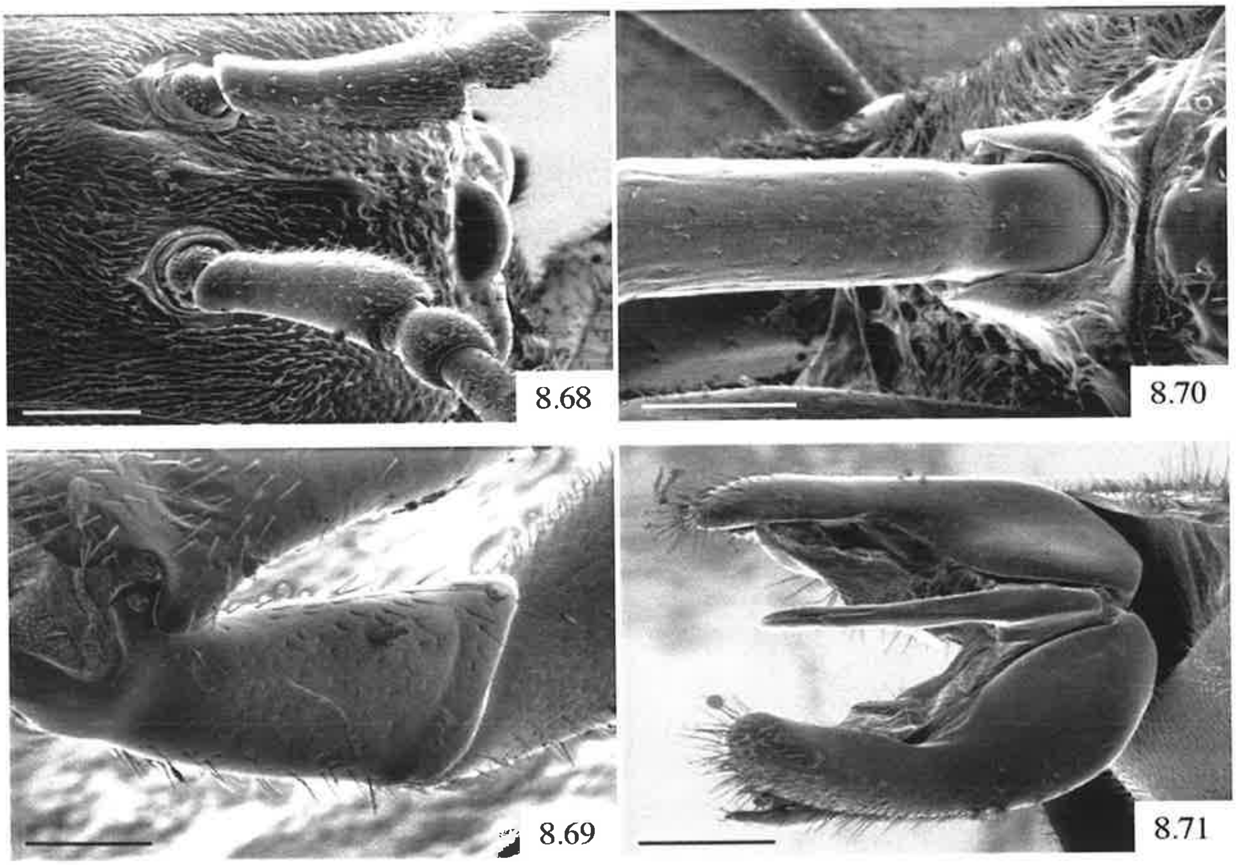
Figures 8.55-8.58. *Pseudofoenus crosskeyi* sp. nov. **8.55.** dorsal view of head, ♀; **8.56**. dorsal view of hind tarsal segments 1-2, ♂; **8.57.** dorsal view of T1, ♀; **8.58.** dorsal view of genitalia, ♂. Scale lines: *8.55*, 500 µm, *8.56-58*, 200 µm.



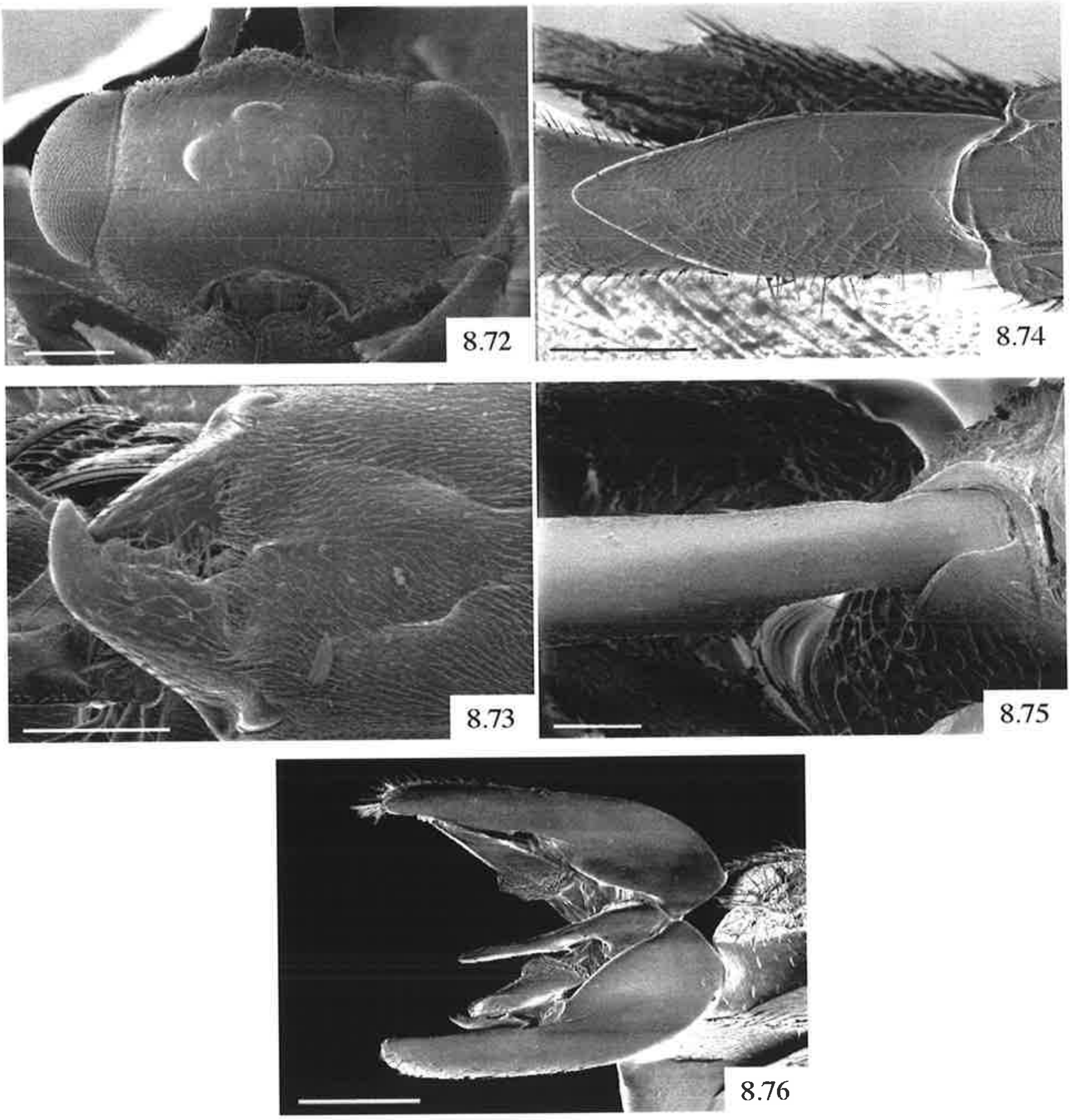
Figures 8.59-8.63. *Pseudofoenus darwini* (Westwood) comb. nov. **8.59.** dorsal view of head, ♀; **8.60.** anterior view of clypeus and mandibles, ♀; **8.61.** lateral view of hind trochanter, ♀; **8.62.** dorsal view of T1, ♂; **8.63.** dorsal view of genitalia, ♂. Scale lines: *8.59-60,* 200 µm, *8.61,* 50 µm, *8.62-63,* 100 µm.



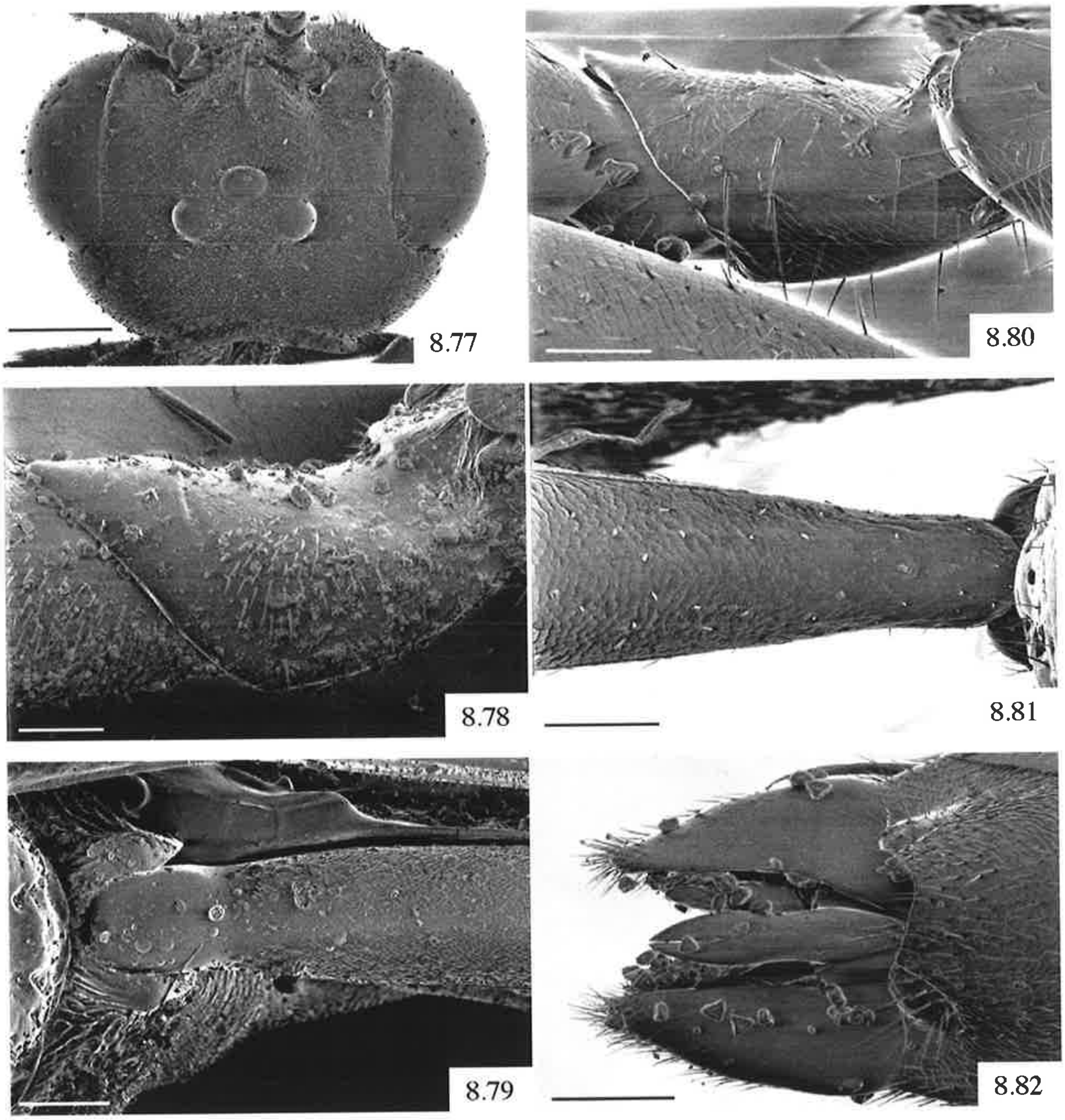
Figures 8.64-8.67. *Pseudofoenus extraneus* (Turner) comb. nov. **8.64.** postero-dorsal view of head ,♀; **8.65.** anterior view of clypeus and mandibles, ♀; **8.66.** lateral view of hind trochanter, ♂; **8.67.** dorsal view of T1, ♀. Scale lines: *8.64-67*, 200 µm.



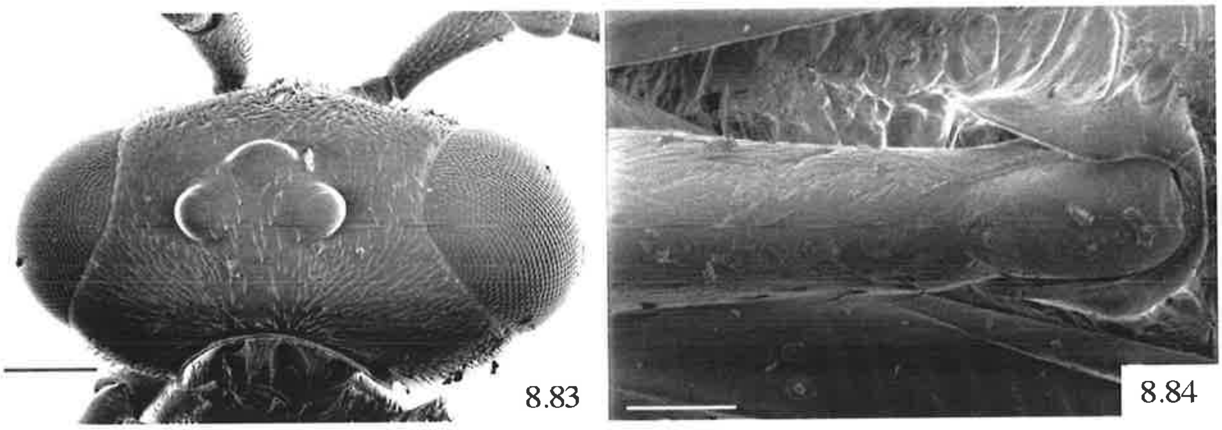
Figures 8.68-8.71. *Pseudofoenus ferrugineus* (Crosskey) comb. nov. **8.68.** anterior view of frontal carina, ♀; **8.69.** dorso-lateral view of hind trochanter, ♂; **8.70.** dorsal view of T1, ♀; **8.71.** dorsal view of genitalia, ♂. Scale lines: *8.68, 70,* 200 µm, *8.69, 71,* 100 µm.



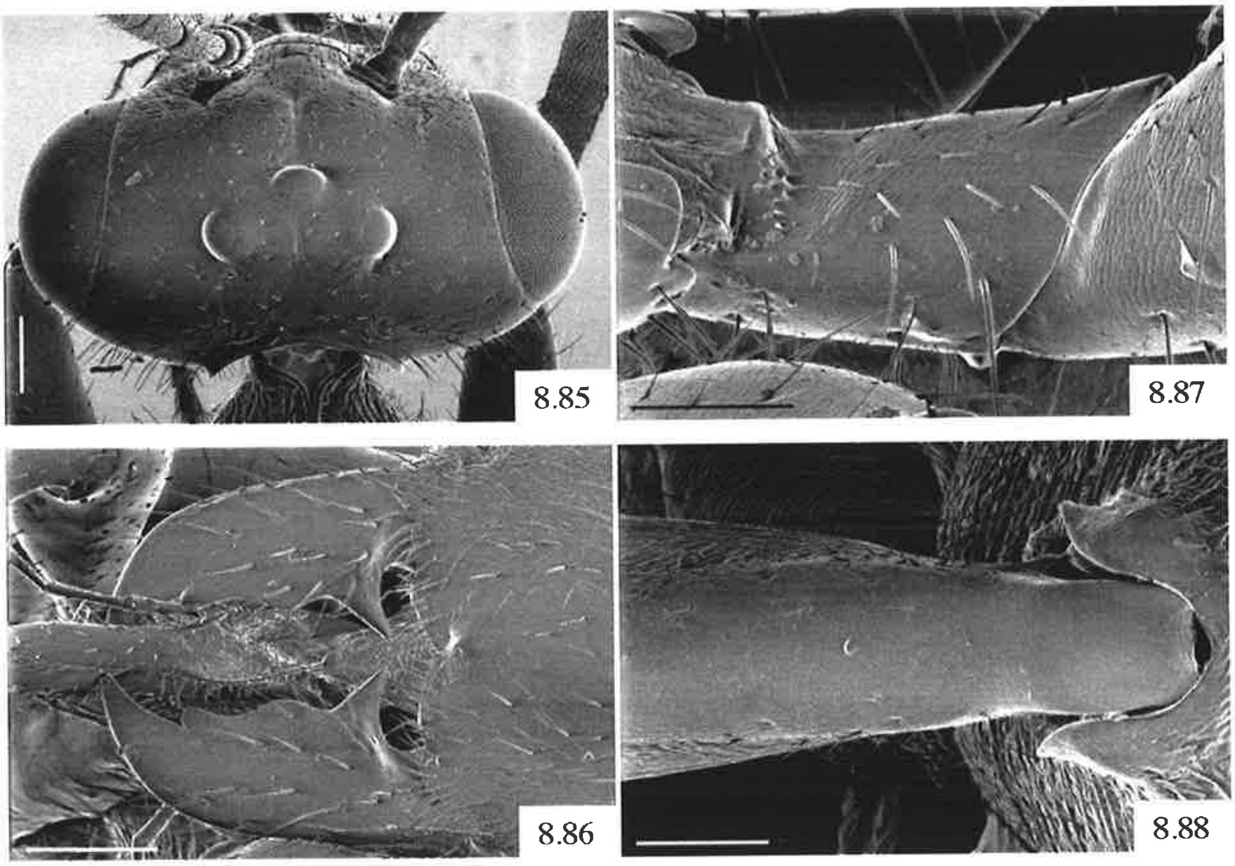
Figures 8.72-8.76. *Pseudofoenus floricolus* (Turner) comb. nov. **8.72.** dorsal view of head, ♀; **8.73.** anterior view of clypeus and mandibles, ♀; **8.74.** dorsal view of hind trochanter,♀; **8.75.** dorsal view of T1, ♀; **8.76.** dorsal view of genitalia, ♂. Scale lines: *8.72-73, 76,* 200 µm, *8.74-75,* 100 µm.



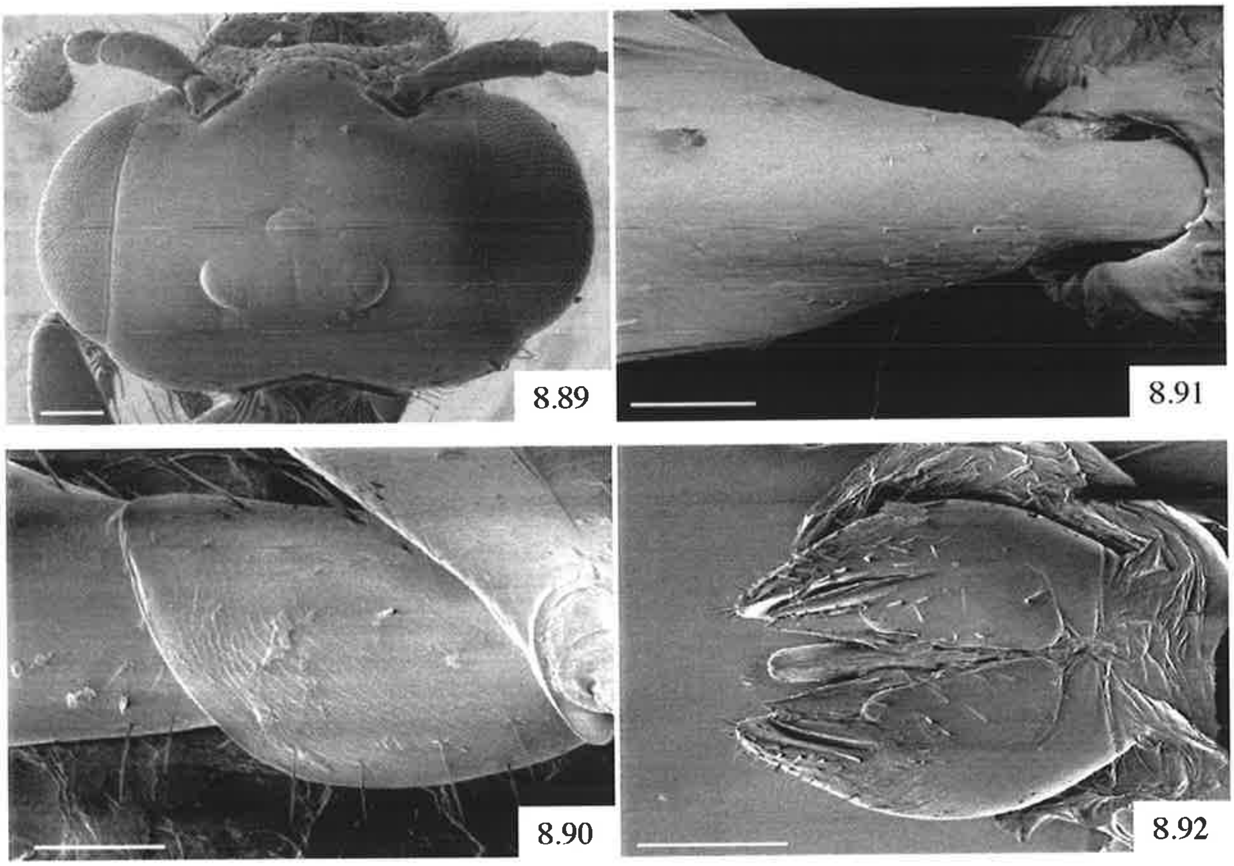
Figures 8.77-8.82. *Pseudofoenus inaequalis* (Turner) comb. nov., ♀. **8.77.** dorsal view of head; **8.78.** lateral view of hind trochanter; **8.79.** dorsal view of T1. *Pseudofoenus iqbali* sp. nov. **8.80.** lateral view of hind trochanter, ♀; **8.81.** dorsal view of hind trochanter, ♀; **8.82.** dorsal view of genitalia, ♂. Scale lines: *8.77*, 500 µm, *8.78, 81-82*, 100 µm, *8.79*, 200 µm, *8.80*, 50 µm.



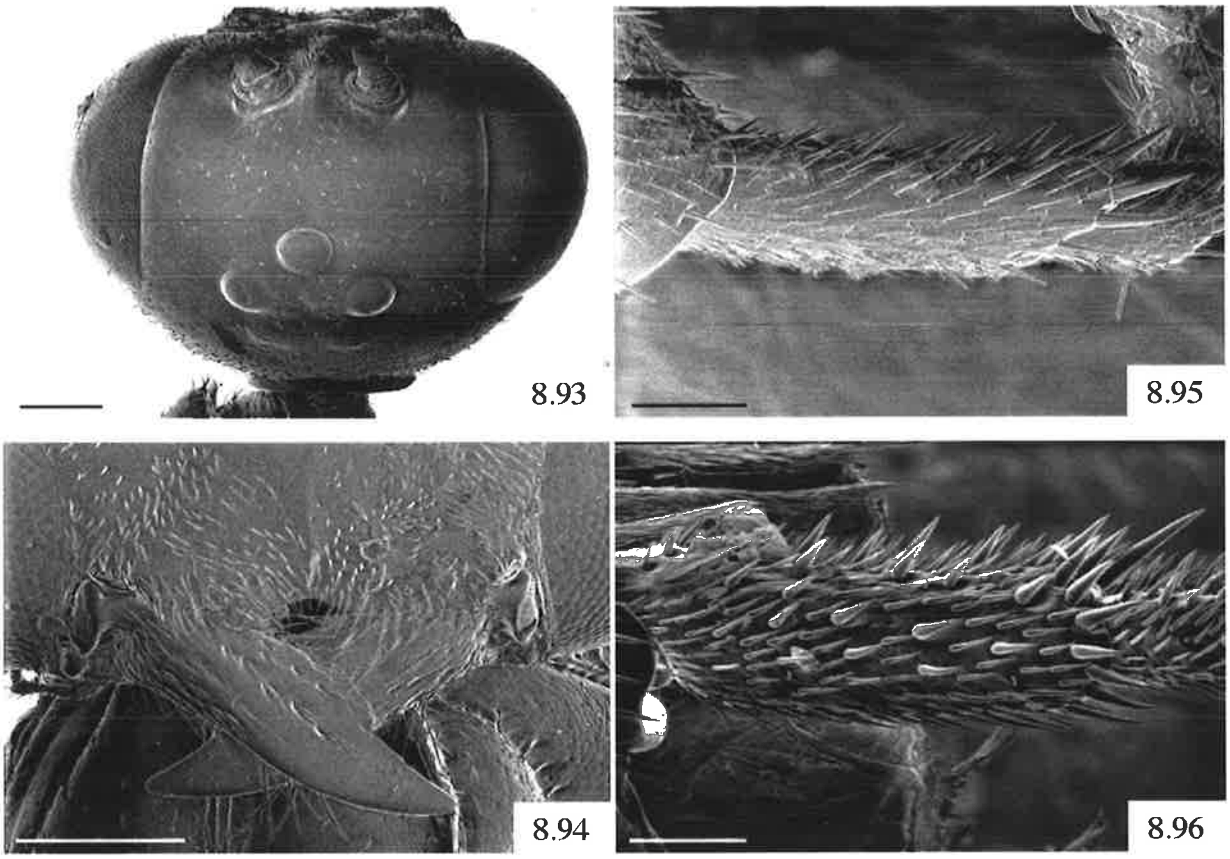
Figures 8.83-8.84. *Pseudofoenus karimuiensis* sp. nov , holotype ♀. **8.83.** dorsal view of head; **8.84.** dorsal view of T1. Scale lines: *8.83*, 200 µm, *8.84*, 100 µm,



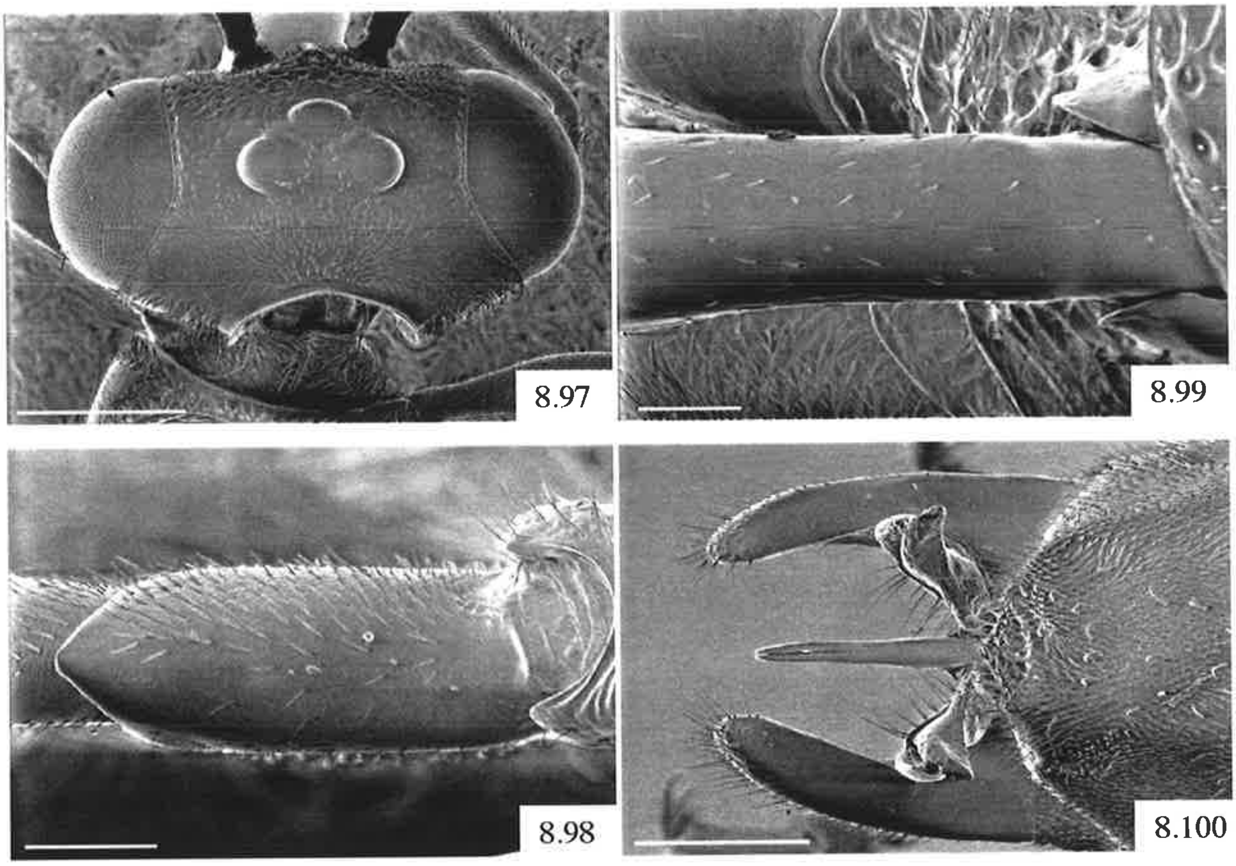
Figures 8.85-8.88. *Pseudofoenus kelleri* sp. nov., paratype ♀. **8.85.** dorsal view of head; **8.86.** anterior view of clypeus and mouthparts; **8.87.** lateral view of hind trochanter; **8.88.** dorsal view of T1. Scale lines: *8.85-86*, 200 µm, *8.87-88*, 100 µm,



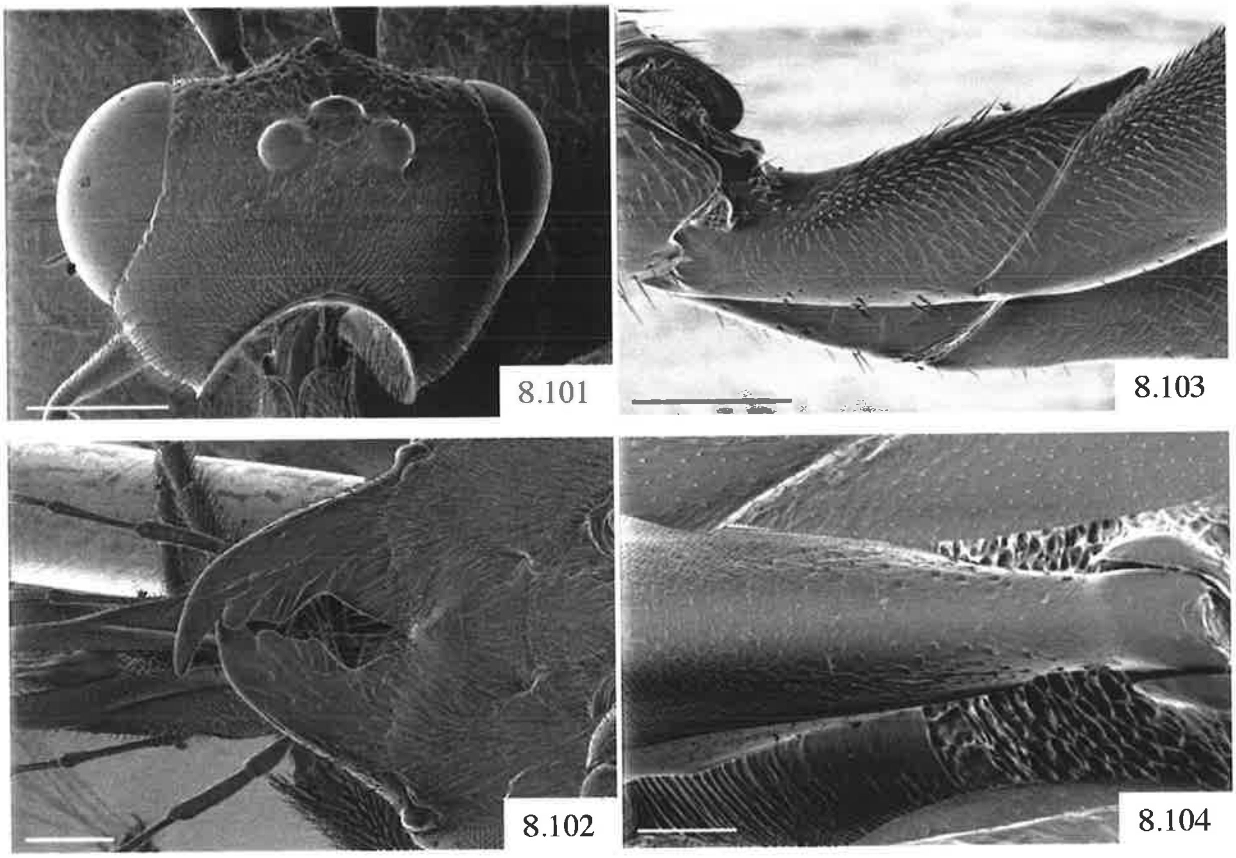
Figures 8.89-8.92. *Pseudofoenus macdonaldi* sp. nov. **8.89.** dorsal view of head, paratype ♀; **8.90.** lateral view of hind trochanter, paratype ♂; **8.91.** dorsal view of T1, paratype ♀; **8.92.** ventral view of genitalia, paratype ♂. Scale lines: *8.89*, 200 µm, *8.90-91*, 50 µm, *8.92*, 100 µm.



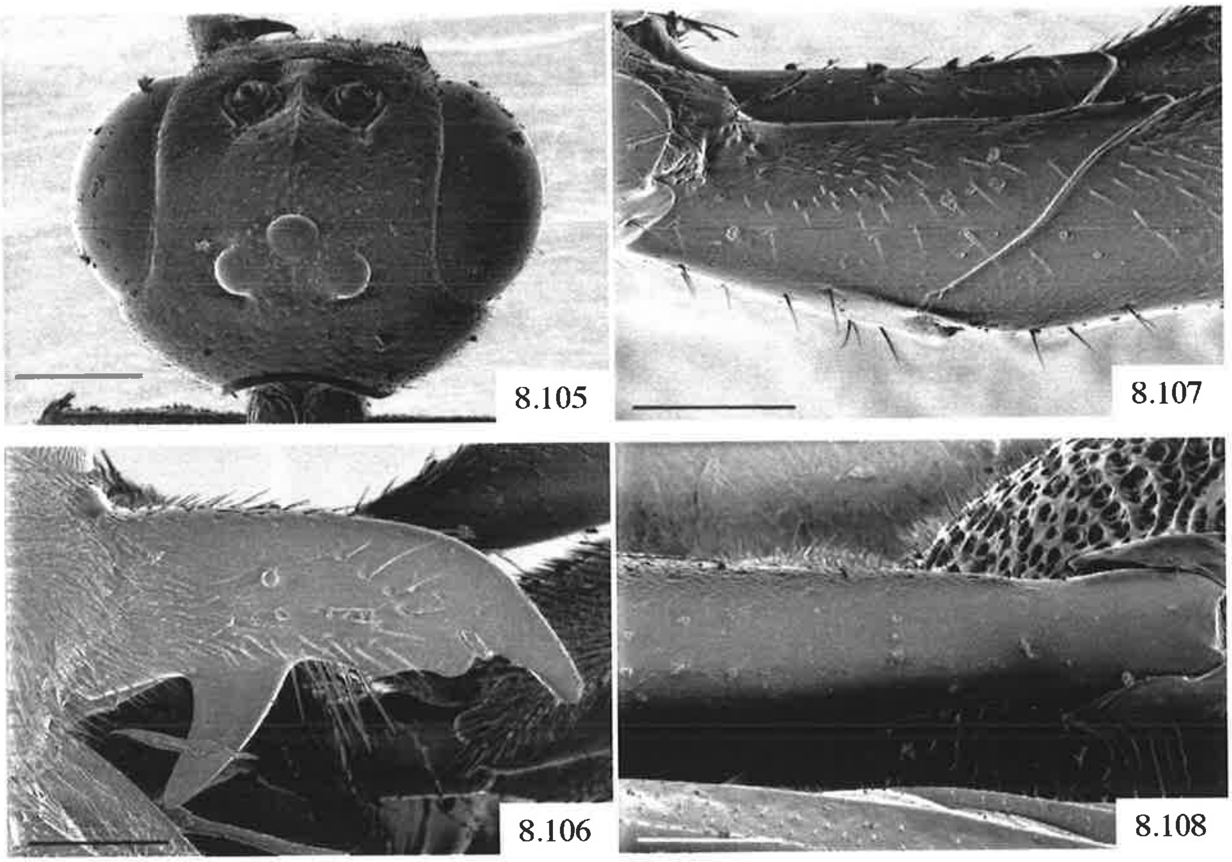
Figures 8.93-8.96. *Pseudofoenus malkini* sp. nov. **8.93.** dorso-anterior view of head, holotype ♀; **8.94.** anterior view of clypeus and mandibles, holotype ♀; **8.95.** lateral view of hind tarsal segment 1, holotype ♀; **8.96.** lateral view of hind tarsal segment 1, paratype ♂. Scale lines: *8.93-94*, 200 μm, *8.95-96*, 100 μm.



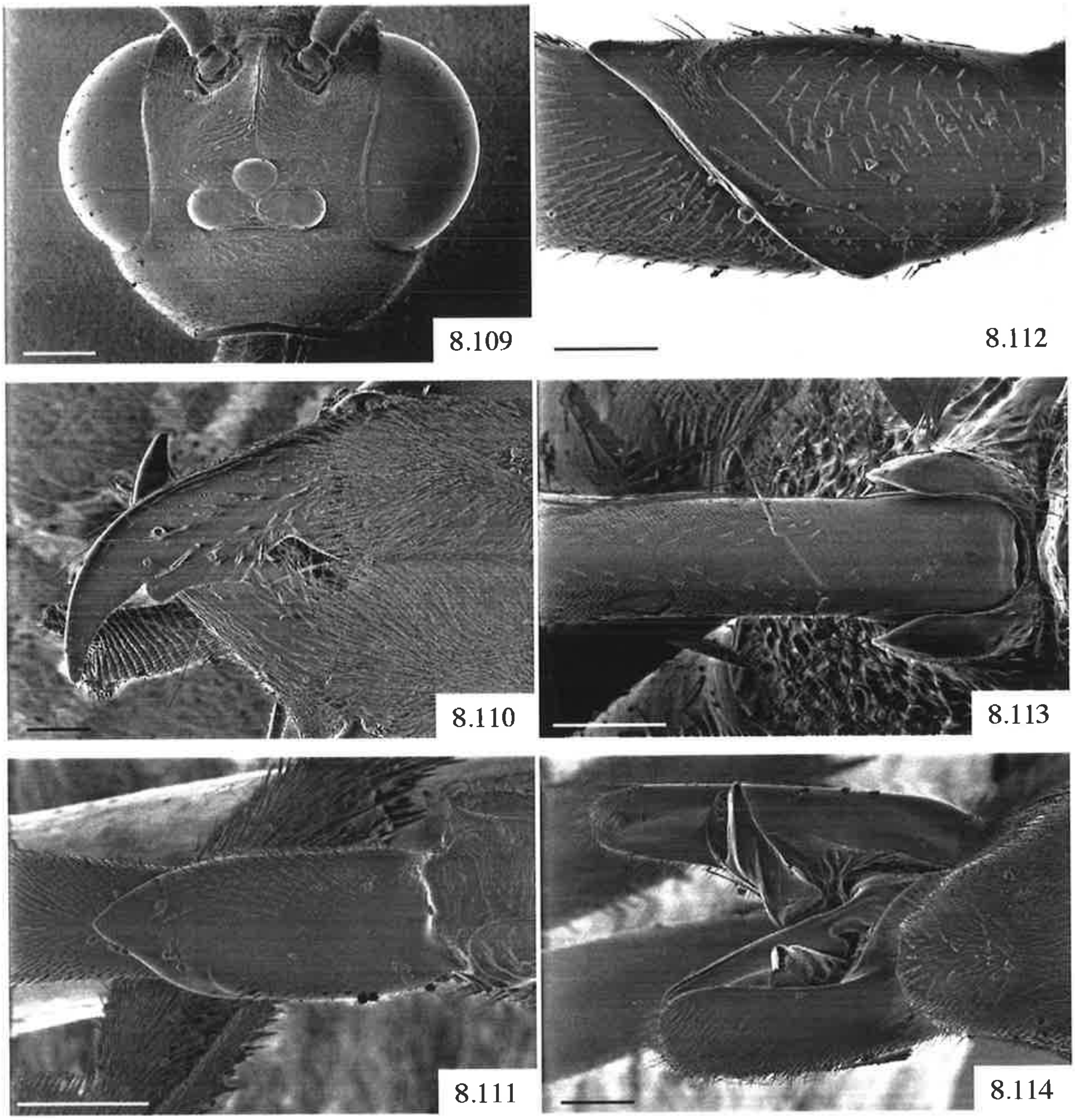
Figures 8.97-8.100. *Pseudofoenus masneri* sp. nov., paratypes. **8.97.** dorsal view of head, ♀; **8.98.** dorsal view of hind trochanter, ♀; **8.99.** dorsal view of T1, ♀; **8.100.** dorsal view of genitalia, ♂. Scale lines: *8.97,* 500 µm, *8.98-99,* 200 µm, *8.100,* 100 µm.



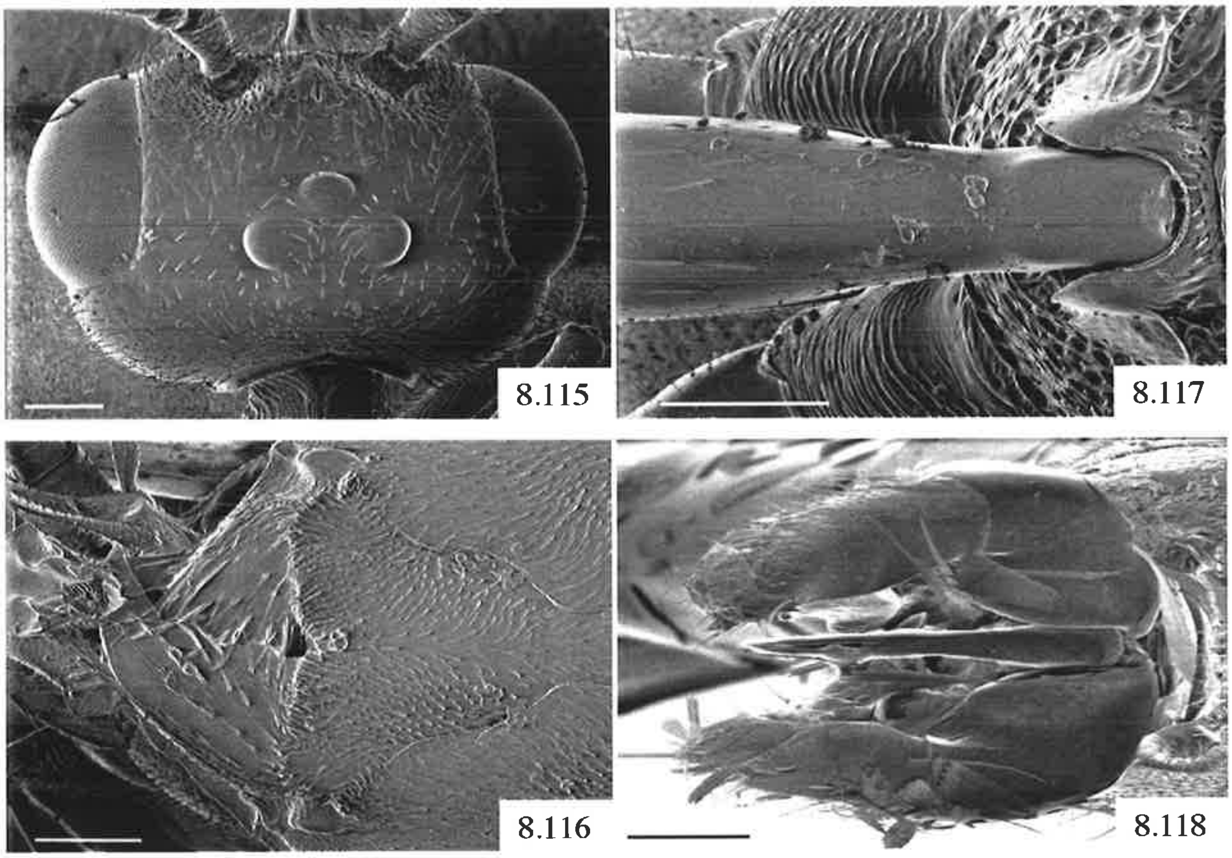
Figures 8.101-8.104. *Pseudofoenus nalbarraensis* sp. nov. **8.101.** dorsal view of head, holotype ♀; **8.102.** anterior view of clypeus and mandibles, holotype ♀; **8.103.** lateral view of hind trochanter, holotype ♀; **8.104.** dorsal view of T1, paratype ♂. Scale lines: *8.101*, 500 µm, *8.102-104*, 200 µm.



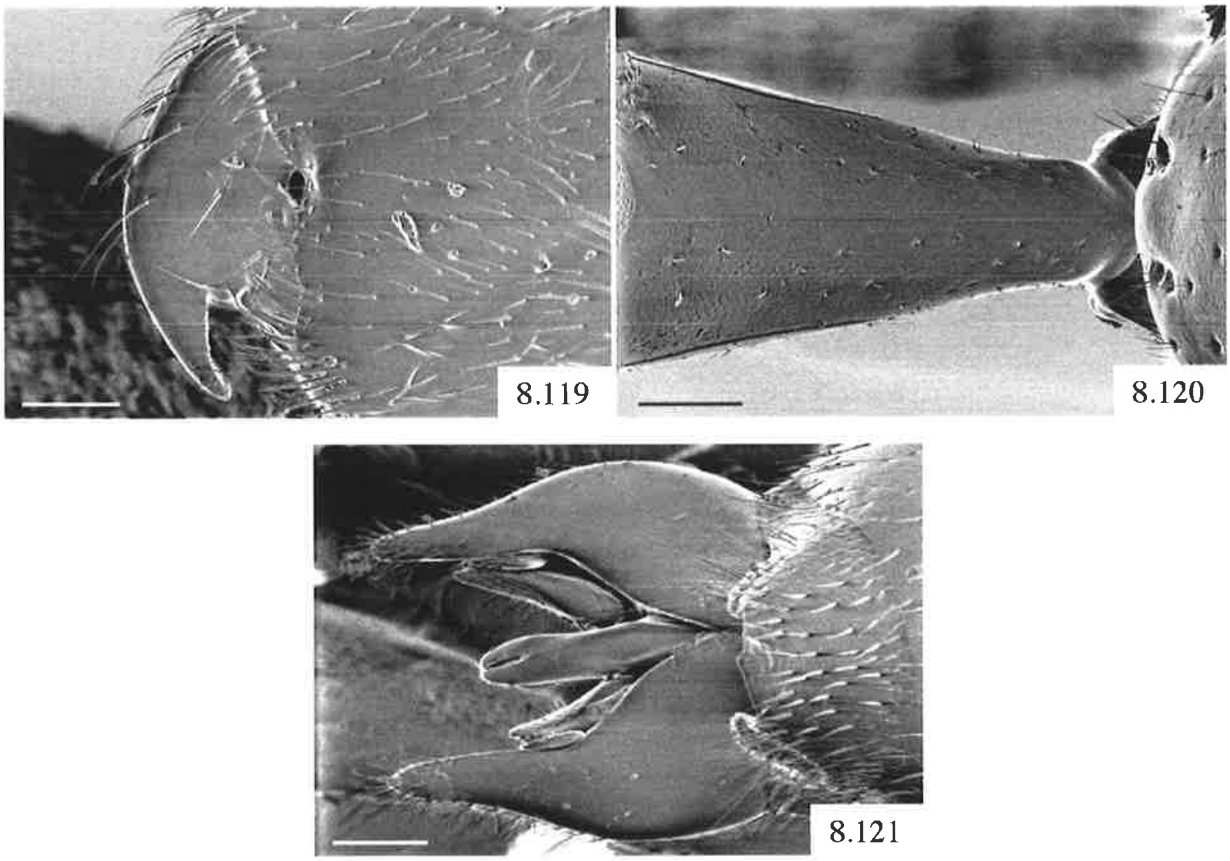
Figuress 8.105-8.108. *Pseudofoenus nitidiusculus* (Turner) comb. nov. **8.105.** dorso-anterior view of head, holotype ♀; **8.106.** anterior view of mandible, ♀; **8.107.** lateral view of hind trochanter, ♀; **8.108.** dorsal view of T1, holotype ♀. Scale lines: *8.105*, 500 µm, *8.106*, 50 µm, *8.107-108*, 200 µm.



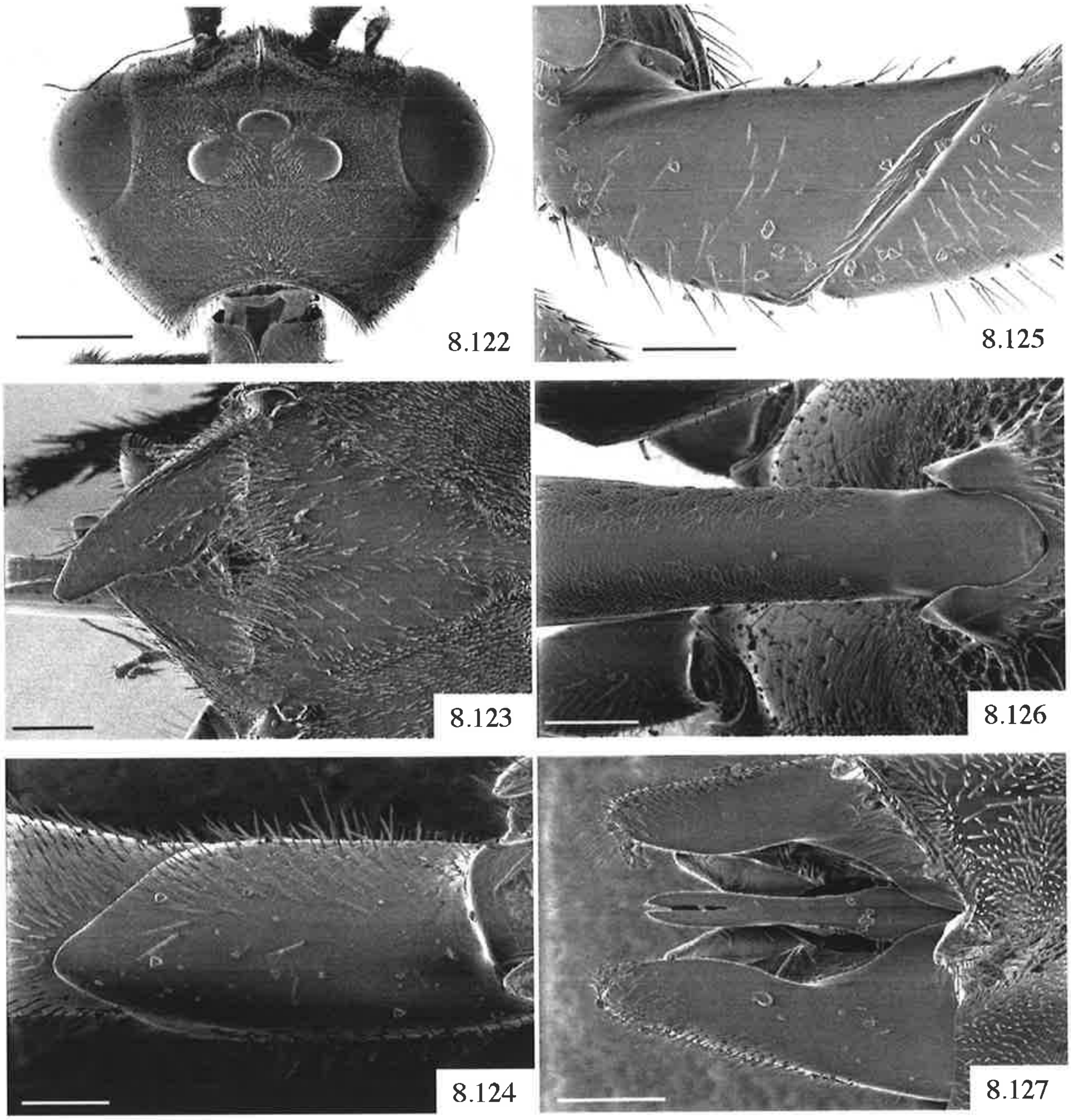
Figures 8.109-8.114. *Pseudofoenus patellatus* (Westwood) comb. nov. **8.109.** dorsal view of head, ♀; **8.110.** anterior view of clypeus and mandibles, ♂; **8.111.** dorsal view of hind trochanter, ♂; **8.112.** lateral view of hind trochanter, ♂; **8.113.** dorsal view of T1, ♀; **8.114.** dorsal view of genitalia,♂. Scale lines: *8.109,* 500µm, *8.110-111, 113-114,* 200 µm, *8.112,* 100 µm.



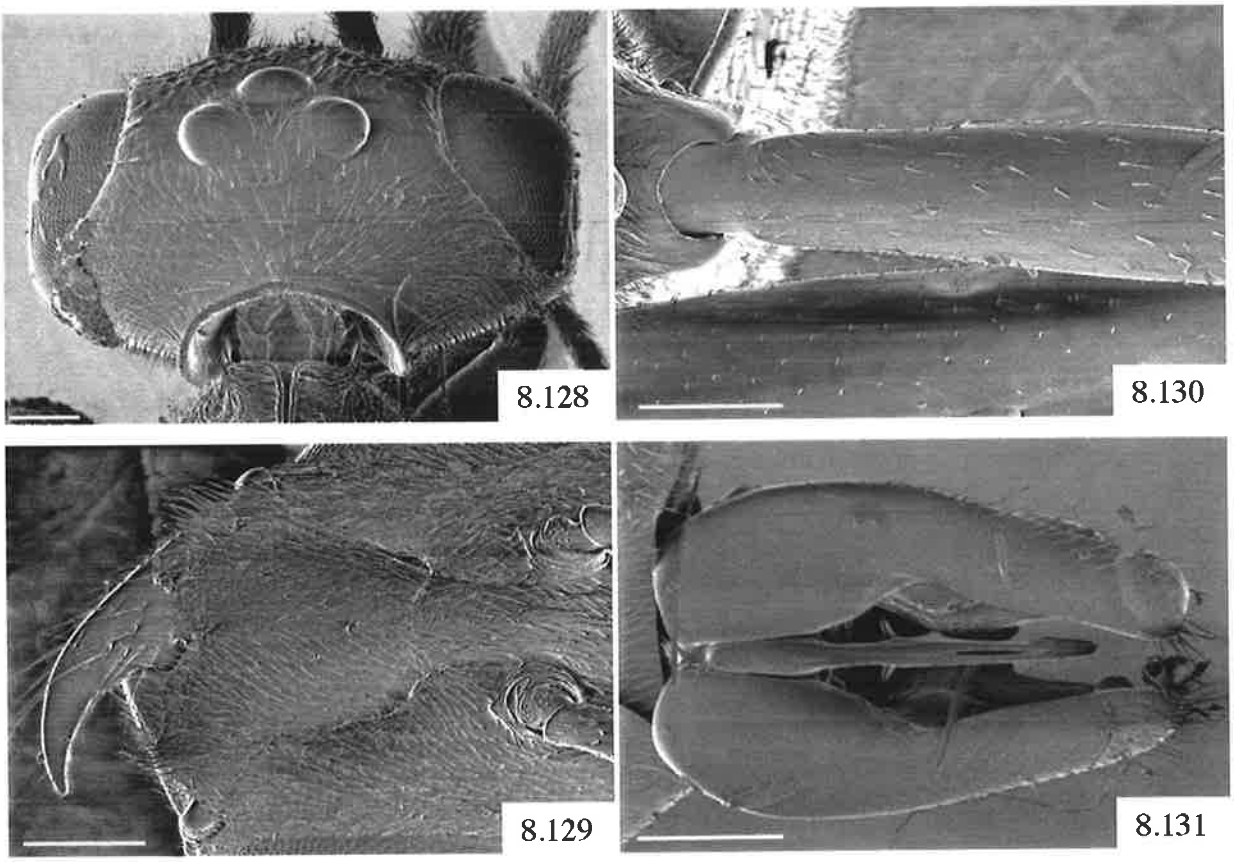
Figures 8.115-8.118. *Pseudofoenus pilosus* (Kieffer) comb. nov. **8.115.** dorsal view of head, ♀; **8.116.** anterior view of head, ♀; **8.117.** dorsal view of T1, ♀; **8.118.** dorsal view of genitalia, ♂. Scale lines: *8.115-118*, 200 μm.



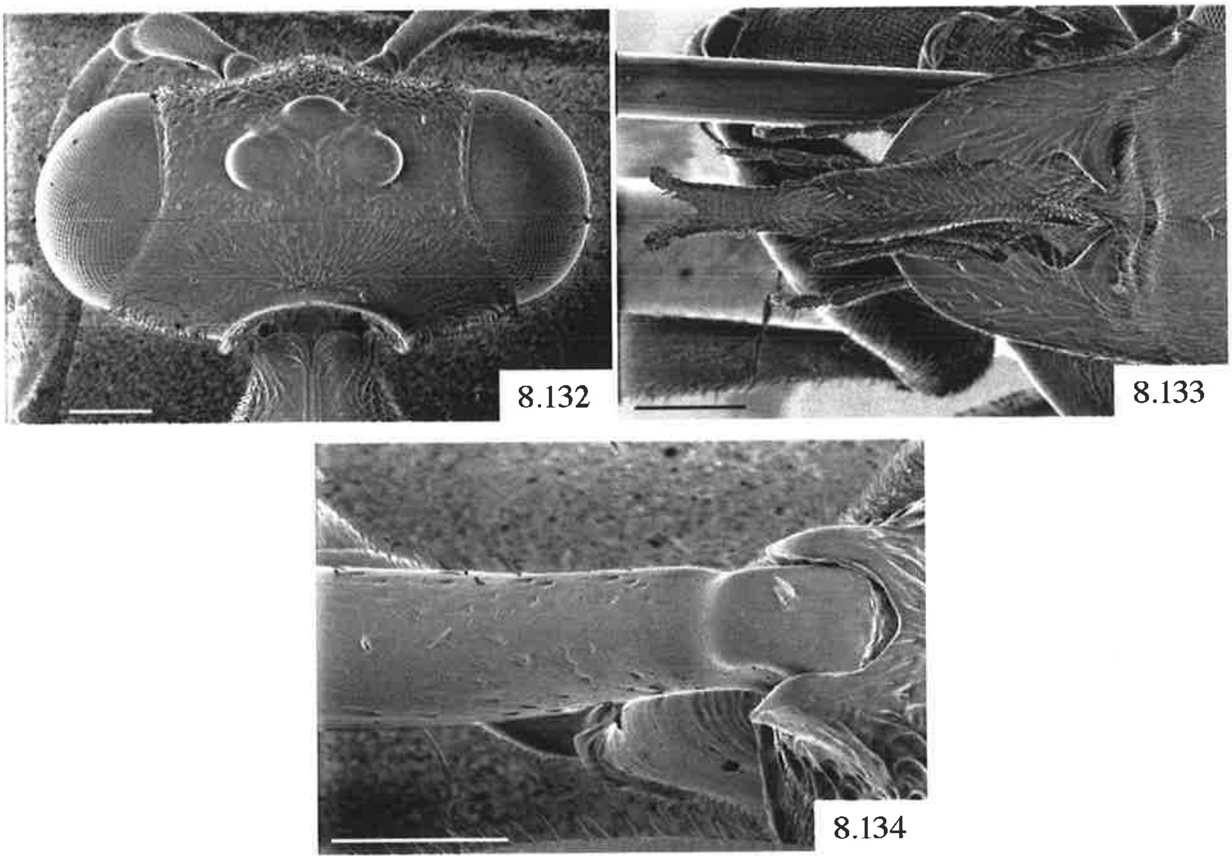
Figures 8.119-8.121. *Pseudofoenus reticulatus* (Crosskey). **8.119.** anterior view of clypeus and mandibles, holotype ♀; **8.120.** dorsal view of T1, holotype ♀; **8.121.** dorsal view of genitalia, paratype ♂. Scale lines: *8.119-121*, 100 μm.



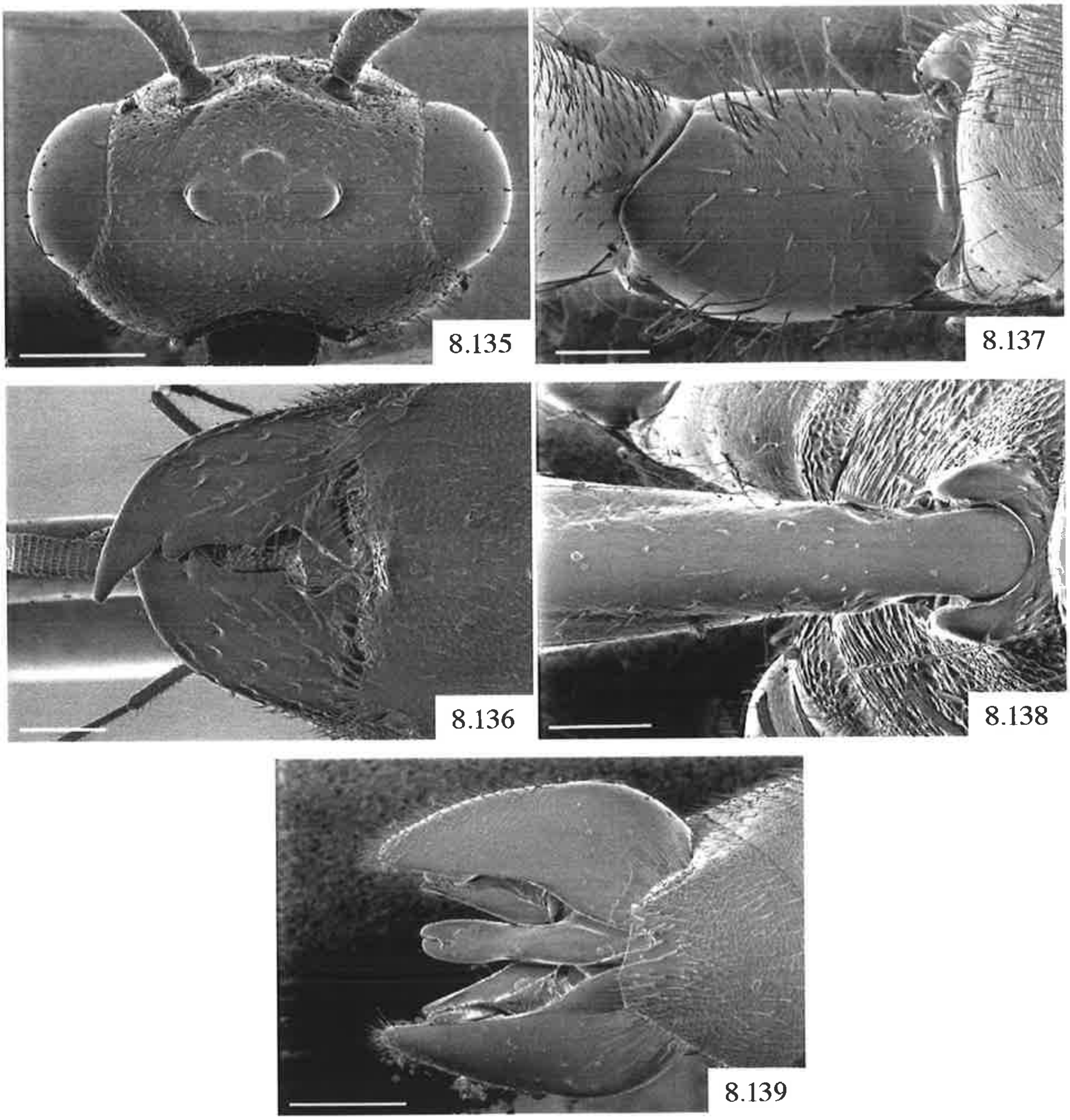
Figures 8.122-8.127. *Pseudofoenus rieki* (Crosskey) comb. nov., paratypes. **8.122.** dorsal view of head, ♀; **8.123.** anterior view of clypeus and mandibles, ♀; **8.124.** dorsal view of hind trochanter, ♂; **8.125.** lateral view of hind trochanter, ♂; **8.126.** dorsal view of T1, ♀; **8.127.** dorsal view of genitalia, ♂. Scale lines: *8.122*, 500 µm, *8.123, 126-127*, 200 µm, *8.124-125*, 100 µm.



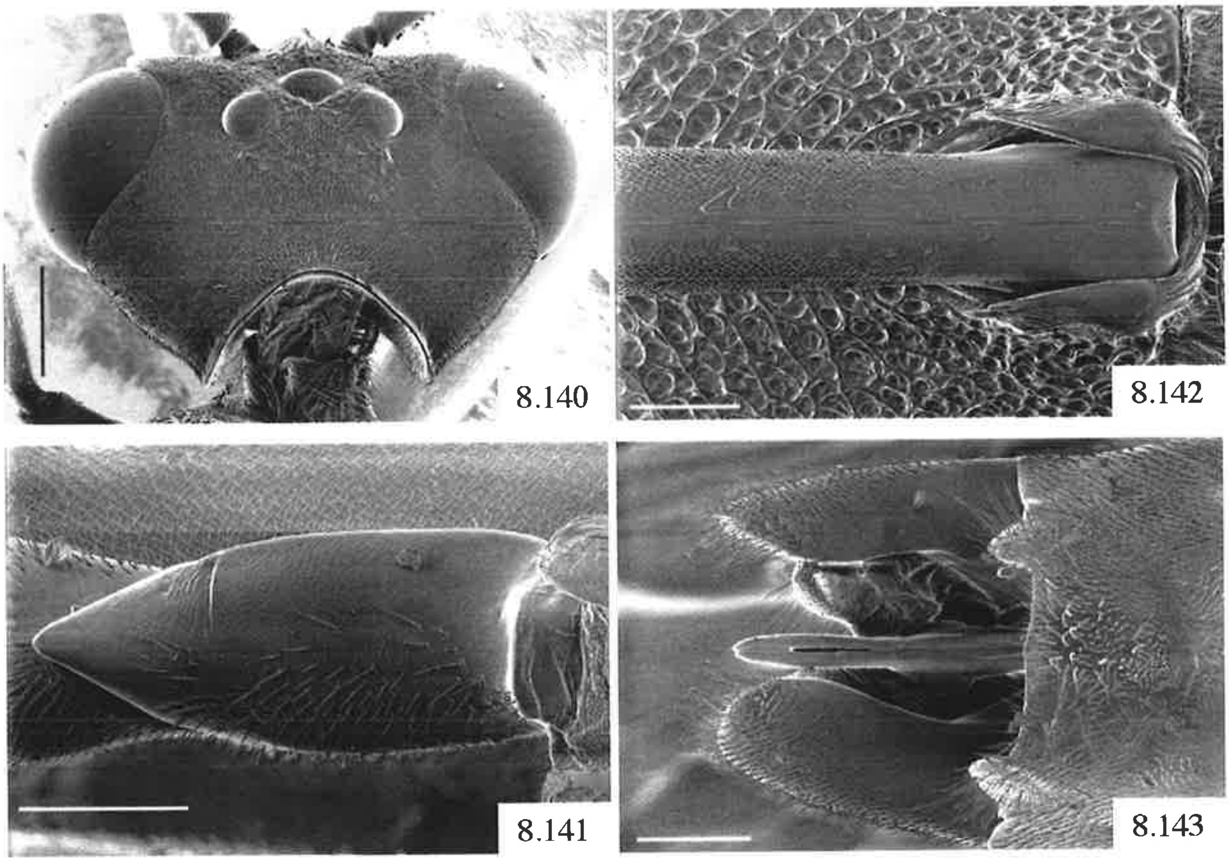
Figures 8.128-8.131. *Pseudofoenus ritae* (Cheesman) comb. nov. **8.128.** dorsal view of head, ♂; **8.129.** anterior view of clypeus and mandibles, ♀; **8.130.** dorsal view of T1 ♀; **8.131.** dorsal view of genitalia, ♂. Scale lines: *8.128-131*, 200 µm.



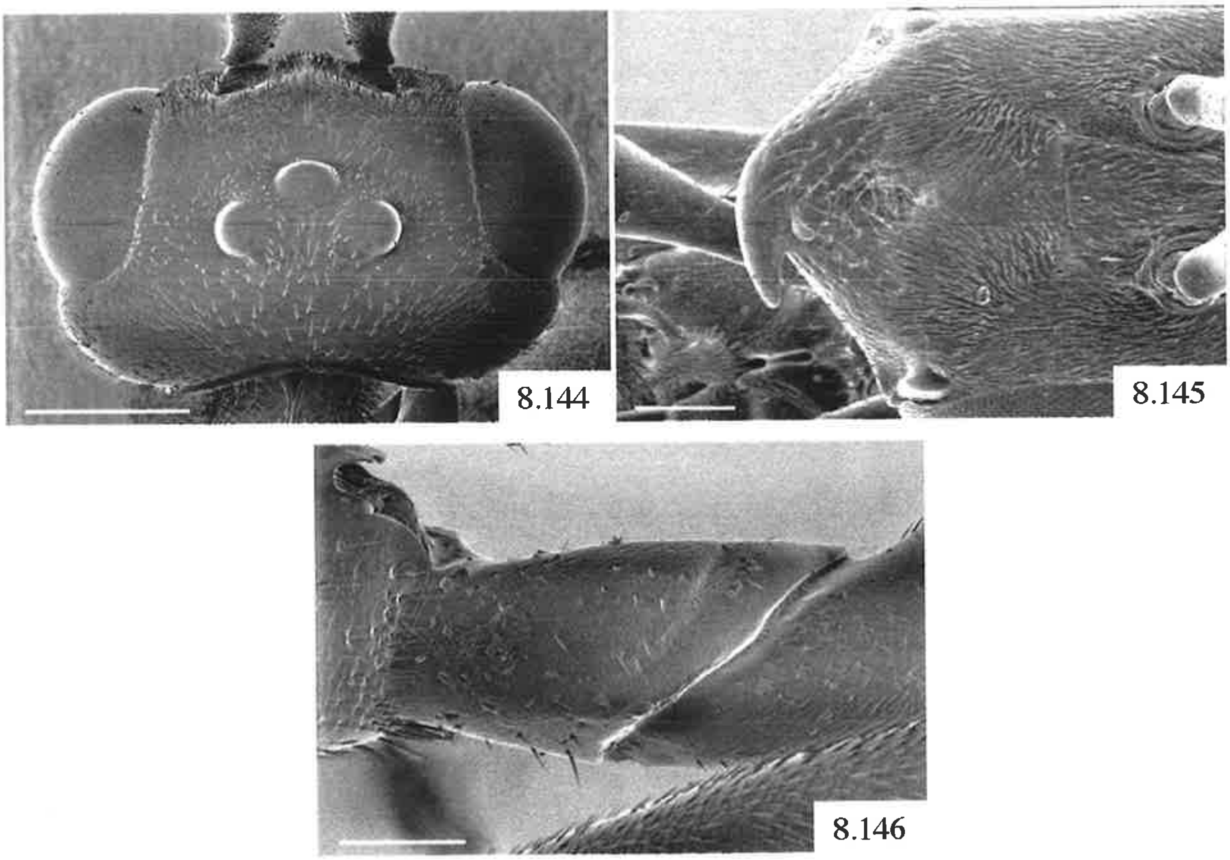
Figures 8.132-8.134. *Pseudofoenus schmidti* sp. nov., holotype ♀. **8.132.** dorsal view of head; **8.133.** anterior view of mouthparts; **8.134.** dorsal view of T1. Scale lines: *8.132*, 250 µm, *8.133-134*, 200 µm.



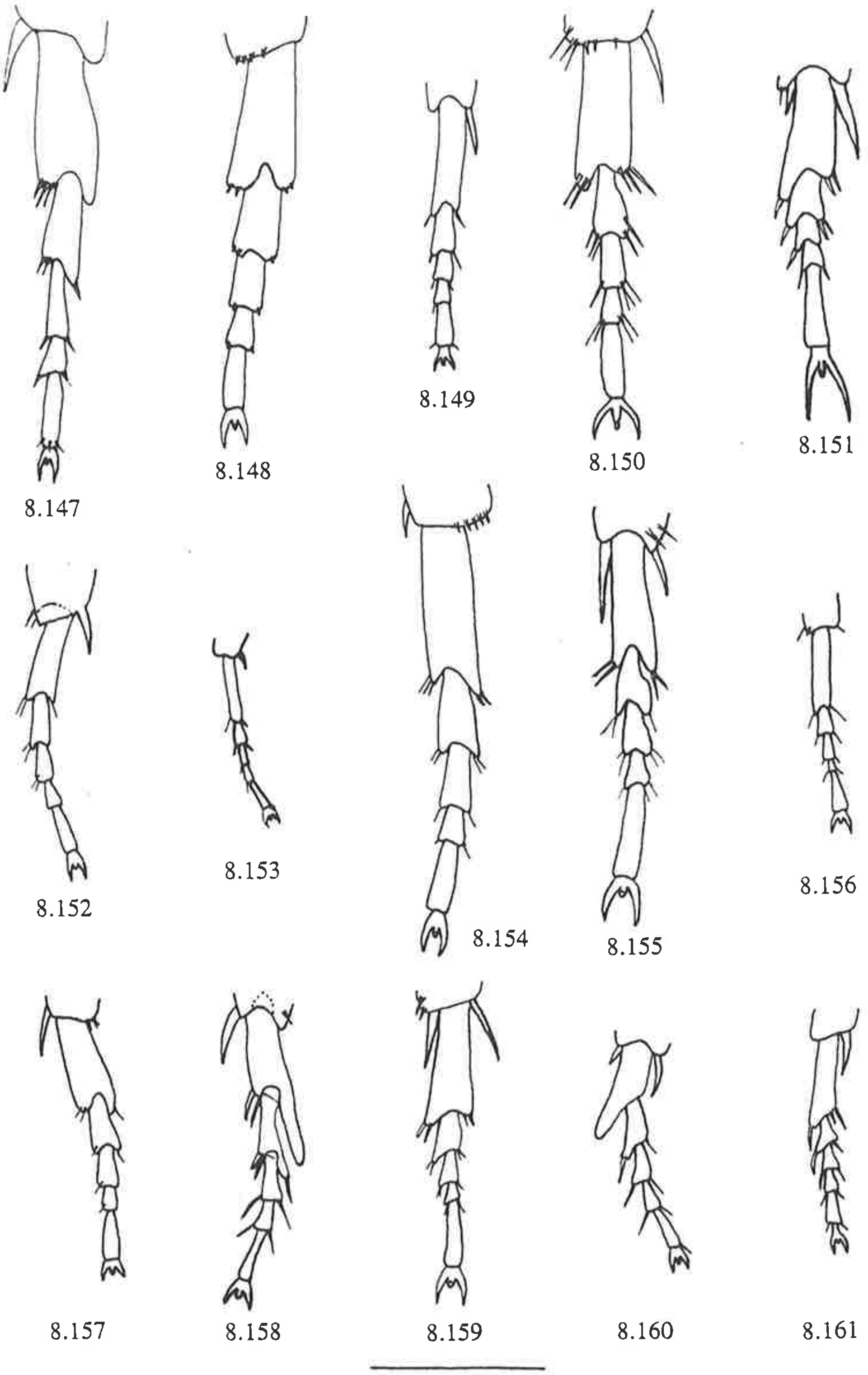
Figures 8.135-8.139. *Pseudofoenus spinitarsis* (Westwood) comb. nov, **8.135.** dorsal view of head, ♀; **8.136.** anterior view of clypeus and mandibles, ♀; **8.137.** dorsal view of hind trochanter, ♀; **8.138.** dorsal view of T1, ♀; **8.139.** dorsal view of genitalia, ♂. Scale lines: *8.135*, 500 µm, *8.136-139*, 200 µm.



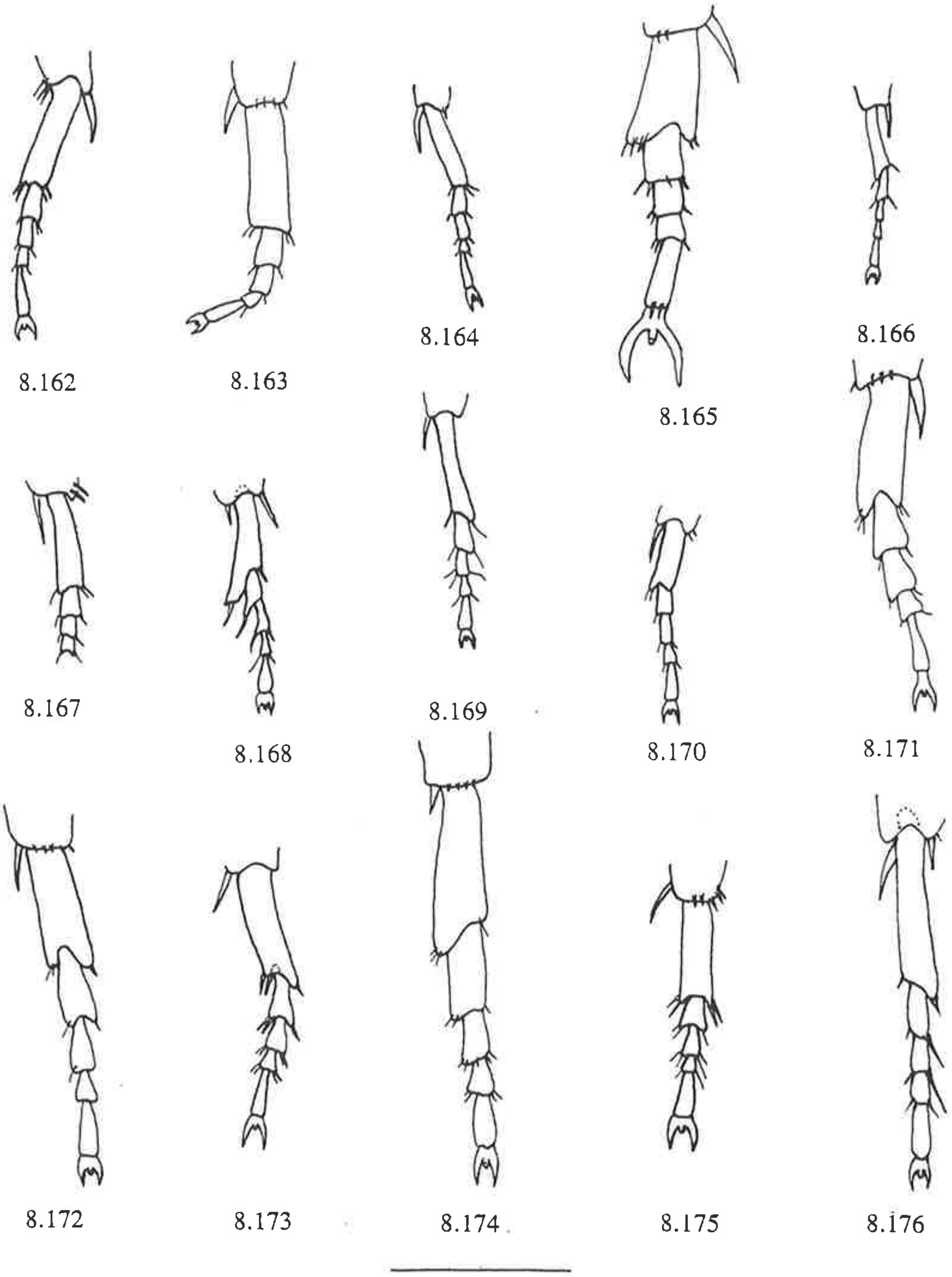
Figures 8.140-8.143. *Pseudofoenus taylori* sp. nov., paratypes. **8.140.** dorsal view of head, ♀; **8.141.** dorsal view of hind trochanter, ♀; **8.142.** dorsal view of T1, ♀; **8.143.** dorsal view of genitalia, ♂. Scale lines: *8.140,* 500 µm, *8.141-143,* 200 µm.



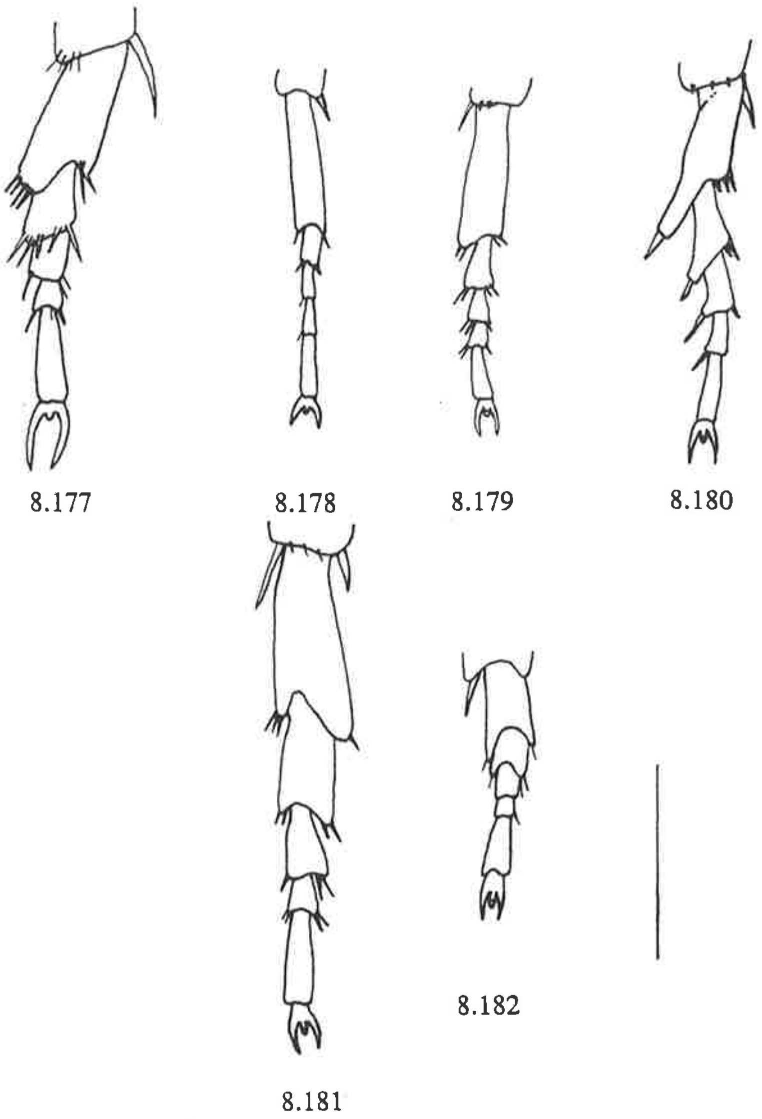
Figures 8.144-8.146. *Eufoenus melanopleurus* (Crosskey), holotype ♂. **8.144.** dorsal view of head; **8.145.** anterior view of clypeus and mandibles; **8.146.** lateral view of hind trochanter. Scale lines: *8.144*, 500 µm, *8.145*, 200 µm, *8.146*, 100 µm.



Figures 8.147-8.161. Dorsal view of hind tarsal segments, ♀ except for 8.152 ♂. **8.147.** *P. morganensis* sp. nov., paratype; **8.148.** *P. cardaleae* sp. nov., holotype; **8.149.** *P. douglasi* sp. nov., paratype; **8.150.** *P. ericae* sp. nov., paratype; **8.151.** *P. feckneri* sp. nov., paratype; **8.152.** *P. microcephalus* (Crosskey) comb. nov.; **8.153.** *P. minimus* (Turner) comb. nov.; **8.154.** *P. antennalis* (Schletterer) comb. nov.; **8.155.** *P. australis* (Westwood) comb. nov.; **8.156.** *P. beverlyae* sp. nov., paratype; **8.157.** *P. collessi* sp. nov., paratype; **8.158.** *P. coorowensis* sp. nov., paratype; **8.159.** *P. crassitarsis* (Kieffer) comb. nov.; **8.160.** *P. crosskeyi* sp. nov., holotype; **8.161.** *P. darwini* (Westwood) comb. nov. Scale line: 1 mm.



Figures 8.162-8.176. Dorsal view of hind tarsal segments, ♀. **8.162** *P. extraneus* (Turner) comb. nov.; **8.163.** *P. ferrugineus* (Crosskey) comb. nov.; **8.164.** *P. floricolus* (Turner) comb. nov.; **8.165.** *P. inaequalis* (Turner) comb. nov.; **8.166.** *P. iqbali* sp. nov., paratype; **8.167.** *P. karimuiensis* sp. nov., holotype (segment 5 and claw missing); **8.168.** *P. kelleri* sp. nov., holotype; **8.169.** *P. macdonaldi* sp. nov., paratype; **8.170.** *P. malkini* sp. nov., paratype; **8.171.** *P. masneri* sp. nov., holotype; **8.172.** *P. nalbarraensis* sp. nov., holotype; **8.173.** *P. nitidiusculus* (Turner) comb. nov.; **8.174.** *P. patellatus* (Westwood) comb. nov.; **8.175.** *P. pilosus* (Kieffer) comb. nov.; **8.176.** *P. reticulatus* (Crosskey) comb. nov., holotype. Scale line: *8. 176-172, 174-175,* 1 mm, *8.173, 176,* 0.5 mm.



8.177 8.178 8.179 8.180

8.182

8.181

Figures 8.177-8.182. Dorsal view of hind tarsal segments, ♀. **8.177.** *P. rieki* (Crosskey) comb. nov., holotype; **8.178.** *P. ritae* (Cheesman) comb. nov., paratype; **8.179.** *P. schmidti* sp. nov., paratype; **8.180.** *P. spinitarsis* (Westwood) comb. nov.; **8.181.** *P. taylori* sp. nov., paratype; **8.182.** *E. melanopleurus* (Crosskey). Scale line: 1 mm.

Figure 8.183. Distribution of *P. douglasi* sp. nov. (●) and *P. ericae* sp. nov. (■).

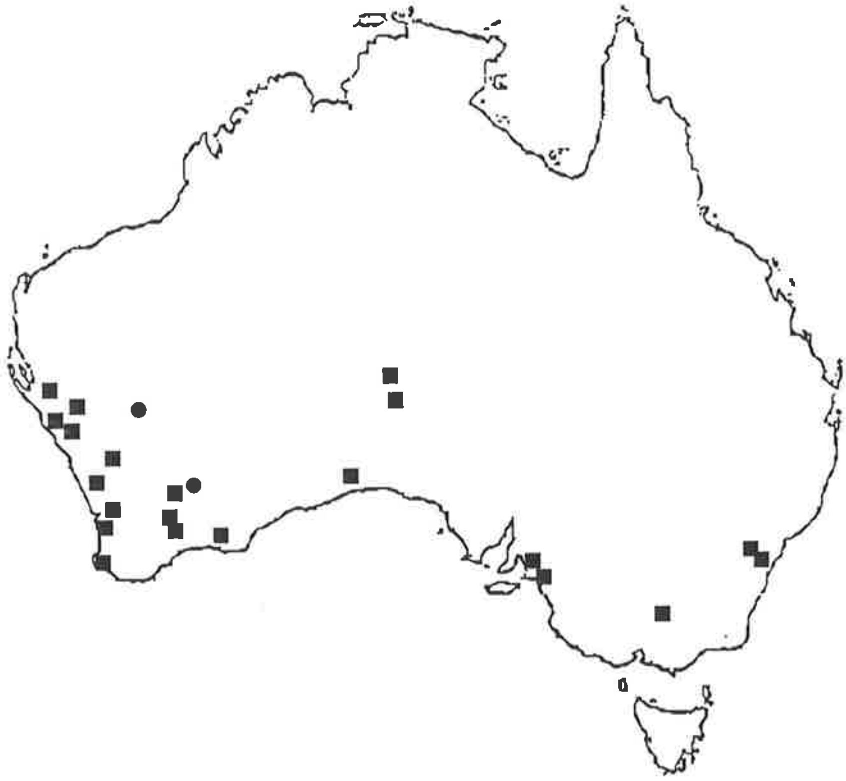


Figure 8.184. Distribution of *P. cardaleae* sp. nov. (●) and *P. feckneri* sp. nov. (■).

Figure 8.185. Distribution of *P. microcephalus* (Crosskey) comb. nov. (●) and *P. minimus* (Turner) comb. nov. (■)

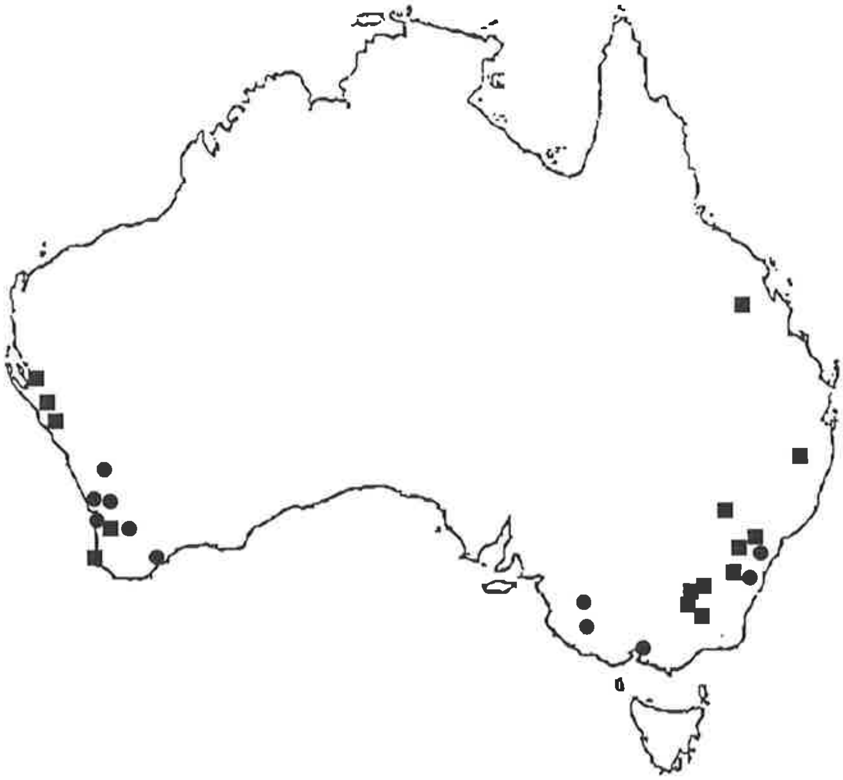


Figure 8.186. Distribution of *P. antennalis* (Schletterer) comb. nov. (●) and *P. australis* (Westwood) comb. nov. (■). Note: South Australian localities for *P. australis* not plotted as precise localities not known.

Figure 8.187. Distribution of *P. beverlyae* sp. nov. (●) and *P. collessi* sp. nov. (■).

Figure 8.188. Distribution of *P. coorowensis* sp. nov. (●) and *P. crassitarsis* (Kieffer) comb. nov. (■).

Figure 8.189. Distribution of *P. crosskeyi* sp. nov. (●) and *P. darwini* (Westwood) comb. nov. (■).

Figure 8.190. Distribution of *P. extraneus* (Turner) comb. nov. (●), *P. karimuiensis* sp. nov. (o), *P. ritae* (Cheesman) comb. nov. (■), and *P. schmidti* sp. nov. (□).

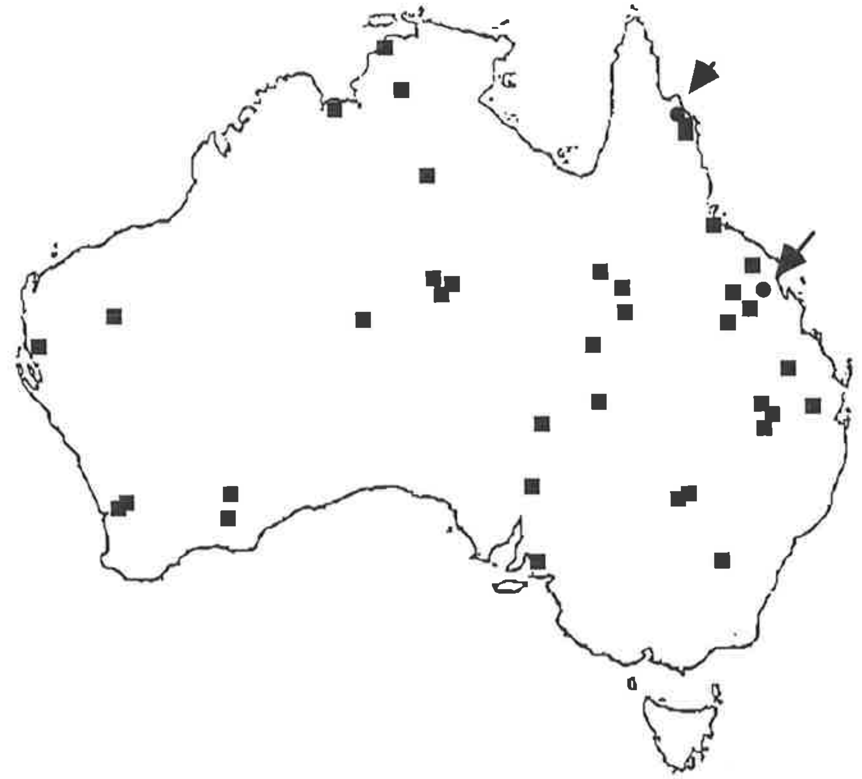


Figure 8.191. Distribution of *P. ferrugineus* (Crosskey) comb. nov. (●) and *P. floricolus* (Turner) comb. nov. (■).

Figure 8.192. Distribution of *P. inaequalis* (Turner) comb. nov. (●) and *P. iqbali* sp. nov. (■).

Figure 8.193. Distribution of *P. kelleri* sp. nov. (●) and *P. macdonaldi* sp. nov. (■).

Figure 8.194. Distribution of *P. malkini* sp. nov. (●) and *P. masneri* sp. nov. (■).

Figure 8.195. Distribution of *P. morganensis* sp. nov. (●) and *P. nalbarraensis* sp. nov (■).

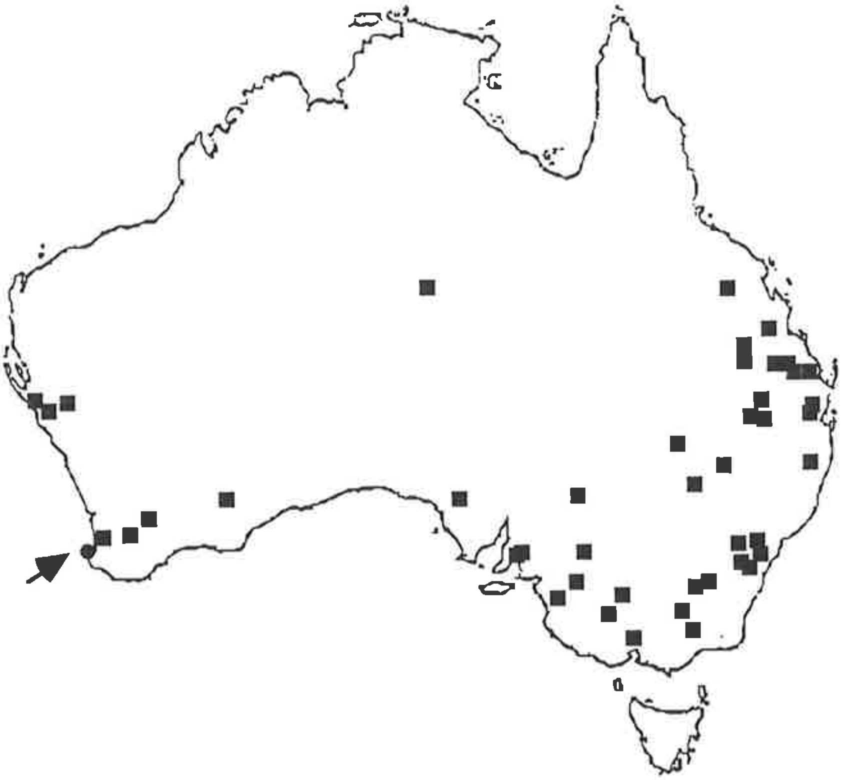


Figure 8.196. Distribution of *P. nitidiusculus* (Turner) comb. nov. (●) and *P. patellatus* (Westwood) comb. nov. (■).

Figure 8.197. Distribution of *P. pilosus* (Kieffer) comb. nov. (●) and *P. reticulatus* (Crosskey) comb. nov. (■).

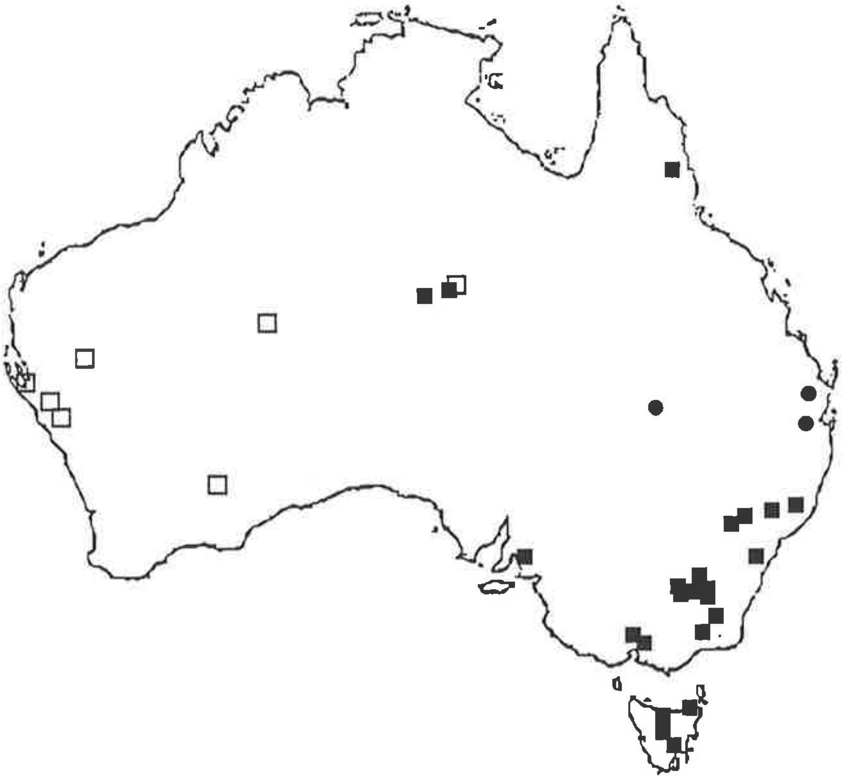


Figure 8.198. Distribution of *P. rieki* (Crosskey) comb. nov. (●), *P. spinitarsis* (Westwood) comb. nov. (■) and *P. taylori* sp. nov. (□). Note: South Australian localities for *P. rieki* not plotted as precise localities not known.

Chapter 9.

General discussion

This study has investigated the phylogenetic relationships among genera and species of hyptiogastrine wasps, examined whether the current distribution of taxa can be explained by vicariance events, and revised the taxonomy of species.

Prior to this study 37 hyptiogastrine species were recognised and this has been increased to 68 species. As well, at least 40 additional undescribed species of *Pseudofoenus s.l.* from the Australian region are currently recognised in museum collections. This represents about a three-fold increase in the number of species, and parallels the situation for many other groups of parasitic Hymenoptera. For example, Iqbal and Austin (1999) found a four-fold increase in *Ceratobaeus* Ashmead (Scelionidae, Baeini). Future collecting in the remote areas of mainland Australia and islands near to Australia, particularly New Guinea, is likely to generate a number of additional hyptiogastrine species. Other Evanioidea, particularly the Aulacidae and Evaniidae, are also probably much more speciose than the literature would suggest. For example, within the Aulacidae, there are more than 40 undescribed Australian species of *Aulacus* and *Pristaulacus* in museum collections, more than double the number of described species.

Perhaps one of the more important aspects of this study relates to the current distribution of the Hyptiogastrinae. The presence of several hyptiogastrine species on oceanic islands in the south-west Pacific shows that the group is capable of dispersal. The lack of any significant speciation in South America compared with Australia, together with the results of the phylogenetic analysis, suggests that the Gondwanan distribution of the subfamily is best explained by having an Australian centre of origin and subsequent radiation, and that the group has reached New Zealand and South America by dispersal more recently than the break-up of the Australian-Antarctic-South American connection. As far is known, this is the first time a vicariance hypothesis has been rejected convincingly for any group of animals that show such a restricted Gondwanan distribution. Whilst a number of other groups have a similar Gondwanan distribution, their phylogeny has not been tested. Monomachidae, for example, have a similar distribution (Naumann 1985), but whether this can be explained by vicariance events or dispersal is as yet untested.

A number of important outcomes were evident as a result of the phylogenetic analyses. Two monophyletic groups within the Hyptiogastrinae are recognised: *Hyptiogaster* Kieffer and *Pseudofoenus* Kieffer *sensu lato*, the latter genus comprising *Aulacofoenus* Kieffer, *Crassifoenus* Crosskey and *Eufoenus* Szépligeti which are synonymised with it. Two monophyletic species groups are designated for *Pseudofoenus s.l.*, with a further 31 species not assigned to any groups. Although there is a high degree of homoplasy in the characters used, it is unlikely that the addition of further, as yet undescribed, species will alter the generic level classification; more likely, however, is the potential for changes to the internal relationships within *Pseudofoenus s.l.*

The results of this phylogenetic study indicate the inadequacy of morphological data to satisfactorily resolve relationships, particularly at species levels, although in this study it has provided the basis for the development of a new classification and to test biogeographic hypotheses. This situation is possibly indicative of other diverse groups of wasps. In the future, relationships may be more completely resolved by using molecular data sets. The comparison of molecular data, such as those produced from a range of mitochondrial or nuclear genes by the direct sequencing of amplified DNA segments, provides a means for examining phylogenetic problems that have not been satisfactorily resolved by the use of morphological data. For example, Dowton & Austin (1994) and Dowton *et al.* (1998), using mitochondrial sequence data from the 16S and COI genes, have been able to successfully generate more robust phylogenies for major groups of Hymenoptera. Belshaw *et al.* (1998) used the D2 variable region of 28S rRNA to provide a phylogenetic reconstruction of the Ichneumonoidea. Increasingly, molecular sequence data are being used across most insect orders to infer aspects of phylogeny, mostly at generic and higher levels, for example, Libellulidae (Odonata) (Kambhampati and Charlton 1999), and Carabidae (Coleoptera) (Maddison *et al.* 1999), whilst Moran *et al.* (1999) have examined phylogenetic relationships within *Uroleucon* (Hemiptera, Aphidae). Some studies have employed a combination of molecular and morphological data, for example, Whitfield's (1997) study on the origin of polydnaviruses among braconid wasps, but the combination of such data are as yet uncommon. An examination of molecular data for the Hyptiogastrinae may more completely resolve their phylogeny, but equally, molecular data may not elucidate the phylogeny if the high degree of homoplasy shown in the morphological data is mirrored in the molecular data. However, apparent from this work and that of recent phylogenetic projects is that a solid foundation must be first developed based on the morphology of a group. Undertaking a morphological approach first has the advantages of 1) determining the limits of morphological data-sets and the development of hypotheses to better focus molecular work; 2) developing a better understanding of the morphological diversity, and associated with this, the biology of the group; 3) generating a comprehensive data-set that can be viewed as complimentary (additive) to molecular data; and 4) development of a framework for identification of taxa. It is hoped that the present study, in focusing on the taxonomy and morphologically based phylogeny of the Hyptiogastrinae, has made a small but significant contribution to the development of a definitive understanding of this subfamily and the parasitic Hymenoptera in general.

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Appendices

Appendix A1.1. Recorded plant associations for the genus *Pristaulacus* (Aulacidae). n.r. = new record; ? = uncertain record.

Pristaulacus species	Plant Species	Distribution	References
P. ater (Westwood)	*Pinus* spp. (Pinaceae)	USA	Townes 1950
P. bilobatus (Provancher)	*Tsuga canadensis* (Pinaceae)	USA	Townes 1950; Carlson 1979
P. bimaculatus Kieffer	*Ceratonia siliqua* (Fabaceae)	Europe	Oehlke 1983a
P. boninensis Konishi	*Ardisia sieboldii* (Myrsinaceae)	Japan	Konishi 1989
	Leucaena leucocephala (Fabaceae)	Japan	Konishi 1989
P. californicus (Townes)	*Pinus attenuata* (Pinaceae)	California	Townes 1950
P. editus (Cresson)	*Pinus attenuata* (Pinaceae)	Washington, California	Townes 1950
	Thuja plicata (Pinaceae)	British Columbia	Townes 1950
P. fasciatus (Say)	*Carya ovata* (Juglandaceae)	N. E. USA	Townes 1950
	Carya sp. (Juglandaceae)	N. E. USA	Carlson 1979
P. foxleei (Townes)	?*Pinus contorta* (Pinaceae)	Idaho	Townes 1950
	P. ponderosa (Pinaceae)	Montana, Idaho	Townes 1950
P. gibbator (Thunberg)	*Picea abies* (Pinaceae)	Sweden	Hedqvist 1973
P. minor (Cresson)	*Abies concolor* (Pinaceae)	USA	Townes 1950
	A. magnifica (Pinaceae)	USA	Townes 1950
	Picea sitkensis (Pinaceae)	USA	Townes 1950
	Pinus ponderosa (Pinaceae)	USA	Carlson 1979
	Pseudotsuga taxifolia (Pinaceae)	W. USA,British Columbia	Townes 1950
	Tsuga heterophylla (Pinaceae)	USA	Townes 1950
P. montanus (Cresson)	*Quercus kelloggii* (Fagaceae)	S. E. USA	Townes 1950
	?apricot (Rosaceae)	California	Townes 1950
P. niger Shuckard	*Pinus* spp. (Pinaceae)	USA	Carlson 1979
	P. elliottii (Pinaceae)	Florida	Haack & Wilkinson 1987
	P. rigida (Pinaceae)	New York	Smith 1996
	P. echinata (Pinaceae)	Georgia	Smith 1996

Pristaulacus species	Plant Species	Distribution	References
(contin.)			
	P. virginiana (Pinaceae)	Virginia	Smith 1996
	P. taeda (Pinaceae)	North Carolina	Smith 1996
	Abies balsamea (Pinaceae)	Minnesota	Smith 1996
	Larix laricina (Pinaceae)	Minnesota	Smith 1996
P. nigripes Kieffer	*Shorea robusta* (Dipterocarpaceae)	N. India	Mani & Muzaffer 1943
P. occidentalis (Townes)	*Abies concolor* (Pinaceae)	California	Meyer *et al.* 1978
P. obscuripennis (Westwood)	?*Quercus* sp. (Fagaceae)	Europe	Sedivy & Capek 1988
P. ornatus (Kieffer)	*Citrus sinensis* (Rutaceae)	NSW	Chadwick & Nikitin 1976
P. patrati Serville	*Euonymus japonicus* (Celestraceae)	Austria	Schletterer 1901
P. resutorivorus (Westwood)	*Pinus* spp. (Pinaceae)	N. USA, Canada	Townes 1950
	P. lambertiana (Pinaceae)	Oregon	Smith 1996
	Pseudotsuga menziesii (Pinaceae)	Montana	Smith 1996
P. rufitarsis (Cresson)	*Abies concolor* (Pinaceae)	California	Townes 1950; Meyer *et al.* 1978; Smith 1996
	Libocedrus decurrens (Cupressaceae)	California	Smith 1996
	Pinus arizonica (Pinaceae)	USA	Townes 1950
	P. attenuata (Pinaceae)	California	Smith 1996
	P. ponderosa (Pinaceae)	USA, Canada	Townes 1950
	P. lambertiana (Pinaceae)	California	Smith 1996
	P. flexilus (Pinaceae)	Idaho	Smith 1996
	Populus tremuloides (Salicaceae)	Colorado	Townes 1950
	Tsuga canadensis (Pinaceae)	New Hampshire	Townes 1950
	T. mertensiana (Pinaceae)	USA	Townes 1950
P. strangaliae Rohwer	*Alnus* sp. (Betulaceae)	N. E. USA	Townes 1950
	Carpinus sp. (Betulaceae)	N. E. USA	Townes 1950
	Fagus sp. (Fagaceae)	N. E. USA	Townes 1950
	Ostrya sp. (Betulaceae)	N. E. USA	Townes 1950
	Tsuga sp. (Pinaceae)	N. E. USA	Townes 1950
Pristaulacus sp.	*Acacia dealbata* (Fabaceae)	Tas	n.r. (TFIC)

Appendix A1.2. Records of flowers visited by adult Gasteruptiidae. (n.r. = new record; ? = uncertain record)

Gasteruptiid species	Plant species	Distribution	References
GASTERUPTIINAE			
G. assectator (L.)	*Aegopodium podagraria* (Umbelliferae)	Europe	Hedqvist 1973
	Anethum graveolens (Umbelliferae)	France	Dominique 1893
	Angelica sylvestris (Umbelliferae)	Europe	Dominique 1893 Crosskey 1951 Hedqvist 1973
	Anthriscus cerefolium (Umbelliferae)	Europe	Crosskey 1951
	A. sylvestris (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Chaerophyllum temulum (Umbelliferae)	France	Dominique 1893
	Daucus carota (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Euonymus sp. (Celestraceae)	Europe	Crosskey 1951
	Gypsophila paniculata (Caryophyllaceae)	France	Dominique 1893
	Heracleum sphondylium (Umbelliferae)	Europe	Crosskey 1951
	Pastinaca sativa (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Pimpinella saxifraga (Umbelliferae)	Europe	Crosskey 1951
	P. major (Umbelliferae)	Europe	Crosskey 1951
	Rhododendron sp. (Ericaceae)	United Kingdom	Crosskey 1951
	Rhus spp. (Anacardiaceae)	France	Dominique 1893
G. diversipes (Abeille)	*Daucus carota* (Umbelliferae)	France	Dominique 1893
	Rhus spp. (Anacardiaceae)	France	Dominique 1893
G. fluvialis (Turner)	*Eucalyptus calophylla* (Myrtaceae)	Australia	Turner 1918a
G. goberti (Tournier)	*Allium porrum* (Alliaceae)	France	Dominique 1893
G. hastator (F.)	*Anthriscus cerefolium* (Umbelliferae)	Europe	Crosskey 1951
	Daucus carota (Umbelliferae)	Europe	Crosskey 1951
	Pimpinella saxifraga (Umbelliferae)	Europe	Crosskey 1951
G. jaculator (L.)	*Aegopodium podagraria* (Umbelliferae)	Europe	Dominique 1893 Crosskey 1951 Hedqvist 1973
	Anethum graveolens (Umbelliferae)	France	Dominique 1893

Gasteruptiid species	Plant species	Distribution	References
(contin.)			
G. jaculator (L.)	*Angelica sylvestris* (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Carduus spp. (Compositae)	Europe	Crosskey 1951
	Chaerophyllum hirsutum (Umbelliferae)	France	Dominique 1893
	C. temulum (Umbelliferae)	Europe	Crosskey 1951
	Daucus carota (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Gypsophila paniculata (Caryophyllaceae)	France	Dominique 1893
	Heracleum sphondylium (Umbelliferae)	Europe	Crosskey 1951
	Mentha sp. (Labiatae)	Europe	Crosskey 1951
	Pastinaca sativa (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Pastinaca sp. (Umbelliferae)	United Kingdom	Capron 1879
	Pimpinella saxifraga (Umbelliferae)	Europe	Crosskey 1951
	Ruta graveolens (Rutaceae)	France	Dominique 1893
G. minutum (Tournier)	*Saxifraga aizoides* (Saxifragaceae)	Europe	Kohl 1912
	Sonchus arvensis (Compositae)	Europe	Crosskey 1951
G. montanus Cresson	*Pastinaca sativa* (Umbelliferae)	Connecticut	Viereck 1916
G. nigrescens Schletterer	*Euphorbia* spp. (Euphorbiaceae)	W. Europe	Kokujev 1910
G. opacum (Tournier)	*Banksia* sp. (Proteaceae)	France	Dominique 1893
G. pedemontanum (Tournier)	*Anthriscus sylvestris* (Umbelliferae)	Europe	Crosskey 1951 Hedqvist 1973
	Daucus carota (Umbelliferae)	Europe	Dominique 1893 Hedqvist 1973
	Eryngium sp. (Umbelliferae)	Europe	Dominique 1893
	Euphorbia spp. (Euphorbiaceae)	Europe	Crosskey 1951
	Heracleum sphondylium (Umbelliferae)	Europe	Crosskey 1951
	Levisticum sp. (Umbelliferae)	France	Dominique 1893
	Pastinaca sativa (Umbelliferae)	Europe	Hedqvist 1973
	Pimpinella saxifraga (Umbelliferae)	Europe	Crosskey 1951
	?*Pteroselinum crispum* (Umbelliferae)	Europe	Crosskey 1951
	Solidago canadensis (Compositae)	Europe	Crosskey 1951

Gasteruptiid species	Plant species	Distribution	References
(contin.)			
G. pyrenaicum Guérin Menéville	*Euphorbia* spp. (Euphorbiaceae)	Europe	Kokujev 1910
G. sowae Schletterer	*Dorycnium herbaceum* (Fabaceae)	Europe	Schletterer 1901
	Paliurus australis (Rhamnaceae)	Europe	Schletterer 1901
G. tarsatorius (Say)	*Solidago canadensis* (Compositae)	Connecticut	Viereck 1916
G. tenue Kieffer	*Ammi visnaga* (Umbelliferae)	NT	Kieffer 1922
G. tourneri Schletterer	*Achillea millefolium* (Compositae)	Europe	Crosskey 1951
	Anthriscus cerefolium (Umbelliferae)	Europe	Crosskey 1951
	Daucus carota (Umbelliferae)	Europe	Crosskey 1951
	Heracleum sphondylium (Umbelliferae)	Europe	Crosskey 1951
	Pastinaca sativa (Umbelliferae)	Europe	Kokujev 1910
	Solidago canadensis (Compositae)	Europe	Crosskey 1951
Gasteruption sp.	*Alphitonia excelsa* (Rhamnaceae)	NT	n.r. (SAMA)
Gasteruption sp.	*Angophora floribunda* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Atalaya hemiglauca* (Sapindaceae)	Qld	n.r. (UQIC)
	Eucalyptus camaldulensis (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Atalaya hemiglauca* (Sapindaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Banksia* sp. (Proteaceae)	WA	n.r. (SAMA)
	Leptospermum sp. (Myrtaceae)	WA	n.r. (SAMA)
Gasteruption sp.	*Bursaria* sp. (Pittosporaceae)	SA	n.r. (SAMA)
Gasteruption sp.	*Eucalyptus argillacea* (Myrtaceae)	NT	n.r. (UQIC)
Gasteruption sp.	*Eucalyptus camaldulensis* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Eucalyptus confertiflora* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Eucalyptus crebra* (Myrtaceae)	Qld	n.r. (UQIC)

Gasteruptiid species	Plant species	Distribution	References
(contin.)			
Gasteruption sp.	*Eucalyptus dealbata* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Eucalyptus ficifolia* (Myrtaceae) *E. salubris* (Myrtaceae)	WA WA	n.r. (UQIC) n.r. (UQIC)
Gasteruption sp.	*Eucalyptus intermedia* (Myrtaceae)	Qld	n.r. (SAMA)
Gasteruption sp.	*Eucalyptus odontocarpa* (Myrtaceae)	NT	n.r. (UQIC)
Gasteruption sp.	*Eucalyptus papuana* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	?*Eucalyptus populnea-crebra* hybrid (Myrtaceae)	NSW	n.r. (UQIC)
Gasteruption sp.	*Eucalyptus tereticornis* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Frankenia* sp. (Frankeniaceae)	SA	n.r. (SAMA)
Gasteruption sp.	*Grevillea* sp. (Proteaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Leptospermum trinervium* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Leptospermum* sp. (Myrtaceae)	Qld	n.r. (SAMA)
Gasteruption sp.	*Leptospermum* sp. (Myrtaceae)	NSW	n.r. (SAMA)
Gasteruption spp.	*Leptospermum* sp. (Myrtaceae)	NSW	n.r. (AMSA)
Gasteruption sp.	*Leptospermum* sp. (Myrtaceae)	Tas	n.r. (UQIC)
Gasteruption sp.	*Lophostemon conferta* (Myrtaceae)	Qld	n.r (UQIC)
Gasteruption sp.	*Lophostemon suaveolens* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Melaleuca linariifolia* (Myrtaceae)	Qld	n.r. (UQIC)
Gasteruption sp.	*Schinus areira* (Anacardiaceae)	SA	n.r. (SAMA)

Gasteruptiid species	Plant species	Distribution	References
(contin.)			
Gasteruption sp.	*Syzygium cormiflora* (Myrtaceae)	Qld	n.r. (UQIC)
HYPTIOGASTRINAE			
A. thoracicus (Guérin Menéville)	*Daviesia mimosoides* (Fabaceae)	ACT	Jennings & Austin 1997a
	Daviesia costata (Fabaceae)	WA	Jennings & Austin 1997a
	Dicrastylis flexuosa (Chloanthaceae)	WA	Jennings & Austin 1997a
A. fletcheri Jennings & Austin	*Lechenaultia stensepala* (Goodeniaceae)	WA	Jennings & Austin 1997a
A. perenjorii Jennings & Austin	*Boronia capitata* (Rutaceae)	WA	Jennings & Austin 1997a
C. grossitarsis (Kieffer)	*Melaleuca* sp. (Myrtaceae)	WA	Jennings & Austin 1994a
C. macronyx (Schletterer)	*E. camaldulensis* (Myrtaceae)	NSW	Jennings & Austin 1994a
Eufoenus sp.	*Acacia aciphylla* (Fabaceae)	WA	n.r. (WAMP)
Eufoenus sp.	*Angophora floribunda* (Myrtaceae)	Qld	n.r. (UQIC)
Eufoenus sp.	*Baeckea stowardii* (Myrtaceae)	WA	n.r. (WAMP)
Eufoenus sp.	*Bursaria spinosa* (Pittosporaceae)	SA	n.r. (SAMA)
Eufoenus sp.	*Calytrix oldfieldii* (Myrtaceae)	WA	n.r. (WAMP)
Eufoenus sp.	*Dicrastylis flexuosa* (Verbenaceae)	WA	n.r. (WAMP)
	Ptilotus sp. (Amaranthaceae)	WA	n.r. (WAMP)
Eufoenus sp.	*Grevillea* sp. (Proteaceae)	SA	n.r. (SAMA)
Eufoenus sp.	*Hakea* sp. (Proteaceae)	NT	n.r. (SAMA)
		WA	n.r. (WAMP)
Eufoenus sp.	*Micromyrtus flaviflora* (Myrtaceae)	WA	n.r. (WAMP)
	M. hymenonema (Myrtaceae)	WA	n.r. (WAMP)
Eufoenus sp.	*Prostanthera wilkieana* (Labiatae)	WA	n.r. (WAMP)

Gasteruptiid species	Plant species	Distribution	References
(contin.)			
Eufoenus sp	*Taraxacum officinale* (Compositae)	SA	n.r. (SAMA)
Hyptiogaster arenicola Turner	*Jacksonia sericea* (Fabaceae)	WA	Jennings & Austin 1997b
	Lechenaulti stenosepala (Goodeniaceae)	WA	Jennings & Austin 1997b
	Scholtzia sp. (Myrtacea)	WA	Jennings & Austin 1997b
H. humeralis (Kieffer)	*Eucalyptus cylindriflora* (Myrtaceae)	WA	n.r. (WAMP)
H. rufus (Westwood)	*Acacia* sp. (Fabaceae)	WA	n.r. (WAMP)
Hyptiogaster sp.	*Callistemon citrinus* (Myrtaceae)	Tas	n.r. (DPIT)
Hyptiogaster sp.	*Eucalyptus* sp. (Myrtaceae)	Tas	n.r. (DPIT)
Hyptiogaster sp.	*Prostanthera lasianthos* (Labiatae)	Tas	n.r. (DPIT)
Pseudofoenus spp.	*Leptospermum* sp. (Myrtaceae)	NZ	n.r. (NZAC)
	L. scoparium (Myrtaceae)	NZ	n.r. (NZAC)
	Metrosideros perforata (Myrtaceae)	NZ	n.r. (NZAC)
	Veronica (Scrophulariaceae)	NZ	n.r. (NZAC)

Appendix A1.3. Host records of Aulacidae. The following abbreviations are used: Bos = Bostrychidae; Bup = Buprestidae; Cer = Cerambycidae; Cler = Cleridae; Hem = Hemiptera; n.r. = new record; Scol = Scolytidae; Xip = Xiphydriidae. An "?" before a species indicates an uncertain record. Distribution abbreviations are as follows: NSW = New South Wales; NT = Northern Territory; NZ = New Zealand; Qld = Queensland; SA = South Australia; Tas = Tasmania; Vic = Victoria; WA = Western Australia.

Species	Distribution	Host	References
Aulacus albimanus Kieffer	NSW	*Coptocercus rubripes* (Boisduval) (Cer)	n.r. (NSWA)
A. aneurus Walkley	New Mexico	?*Dendroctonus* sp. (Scol) ?*Dendroctonus adjunctus* Bland (Scol)	Walkley 1952 Krombein, *et al.* 1958; Carlson 1979
A. apicalis Westwood	NSW	*Piesarthrius marginellus* Hope (Cer)	Schulz 1906; Cameron 1911; Clausen 1940
A. burquei (Provancher)	N.E. USA Quebec	*Xiphydria abdominalis* Say (Xip) *X. champlaini* Rohwer (Xip) *X. maculata* Say (Xip)	Viereck 1916 Champlain 1922 Bradley 1908; Champlain 1922 Champlain 1922; Townes 1950, 1951 Carlson 1979; Deyrup 1984; Smith 1996
A. digitalis Townes	USA	*X. maculata*	Deyrup 1984; Smith 1996
A. fuscicornis Cameron	NSW	?unknown cerambycid (Cer)	Cameron 1911
A. lovei (Ashmead)	N.E. USA, Quebec	*Xiphydria abdominalis* Say (Xip) *X. champlaini* (Xip) *X. scafa* Smith (Xip) *X. tibialis* Say (Xip)	Townes 1950 Carlson 1979 Carlson 1979 Smith 1996 Townes 1950; Carlson 1979
A. pallidicaudis (Cameron)	NSW	*Piesarthrius marginellus* (Cer)	Cameron 1911
A. pallipes Cresson	N.E. USA	*X. mellipes* Harris (Xip)	Ashmead 1901; Bradley 1901 Viereck 1916; Townes 1950, 1951 Carlson 1979; Smith 1996
A. striatus Jurine	Europe	*Xiphydria* sp. (Xip)	Bugnion & Popoff 1911 Lindemans 1921; Hellèn 1950 Oehlke 1983b

Species	Distribution	Host	References
(contin.)		*X. annulata* Jurine (Xip)	Györfi & Bajári 1962; Györfi 1964
		X. camelus (Xip)	Dahlbom 1837; Ratzeburg 1852 Giraud 1877; Kokujev 1910 Smits van Burgst 1920; Crosskey 1951 Györfi & Bajári 1962; Györfi 1964 Hedqvist 1973; Schimitschek 1974 Evenhuis & Vlug 1975; Gorny 1979 Oehlke 1983a; Sedivy & Capek 1988
		X. dromedarius F. (Xip)	Dahlbom 1837; Ratzeburg 1852 Giraud 1877; Crosskey 1951 Györfi & Bajári 1962; Györfi 1964 Oehlke 1983b
		X. longicollis Geoffroy (Xip)	Györfi 1964; Schimitschek 1974
		Xylotrechus capricornis (Gebler) (Cer)	Sedivy & Capek 1988
		? *Purpuricenus koehleri* L. (Cer)	Giraud 1877; Gaulle 1908
Aulacus sp.	Vic	*Scolecobrotus westwoodi* Hope (Cer)	n.r. (MVMA)
Aulacus sp.	Tas	*Nascoides quadrinotata* Van de Poll (Bup)	n.r. (ANIC); (TFIC)
Aulacus sp.	Tas	*Epithora dorsalis* MacLeay (Cer)	n.r. (TFIC)
Aulacus sp.	Qld	*Chlorophorus annularis* F. (Cer)	n.r. (QDPI)
Aulacus sp.	Qld	"borer" in cypress pine	n.r. (QDPI)
Aulacus sp.	Qld	"borer" in citrus	n.r. (QDPI)
Aulacus sp.	Tas	?*Coptocerus rubripes* (Cer)	n.r. (TFIC)
		?*Epithora dorsalis* (Cer)	n.r. (TFIC)
		?*Tessaromma undatum* Newman (Cer)	n.r. (TFIC)
Aulacus sp.	Vic	*Uracanthus acutus* Blackburn (Cer)	n.r. (MVMA)

Species	Distribution	Host	References
(contin.)			
Pristaulacus angularis (Crosskey)	NSW	*Phoracantha recurva* Newman (Cer)	Crosskey 1953b
	Qld	unknown cerambycid (Cer)	n.r. (BMNH)
P. barbeyi Ferrière	Algeria	unknown buprestid (Bup)	Ferrière 1933
P. beesoni Turner	N. India	*Chrysobothris beesoni* Obenberger (Bup)	Beeson 1941
		Xylotrechus smei Castelnau & Gory (Cer)	Beeson 1941
P. bilobatus (Provancher)	N.E. USA	*Melanophila fulvoguttata* (Harris) (Bup)	Champlain 1922 Townes 1950, 1951; Carlson 1979
P. bimaculatus Kieffer	Europe	*Purpuricenis koehleri* L. (Cer)	Lichtenstein & Picard 1918 Györfi & Bajári 1962; Oehlke 1983b
		?*Denops albofasciata* Charpentier (Cler)	Györfi & Bajári 1962; Oehlke 1983b
		?*Scobicia pustulata* F. (Bos)	Oehlke 1983b
P. boninensis Konishi	Japan	*Ceresium unicolor* (F.) Cer)	Konishi 1989
P. californicus (Townes)	California	*Chrysophania placida* (Le Conte) (Bup)	Townes 1950
		Paratimia conicola Fisher (Cer)	Townes 1950, 1951; Carlson 1979
P. chlapowskii Kieffer	Hungary; Czechoslovakia	*Chlorophorus pilosus* Forster (Cer)	Oehlke 1983b
		?*Isotomus speciosus* Schneider (Cer)	Sedivy & Capek 1988
P. comptipennis Enderlein	Japan	*Ceresium elongatum* Matushita (Cer)	Konishi 1991
P. editus (Cresson)	Washington	*Chrysophania placida* (Bup)	Townes 1950, 1951; Carlson 1979
	California	*Paratimia conicola* (Cer)	Townes 1950, 1951
	British Columbia	*Trachykele blondeli* Marseul (Bup)	Townes 1950
P. flavoguttatus (Westwood)	Qld	*Zygocera plumifer* Pascoe (Cer)	n.r. (QDPI)
P. flavimanus (Kieffer)	NSW	*Piesarthrius marginellus* (Cer)	Chadwick & Nikitin 1976
P. foxleei (Townes)	California, N.W. USA	*Anoplodera sanguinea* Le Conte (Cer)	Townes 1950
		Leptura obliterata Haldane (Cer)	Townes 1950, 1951; Carlson 1979

Species	Distribution	Host	References
(contin.)		*L. plagifera* Le Conte (Cer)	Townes 1950
P. gibbator (Thunberg)	Sweden	*Callidium coriaceum* Paykull (Cer)	Hedqvist 1973
P. gloriata (F.)	Europe, Asia	?*Callidium violaceum* (L.)(Cer)	Sedivy & Capek 1988
		?*Chlorophorus figuratus* (Scop.[ ]) (Cer)	Sedivy & Capek 1988
		Chrysobothris igniventris Reitter (Bup)	Sedivy & Capek 1988
		?*Dicerca berolinensis* Herbst (Bup)	Sedivy & Capek 1988
P. minor (Cresson)	USA, Canada	*Hylotrupes ligneus* (F.) (Cer)	Townes 1950
		Melanophila drummondi Kirby (Bup)	Townes 1950, 1951
		M. intrusa Horn (Bup)	Townes 1951; Carlson 1979
		Semanotus ligneus (F.) (Cer)	Townes 1951; Carlson 1979
P. montanus (Cresson)	W. USA, Canada	*Chrysobothris femorata* (Olivier) (Bup)	Townes 1950, 1951 Carlson 1979
		Xylotrechus nauticus (Mann) (Cer)	Townes 1950, 1951; Carlson 1979
P. niger Shuckard	Florida	*Monochamus titillator* (F.) (Cer)	Haack & Wilkinson 1987
		Mechanthocinus obsoletus (Olivier) Cer)	Haack & Wilkinson 1987
		Tylocerina nodosus (F.) (Cer)	Haack & Wilkinson 1987
		Xylotrechus sagittatus (Germar) (Cer)	Haack & Wilkinson 1987
P. nigripes Kieffer	India	*Xylotrechus quadripes* Chevreul (Cer)	Beeson 1941
P. obscuripennis (Westwood)	Europe, Asia Minor	*Xylotrechus arvicola* (Olivier) (Cer)	Sedivy & Capek 1988
P. ornatus Kieffer	Qld	*Zygocera plumifera* (Cer)	n.r. (BMNH)
P. sp. nr *ornatus* Kieffer	NSW	?*Coptopterus thoracicus* (Pascoe) (Cer)	Chadwick & Nikitin 1976
P. patrati Audinet-Serville	central Europe	*Xiphydria annulata* (Xip)	Lichtenstein & Picard 1918 Györfi 1964; Oehlke 1983b
		X. longicollis (Xip)	Schimitschek 1974
P. resutorivorus (Westwood)	N. USA, Canada	?*Arhopalus productus* (Le Conte) (Cer)	Carlson 1979
		Monochamus resutoris ⊔(Cer)	Westwood 1851
P. rufitarsis (Cresson)	N. USA,	*Chrysobothris caurina* Horn (Bup)	Carlson 1979

Species	Distribution	Host	References
(contin.)	Canada	*Graphisurus* sp. (Cer)	Carlson 1979
		Melanophila drummondi (Kirby) (Bup)	Townes 1950, 1951; Carlson 1979
		Melanophila fulvoguttata (Bup)	Townes 1950, 1951; Carlson 1979
		Saperda calcarata Say (Cer)	Townes 1950, 1951; Carlson 1979
P. strangaliae Rohwer	N. USA, Canada	*Anoplodera proxima* (Say) (Cer)	Smith 1996
		A. mutabilis (Newman) (Cer)	Townes 1950, 1951
		A. rubrica (Say) (Cer)	Townes 1950, 1951
P. variegatus Shuckard	Tas	*Ancita crocogaster* Boisduval (Cer)	n.r. (TFIC)
Pristaulacus sp.	NSW	*Aphanasium australe* (Boisduval) (Cer)	Moore 1964
Pristaulacus sp.	Tas	*Bethelium signiferum* Newman (Cer)	n.r. (TFIC)
Pristaulacus sp.	Thailand	*Xylotrechus quadripes* Chevrolat (Cer)	Visitipanich 1994
Pristaulacus sp.	NSW	unknown cerambycid (Cer)	Hadlington & Gardner 1959

Appendix A1.4. Host records of the Gasteruptiidae. The following family abbreviations are used: Coll = Colletidae; Hal = Halictidae; Lep = Lepidoptera; Mas = Masarinae; Meg = Megachilidae; Sph = Sphecidae; Sten = Stenotritidae; Trig = Trigonalyidae; n.r. = new record; ? indicates an uncertain record. Distribution abbreviations are as follows: ACT = Australian Capital Territory; NT = Northern Territory; P.N.G. = Papua New Guinea; Qld = Queensland; SA = South Australia; Tas = Tasmania; Vic = Victoria; WA = Western Australia.

Species	Distribution	Host	References
GASTERUPTIINAE			
Gasteruption assectator (L.)	Europe, N America	*Chelostoma florisomne* (L.) (Meg)	Nicholson 1928
		Colletes daviesanus Smith (Coll)	O'Toole, pers. comm.
		Heriades florisomne (L.) (Sph)	Lindemans 1921
		Hylaeus annularis Kirby (Coll)	Höppner 1904
		H. brevicornis (Nylander) (Coll)	Höppner 1904
		H. communis (Nylander) (Coll)	Höppner 1904
		H. cervicornis Costa (Coll)	Höppner 1904
		H. ellipticus (Kirby) (Coll)	Carlson 1979
		H. kriechbaumeri (Foerster) (Coll)	Höppner 1904
		H. rinki Gorsky (Coll)	Höppner 1904
		H. signatus Smith (Coll)	O'Toole & Raw 1991
		Hylaeus sp. (Coll)	Ferrière 1946
		Megachile rotundata (F.) (Meg)	Carlson 1979
		Odynerus spinipes (L.) (Vesp)	Györfi & Bajári 1962; Oehlke 1983a
		Passaloecus distinctus Fox (Sph)	Bradley 1908
		Pemphredon lethifer Shuckard (Sph)	Györfi & Bajári 1962; Oehlke 1983a
		Trypoxylon figulus (L.) (Sph)	Giraud 1877 Höppner 1904; Farhinger 1922 Ferrière 1946; Sedivy 1958 Györfi & Bajári 1962
		Trypoxylon sp. (Sph)	Oehlke 1983a
G. brachyurum Schletterer	SA	*Callomelitta picta* Smith (Coll)	n.r. (ANIC)
G. caffrarium Schletterer	southern Africa	*Hylaeus* sp. (Coll)	Skaife 1953
		Immanthidium junodi (Meg)	Prins 1978
G. caudatum Szépligeti	Europe	*Osmia leucomelena* (Kirby) (Meg)	Malyshev 1964, 1966
		Osmia parvula Dufour & Perris (Meg)	Malyshev 1937, 1949, 1964

Species	Distribution	Host	References
(contin.)			
G. deivitsi Schletterer	ACT	?*Sceliophron* sp. (Sph)	n.r. (ANIC)
G. diversipes (Abeille)	Europe	*Eumenes* sp. (Vesp)	Dominique 1893; Ferrière 1946 Sedivy 1958; Györfi & Bajári 1962 Oehlke 1983a
		Heriades sp. (Sph)	Ferrière 1946; Hellèn 1950
		Hylaeus deceptoria Perez (Coll)	Ferton 1910
		Hylaeus sp. (Coll)	Ferrière 1946; Oehlke 1983a
		Odynerus sp. (Vesp)	Dominique 1893; Ferrière 1946 Sedivy 1958; Györfi & Bajári 1962 Oehlke 1983a
		Osmia sp. (Meg)	Hellèn 1950
G. erythrostonum (Dahlbohm)	Europe	*Hylaeus pectoralis* (Coll)	Oehlke 1983a
G. freyi (Tournier)	Europe	*Hylaeus pectoralis* (Coll)	Ferrière 1946; Oehlke 1983a
		Hylaeus sp. (Coll)	Malyshev 1966
G. hastator (F.)	Europe, N. Africa	*Hylaeus variegata* (F.) (Coll)	Höppner 1904 Stöckhert 1922; Oehlke 1983a
		?*Lestica subterranea* (F.) (Sph)	Oehlke 1983a
		Odynerus sp. (Vesp)	Sedivy 1958
		Odynerus lavigata Shuckard (Vesp)	Crosskey 1951; Oehlke 1983a Györfi & Bajári 1962
		Osmia tridentata Dufour & Perris (Meg)	Crosskey 1951; Oehlke 1983a
		Osmia sp. (Meg)	Sedivy 1958; Györfi & Bajári 1962
? *G. incertus* (Cresson)	USA	*Passaloecus distinctus* Fox (Sph)	Bradley 1908
G. jaculator (L.)	N. Europe	*Chelostoma florisomne* (L.) (Meg)	Oehlke 1983a
		Colletes daviesanus Smith (Coll)	Höppner 1904 Malyshev 1966; Oehlke 1983a
		Heriades truncorum (L.) (Sph)	Höppner 1904; Oehlke 1983a
		Hylaeus ?*bicinctus* (Coll)	Oehlke 1983a
		H. pectoralis (Forster)	BMNH (nr)
		?*Odynerus spinipes* (Vesp)	Oehlke 1983a
		Osmia bicornis L. (Meg)	Dominique 1893 Höppner 1904; Oehlke 1983a

Species	Distribution	Host	References
(contin.)		*Osmia leaiana* Kirby (Meg)	Morley 1916
		Osmia tridentata (Meg)	Dominique 1893; Höppner 1904; Oehlke 1983a
		Pemphredon lugubris (F.) (Sph)	Morley 1937; Oehlke 1983a
		Trypoxylon figulus (Sph)	Giraud 1866; Höppner 1904
G. kaweahense (Bradley)	S. W. USA	*Ceratina pacifica* (Smith) (Coll)	Daly *et al.* 1967; Carlson 1979
G. kirbii (Westwood)	N. America	*Hoplitis sambuci* Titus (Meg)	Carlson 1979
		Hylaeus modestus Say (Coll)	Carlson 1979
		Megachile rotundata (F.) (Meg)	Carlson 1979
G. laticeps (Tournier)	Italy	*Pemphredon* sp. (Sph)	Györfi & Bajári 1962
G. opacum (Tournier)	Europe	*Trypoxylon figulus* (Sph)	Magretti 1882; Ferrière 1946; Sedivy 1958; Györfi & Bajári 1962; Oehlke 1983a
G. pattersonae Melander & Brues	W. USA	*Dianthidium curvatum sayi* Cockerell (Meg)	Carlson 1979
G. pedemontanum Tournier	Europe	*Osmia versicolor* Latrielle (Meg)	Fahringer 1922; Ferrière 1946 Sedivy 1958; Györfi & Bajári 1962 Oehlke 1983a
		Osmia sp. (Meg)	Hellèn 1950 Crosskey 1951; Hedqvist 1958
	Holland	?*Trigonalis hahnii* Spinosa (Trig)	Lindemans 1921
G. punctulatum Schletterer	sth. Africa	*Hylaeus (Notohylaeus) heraldicus* Smith (Coll)	Kieffer 1956b; Prins 1978
G. pyrenaicum (Guérin Méneville)	Europe	*Cemonus unicolor* (Panzer) (Sph)	Dominique 1893 Höppner 1904; Ferrière 1946 Sedivy 1958; Györfi & Bajári 1962 Oehlke 1983a
		Ceratina callosa (F.) (Coll)	Malyshev 1964 1966; Oehlke 1983a
		C. caerula (Villers) (Coll)	Malyshev 1966; Oehlke 1983a
		C. cyanea K{ } (Coll)	Malyshev 1964
G. robustum Kieffer	sth. Africa	*Xylocopa sicheli* Vachal (Anth)	Whatmough 1974
		Xylocopa sp. (Anth)	Prinsloo 1985

Species	Distribution	Host	References
(contin.)			
G. rugulosum {?}	?	*Colletes* sp. *Hylaeus* sp.	Malyshev 1964 Malyshev 1964
G. simillinum Schletterer	NSW	unknown beetle	n.r. (ANIC)
G. terrestre Tournier	Europe	*Osmia versicolor* (Meg)	Farhinger 1922
G. thompsoni {?}	?	*Colletes* sp. *Hylaeus* sp.	Malyshev 1964 Malyshev 1964
G. trigonum Pasteels	Zaire, Zambia	*Xylocopa carinata* Smith (Anth)	Pasteels 1956b; Prins 1978
G. varians Pasteels	N. Qld, P.N.G.	*Megachile kuehni* Friese (Meg)	Pasteels 1956c
G. variolosum Abeille	Italy	?*Pemphredon lethifer* Shuckard (Sph)	Grandi 1959
G. visiliae (Bradley)	S. W. USA	*Hylaeus cressoni* Cockerell (Coll)	Carlson 1979
G. xylocopae Kieffer	southern Africa	*Xylocopa sicheli* Vachal (Anth) *Xylocopa* sp. (Anth)	Kieffer 1911; Pasteels 1956a; Prins 1978 Malyshev 1931
Gasteruption sp.	?SA	*Amphylaeus nubilosellus mediostrictus* (Cockerell)(Coll)	n.r. (WAMP)
Gasteruption sp.	Qld	*Amphylaeus sculptifrons* (Cockerell) (Coll)	n.r. (WAMP)
Gasteruption sp.	SA	*Callomelitta* sp. (Coll)	n.r. (WAMP)
Gasteruption sp.	SA	*Callomelitta picta* Smith (Coll)	n.r. Houston, pers. comm.
Gasteruption sp.	SA	*Euryglossa (Euhesma)* sp. (Coll)	n.r. (WARI)
Gasteruption sp.	Australia	*Euryglossina lynettae* (Rayment) (Coll)	Rayment 1955
Gasteruption sp.	SA	*Euryglossina pulchra* Exley (Coll) *Pachyprosopis haematostomata* (Coll)	Houston 1969 Houston 1969
Gasteruption sp.	Tas	*Herohesma weiri* Exley (Coll)	n.r. (ANIC)

Species	Distribution	Host	References
(contin.) *Gasteruption* sp.	Australia	*Hylaeorhiza nubilosa* (Smith) (Coll)	n.r. (ANIC)
Gasteruption sp.	Qld	*Hylaeorhiza nubilosa* (Coll) *Amphylaeus morosus* (Smith) (Coll) *Chalicodoma* sp. (Coll)	n.r. (WAMP) n.r. (WAMP) n.r. (WAMP)
Gasteruption sp.	Australia	*Hylaeus chrysognatha* Cockerell (Coll)	n.r. (ANIC)
Gasteruption sp.	Qld	*Hylaeus quadratus* (Smith) (Coll)	n.r. (ANIC)
Gasteruption sp.	Vic	*Hylaeus* sp. (Coll)	n.r. (BMNH)
Gasteruption sp.	Qld	*Hylaeus obtusatus* (Smith) (Coll)	n.r. (WAMP)
Gasteruption sp.	Qld	*Hylaeus (Eurosopsis)* sp. (Coll)	n.r. (WAMP)
Gasteruption sp.	WA	*Hyleoides zonalis* Smith (Coll)	n.r. (WAMP)
Gasteruption sp.	SA	*Meroglossa* sp. (Coll)	n.r. (WAMP)
Gasteruption sp.	Qld	*Pachyprosopis haematostoma* Cockerell (Coll)	Houston 1969
Gasteruption sp.	SA	unknown colletid (Coll)	n.r. (WARI)
Gasteruption sp.	SA	unknown eumenid (Vesp)	n.r. (SAMA)
Gasteruption sp.	NT	unknown wasp mud nest (Vesp?)	n.r. (SAMA)
Gasteruption sp.	Qld	unknown hyaleine (Coll)	n.r. (WAMP)
HYPTIOGASTRINAE *Aulacofoenus asymmetricus* (Turner)	SA	*Nomia australica* Smith (Hal)	n.r. (WAMP)
Crassifoenus macronyx (Schletterer)	SA	*Stenotritus* sp. (Sten)	Jennings & Austin 1994a
C. houstoni Jennings & Austin	WA	*Ctenocolletes albomarginatus* Michener (Sten) *C. fulvescens* Houston (Sten)	Houston 1987; Jennings & Austin 1994a Houston 1987; Jennings & Austin 1994a

Species	Distribution	Host	References
(contin.)			
		Ctenocolletes nicholsoni (Cockerell) (Sten)	Houston 1987; Jennings & Austin 1994a
		C. ordensis Michener (Sten)	Houston 1984, 1987; Jennings & Austin 1994a
		C. smargdinus (Smith) (Sten)	Houston 1987; Jennings & Austin 1994a
Eufoenus inaequalis (Turner)	WA	*Cladocerapis persooniae* Rayment (Coll]	Parrott 1955
Eufoenus sp.	Qld	*Euryglossula chalcosoma* (Cockerell) (Coll)	Houston 1969
Eufoenus sp.	WA	*Euryglossa (Dermatomesma)* sp. (Coll)	n.r. (WAMP)
Eufoenus sp.	NT	*Hylaeus* sp. (Coll)	Naumann 1983
Eufoenus sp.	ACT	*Leioproctus nigrifulvus* [ ] (Coll)	n.r. (ANIC)
Eufoenus sp.	WA	*Neopasiphe* sp. (Coll)	n.r. (WAMP)
Eufoenus sp.	WA	*Nomia australica* Smith (Hal)	n.r. (WAMP)
Eufoenus sp.	Qld	*Paracolletes* sp. (Coll)	n.r. (QDPI)
Eufoenus sp.	SA	*Xanthesma furcifera* (Cockerell) (Coll)	Houston 1969
Hyptiogaster arenicola Turner	WA	*Rolandia maculata* (Meade-Waldo) (Mas)	Houston 1995; Jennings & Austin 1997b
H. humeralis (Schletterer)	WA	*Paragia tricolor* Smith (Mas)	Jennings & Austin 1997b
H. rufus (Westwood)	SA	*Callomellita* sp. (Coll)	Jennings & Austin 1997b
H. pinjarraegaensis Jennings & Austin	WA	?*Paragia* sp. (Mas)	Jennings & Austin 1997b
Pseudofoenus crassipes (Smith)	NZ	*Paracolletes* sp. (Coll)	Jennings & Austin 1994b
P. pedunculatus (Schletterer)	NZ	*Leioproctus metallicus* (Smith) (Coll)	Gourlay 1930; Valentine & Walker 1991
P. unguicularis (Smith)	NZ	*Paracolletes* sp. (Coll)	Jennings & Austin 1994b

Appendix A2.1. Data matrix for preliminary analyses (Section 6.4). Missing data indicated by '?'. Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Taxon/Character		1	11111	11112	22222	22223	33333	33334	44444	44445	55555	555
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	678
Schlettererius cinctipes	00010	00100	01100	21001	01001	10001	10110	01000	00000	01011	10000	110
Aulacus atriceps	11100	11000	01110	0-010	10102	00011	00010	01000	11000	00001	11101	010
Aulacus sp. 1	11100	11000	01110	0-010	10112	00011	00010	01000	11000	00001	11101	010
Aulacus sp. 2	11100	11000	01110	0-010	10102	00011	00010	01000	11000	00001	10101	010
Pristaulacus cinguiculatus	11100	01000	01110	10010	10102	00011	00010	01000	11100	00001	10101	010
Pristaulacus variegatus	11100	01000	01110	10010	10102	00011	00010	01000	11100	00001	10101	010
Pristaulacus sp. 1	11100	01000	01110	10010	10102	00011	00010	01000	11100	00001	11101	010
Gasteruption brachyurum	21110	00000	00001	20110	10110	00010	10111	10101	01000	01001	10111	010
Gasteruption fluviale	21110	00000	00001	20110	10111	00000	10111	10101	01000	01001	10111	010
Gasteruption spinigerum	21110	00000	01001	20110	10111	00000	11111	10101	01000	00001	10111	010
Gasteruption ?paradoxale	21110	00010	00001	20110	10111	00000	11111	10101	01000	01001	10111	010
Gasteruption sp. 1	21110	00100	00001	21110	10101	00010	10111	10101	01000	01001	10111	110
Aulacofoenus deletangii	21110	00100	00111	20110	10110	00010	11111	11201	01000	10000	00111	000
Aulacofoenus fallax	21110	00110	00111	21110	10110	00010	11111	11101	01000	00000	00111	000
Aulacofoenus fletcheri	21110	10111	00111	20110	10110	00000	10111	11101	01000	00000	00111	100
Aulacofoenus infumatus	21110	00100	00111	20110	10110	00010	10111	11201	01000	00000	00111	000
Aulacofoenus kurmondi	21110	00110	00111	21110	10100	00010	11111	11101	01000	10000	00111	000
Aulacofoenus marionae	21110	10110	00111	21110	10110	00000	10111	11101	01000	00000	00111	000
Aulacofoenus perenjorii	21110	00110	00111	20110	10110	00000	11111	11101	01000	00000	00111	100
Aulacofoenus thoracicus	21110	00110	00111	20110	10110	00010	11111	11101	01011	00000	00111	100
Aulacofoenus whiani	21110	00110	01111	21110	10110	00000	11111	11101	01000	00000	00111	000
Crassifoenus grossitarsis	21110	00110	11111	20110	10110	00010	11111	11111	01000	10100	00111	001
Crassifoenus houstoni	21110	00110	11111	20110	10110	00010	11111	11111	01000	10100	00111	001
Crassifoenus macronyx	21110	00110	11111	20110	10110	00010	11111	11111	01000	10100	00111	001
Eufoenus antennalis	21110	00110	00111	21110	10110	00010	11111	11101	01000	01000	00111	000
Eufoenus australis	21110	00110	00111	21110	10110	00010	11111	11101	00000	00&1000	00111	000
Eufoenus crassitarsis	21110	00110	00111	21110	10110	00000	10111	11101	00010	01000	00111	000
Eufoenus darwini	21110	00100	00111	21110	10110	00000	10111	11101	00011	00000	00111	000
Eufoenus extraneus	21210	00100	00111	21110	10110	00010	11111	11001	00000	01000	00111	000
Eufoenus ferrugineus	21110	00110	00111	21110	10110	00000	11111	11101	00000	01000	00111	000
Eufoenus floricolus	21110	00100	00111	21110	10110	00010	10111	11101	00000	01000	00111	000

Taxon/Character		1	11111	11112	22222	22223	33333	33334	44444	44445	55555	555
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	678
Eufoenus inaequalis	21110	00110	00111	21110	10110	00000	11111	11101	00000	10000	00111	100
Eufoenus minimus	21110	00100	01111	20110	10110	00010	11111	11101	00000	01000	00111	000
Eufoenus patellatus	21110	00110	00111	21110	10110	00010	11111	11101	00000	00&1000	00111	000
Eufoenus pilosus	21110	00100	00111	21110	10110	00010	00111	11101	00000	00000	00111	000
Eufoenus rieki	21210	00110	00111	21110	10110	00010	10111	11101	00000	01000	00111	000
Eufoenus ritae	21110	10100	00111	21110	10110	00000	11111	11101	00000	01000	00111	000
Eufoenus spinitarsis	21110	00100	01111	21110	10110	00000	11111	11101	00011	00000	00111	000
*'Eufoenus' beverlyae**	21110	00100	00111	21110	10110	00000	11111	11101	00000	00000	00111	000
*'Eufoenus' iqbali**	21110	00100	01111	21110	10110	00010	10111	11101	00010	00000	00111	000
*'Eufoenus' macdonaldi**	21110	00100	01111	21110	10110	00010	10111	11101	00000	00000	00111	000
*'Eufoenus' karimuiensis**	21110	00100	00111	21110	10110	000?0	??111	11101	00000	01000	00111	000
*'Eufoenus' nalbarraensis**	21110	00100	00111	21110	10110	00010	10111	11101	00000	01000	00111	000
*'Eufoenus' douglasi**	21110	00110	00111	20110	10110	00010	11111	11001	00000	00000	00111	100
*'Eufoenus' masneri**	21110	10110	00111	21110	10110	00010	11111	11101	00000	00000	00111	000
*'Eufoenus' malkini**	21110	00110	00111	21110	10110	00000	10111	11001	00000	00000	00111	000
*'Eufoenus' crosskeyi**	21110	10100	01111	21110	10110	00000	11111	11101	00011	00000	00111	000
Hyptiogaster arenicola	21110	00110	10111	21110	10100	00010	10111	11101	01000	01000	00111	010
Hyptiogaster humeralis	21111	00110	10111	21110	10110	01110	11111	11101	01000	10000	00111	010
Hyptiogaster kalbarrii	21111	00010	10121	21110	10100	01110	11111	11101	01000	00000	00111	010
Hyptiogaster pinjarregaensis	21110	00110	11111	21110	10100	00000	10111	11101	01000	01000	00111	010
Hyptiogaster rufus	21110	00010	10111	21110	10100	00000	10111	11101	01000	01000	00111	010
Pseudofoenus crassipes	21110	10110	00111	21110	10110	00010	11101	12101	00010	00000	00111	000
Pseudofoenus unguiculatus	21110	10110	00111	21110	10110	00010	10101	12101	00000	10000	00111	000

Appendix A2.2. Extended data matrix used in Section 6.5.2. Missing data indicated by '?'. Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Taxon/Character	1	11222	23333	34444	44555	66666	6666
	56891	27478	92478	92456	78689	01234	5678
Gasteruption sp. 1	00100	11000	10101	01000	10101	00001	1400
Aulacofoenus deletangii	00100	10100	11112	01001	00000	00420	0210
Aulacofoenus fallax	00110	11100	11111	01000	00001	10102	0220
Aulacofoenus fletcheri	01110	10100	00111	01000	00100	10012	0120
Aulacofoenus infumatus	00100	10100	10112	01000	00000	10200	0110
Aulacofoenus kurmondi	00110	11000	11111	01001	00000	10122	0010
Aulacofoenus marionae	01110	11100	00111	01000	00000	00212	0020
Aulacofoenus perenjorii	00110	10100	01111	01000	00100	10102	0110
Aulacofoenus thoracicus	00110	10100	11111	01110	00100	10001	0320
Aulacofoenus whiani	00110	11100	01111	01000	00001	10013	0120
Crassifoenus grossitarsis	00111	00100	11111	11001	01010	01010	0121
Crassifoenus houstoni	00111	00100	11111	11001	01011	01020	0030
Crassifoenus macronyx	00111	00100	11111	11001	01011	10011	0021
Eufoenus antennalis	00110	11100	11111	01000	10001	10222	0020
Eufoenus australis	00110	11100	11111	00000	10000	10202	0120
				1			
Eufoenus crassitarsis	00110	11100	00111	00100	10000	00011	0120
Eufoenus darwini	00100	11100	00111	00110	00000	20100	0210
Eufoenus extraneus	00100	11100	11110	00000	10000	20300	0020
Eufoenus ferrugineus	00110	11100	01111	00000	10000	20202	0020
Eufoenus floricolus	00100	11100	10111	00000	10000	10201	0110
Eufoenus inaequalis	00110	11100	01111	00001	00100	10210	0120
Eufoenus minimus	00100	00100	11110	00000	10001	20200	0210
Eufoenus patellatus	00110	11100	11111	00000	10001	10112	0120
				1			
Eufoenus pilosus	00100	11100	10111	00000	00000	00200	0120
Eufoenus rieki	00110	11100	00111	00000	10000	00011	0010
Eufoenus ritae	01100	11100	01111	00000	10000	10202	0010
Eufoenus spinitarsis	00100	01100	01111	00110	00000	00010	0210
*'Eufoenus' beverlyae**	00100	11100	11111	00000	00000	00310	0110
*'Eufoenus' iqbali**	00100	01100	10111	00100	00001	20110	0210
*'Eufoenus' macdonaldi**	00100	01100	10111	00000	00000	00201	0210
*'Eufoenus' karimuiensis**	00100	11100	??111	00000	10001	102?2	0020
*'Eufoenus' nalbarraensis**	00100	11100	10111	00000	00000	10110	0410
*'Eufoenus' douglasi**	00110	10100	11110	00000	00100	10102	0110
*'Eufoenus' masneri**	01110	11100	11111	00000	00000	10201	0110
*'Eufoenus' malkini**	00110	11100	00110	00000	00000	00113	0110
*'Eufoenus' crosskeyi**	21100	01100	01111	00110	00001	10000	0110
*'Eufoenus' collessi**	00110	11100	11111	01000	00001	10201	0110
*'Eufoenus' cardaleae**	00110	10100	10111	00000	00000	10101	0310
*'Eufoenus' schmidti**	00100	11100	11111	00000	00000	00202	0120
*'Eufoenus' ericae**	20110	00100	11111	00000	10100	10102	0020
*'Eufoenus' taylori**	01110	11100	00111	01000	10001	10003	0020
'Eufoenus' morganensis8	01110	10100	11111	01110	10001	10001	0020
*'Eufoenus' kelleri**	00100	01100	10111	00100	00001	20100	0210
*'Eufoenus' feckneri**	00110	10100	11111	00001	00000	00211	0110
				1			
*'Eufoenus' coorowensis**	20100	01100	01111	00110	00001	10111	0110
Hyptiogaster arenicola	00111	11000	10111	01000	10001	10302	1040
Hyptiogaster humeralis	10111	11111	11111	01001	00001	21311	1030
Hyptiogaster kalbarrii	10011	11011	11111	01000	00003	40302	1140
Hyptiogaster pinjarregaensis	00111	01000	00111	01000	10001	10111	1140
Hyptiogaster rufus	00011	11000	00111	01000	10002	30202	1130
Pseudofoenus crassipes	01110	11100	11021	00110	00000	00210	0200
Pseudofoenus unguiculatus	01110	11100	10021	00001	00000	00110	0200

Appendix A2.3. Segment coding for character 59 - terminal flagellomere length : width using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean ratio	1 x SD
Gasteruption sp. 1	2.5	1
Aulacofoenus deletangii	1.4	0
Aulacofoenus fallax	2.3	1
Aulacofoenus fletcheri	1.9	0
Aulacofoenus infumatum	1.9	0
Aulacofoenus kurmondi	1.9	0
Aulacofoenus marionae	2.0	0
Aulacofoenus perenjorii	1.8	0
Aulacofoenus thoracicus	1.9	0
Aulacofoenus whiani	2.4	1
Crassifoenus grossitarsis	2.0	0
Crassifoenus houstoni	2.3	1
Crassifoenus macronyx	2.3	1
Eufoenus antennalis	2.6	1
Eufoenus australis	1.7	0
Eufoenus crassitarsis	1.7	0
Eufoenus darwinii	1.9	0
Eufoenus extraneus	2.0	0
Eufoenus ferrugineus	1.8	0
Eufoenus floricolus	1.5	0
Eufoenus inaequalis	1.9	0
Eufoenus minimus	2.5	1
Eufoenus nitidiusculus	1.6	0
Eufoenus patellatus	2.4	1
Eufoenus pilosus	1.6	0
Eufoenus reticulatus	2.7	1
Eufoenus rieki	1.6	0
Eufoenus ritae	2.0	0
Eufoenus spinitarsis	1.8	0
*'Eufoenus' beverlyae**	1.5	0
*'Eufoenus' cardaleae**	1.7	0
*'Eufoenus' collessi**	2.1	1
*'Eufoenus' coorowensis**	2.1	1
*'Eufoenus' crosskeyi**	2.1	1
*'Eufoenus' douglasi**	2.0	0
*'Eufoenus' ericae**	1.8	0
*'Eufoenus' feckneri**	1.8	0
*'Eufoenus' iqbali**	2.4	1
*'Eufoenus' karimuiensis**	2.1	1
*'Eufoenus' kelleri**	2.7	1
*'Eufoenus' macdonaldi**	1.6	0
*'Eufoenus' malkini**	1.7	0
*'Eufoenus' masneri**	1.7	0
*'Eufoenus' morganensis**	2.1	1
*'Eufoenus' nalbarraensis**	1.9	0
*'Eufoenus' schmidti**	2.0	0
*'Eufoenus' taylori**	2.2	1
Hyptiogaster arenicola	2.4	1
Hyptiogaster humeralis	2.3	1
Hyptiogaster kalbarrii	5.1	3
Hyptiogaster pinjarregaensis	2.4	1
Hyptiogaster rufus	3.4	2
Pseudofoenus crassipes	2.0	0
Pseudofoenus unguiculatus	2.0	0
Mean	2.09	
S.D.	0.56	

Appendix A2.4. Segment coding for character 60 - antennal length : lateral head width using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	1.50	0
Aulacofoenus fallax	2.04	1
Aulacofoenus fletcheri	2.05	1
Aulacofoenus infumatum	1.93	1
Aulacofoenus kurmondi	2.00	1
Aulacofoenus marionae	1.68	0
Aulacofoenus perenjorii	2.04	1
Aulacofoenus thoracicus	1.86	1
Aulacofoenus whiani	1.83	1
Crassifoenus grossitarsis	1.70	0
Crassifoenus houstoni	1.66	0
Crassifoenus macronyx	1.83	1
Eufoenus antennalis	1.98	1
Eufoenus australis	2.08	1
Eufoenus crassitarsis	1.63	0
Eufoenus darwinii	2.38	2
Eufoenus extraneus	2.21	2
Eufoenus ferrugineus	2.16	2
Eufoenus floricolus	1.88	1
Eufoenus inaequalis	1.89	1
Eufoenus minimus	2.35	2
Eufoenus nitidiusculus	1.56	0
Eufoenus patellatus	2.04	1
Eufoenus pilosus	1.42	0
Eufoenus reticulatus	1.38	0
Eufoenus rieki	1.73	0
Eufoenus ritae	2.06	1
Eufoenus spinitarsis	1.75	0
*'Eufoenus' beverlyae**	1.56	0
*'Eufoenus' cardaleae**	1.90	1
*'Eufoenus' collessi**	2.00	1
*'Eufoenus' coorowensis**	2.04	1
*'Eufoenus' crosskeyi**	2.00	1
*'Eufoenus' douglasi**	1.93	1
*'Eufoenus' ericae**	1.81	1
*'Eufoenus' feckneri**	1.75	0
*'Eufoenus' iqbali**	2.33	2
*'Eufoenus' karimuiensis**	1.99	1
*'Eufoenus' kelleri**	2.41	2
*'Eufoenus' macdonaldi**	1.56	0
*'Eufoenus' malkini**	1.64	0
*'Eufoenus' masneri**	1.92	1
*'Eufoenus' morganensis**	1.77	1
*'Eufoenus' nalbarraensis**	1.88	1
*'Eufoenus' schmidti**	1.73	0
*'Eufoenus' taylori**	1.95	1
Hyptiogaster arenicola	2.12	1
Hyptiogaster humeralis	2.16	2
Hyptiogaster kalbarrii	3.67	4
Hyptiogaster pinjarregaensis	2.07	1
Hyptiogaster rufus	2.76	3
Pseudofoenus crassipes	1.58	0
Pseudofoenus unguiculatus	1.55	0
Mean	1.93	
S.D.	0.36	

Appendix A2.5. Segment coding for Character 62 - length hind tarsal segment 1 : length segment 2 - using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	1.91	0
Aulacofoenus deletangii	3.80	4
Aulacofoenus fallax	2.40	1
Aulacofoenus fletcheri	1.70	0
Aulacofoenus infumatus	2.80	2
Aulacofoenus kurmondi	2.40	1
Aulacofoenus marionae	2.60	2
Aulacofoenus perenjorii	2.20	1
Aulacofoenus thoracicus	1.40	0
Aulacofoenus whiani	1.90	0
Crassifoenus grossitarsis	1.40	0
Crassifoenus houstoni	1.33	0
Crassifoenus macronyx	1.40	0
Eufoenus antennalis	2.80	2
Eufoenus australis	2.78	2
Eufoenus crassitarsis	2.30	1
Eufoenus darwini	2.50	1
Eufoenus extraneus	3.10	3
Eufoenus ferrugineus	2.83	2
Eufoenus floricolus	2.73	2
Eufoenus inaequalis	2.95	2
Eufoenus minimus	2.60	2
Eufoenus patellatus	2.40	1
Eufoenus pilosus	2.77	2
Eufoenus rieki	1.80	0
Eufoenus ritae	2.60	2
Eufoenus spinitarsis	1.70	0
*'Eufoenus' beverlyae**	3.42	3
*'Eufoenus' cardaleae**	2.00	1
*'Eufoenus' collessi**	2.60	2
*'Eufoenus' coorowensis**	2.07	1
*'Eufoenus' crosskeyi**	1.77	0
*'Eufoenus' douglasi**	2.19	1
*'Eufoenus' ericae**	2.41	1
*'Eufoenus' feckneri**	2.89	2
*'Eufoenus' iqbali**	2.50	1
*'Eufoenus' karimuiensis**	2.67	2
*'Eufoenus' kelleri**	2.16	1
*'Eufoenus' macdonaldi**	2.80	2
*'Eufoenus' malkini**	1.94	1
*'Eufoenus' masneri**	2.90	2
*'Eufoenus' morganensis**	1.60	0
*'Eufoenus' nalbarraensis**	2.00	1
*'Eufoenus' schmidti**	3.00	2
*'Eufoenus' taylori**	1.76	0
Hyptiogaster arenicola	3.30	3
Hyptiogaster humeralis	3.50	3
Hyptiogaster kalbarrii	3.20	3
Hyptiogaster pinjarregaensis	2.40	1
Hyptiogaster rufus	3.00	2
Pseudofoenus crassipes	2.80	2
Pseudofoenus unguiculatus	2.06	1
Mean	2.43	
SD	0.59	

Appendix A2.6. Segment coding for character 63 - hind tarsal claw length : hind tarsal segment 5 length using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	0.61	0
Aulacofoenus deletangii	1.10	2
Aulacofoenus fallax	0.60	0
Aulacofoenus fletcheri	0.70	1
Aulacofoenus infumatus	0.50	0
Aulacofoenus kurmondi	1.10	2
Aulacofoenus marionae	0.70	1
Aulacofoenus perenjorii	0.60	0
Aulacofoenus thoracicus	0.50	0
Aulacofoenus whiani	0.90	1
Crassifoenus grossitarsis	1.00	1
Crassifoenus houstoni	1.15	2
Crassifoenus macronyx	0.87	1
Eufoenus antennalis	1.17	2
Eufoenus australis	0.50	0
Eufoenus crassitarsis	0.95	1
Eufoenus darwini	0.64	0
Eufoenus extraneus	0.65	0
Eufoenus ferrugineus	0.65	0
Eufoenus floricolus	0.67	0
Eufoenus inaequalis	0.91	1
Eufoenus minimus	0.65	0
Eufoenus patellatus	0.73	1
Eufoenus pilosus	0.64	0
Eufoenus rieki	0.90	1
Eufoenus ritae	0.60	0
Eufoenus spinitarsis	0.70	1
*'Eufoenus' beverlyae**	0.70	1
*'Eufoenus' cardaleae**	0.52	0
*'Eufoenus' collessi**	0.65	0
*'Eufoenus' coorowensis**	0.70	1
*'Eufoenus' crosskeyi**	0.68	0
*'Eufoenus' douglasi**	0.65	0
*'Eufoenus' ericae**	0.65	0
*'Eufoenus' feckneri**	1.00	1
*'Eufoenus' iqbali**	0.70	1
*'Eufoenus' karimuiensis**	?	?
*'Eufoenus' kelleri**	0.61	0
*'Eufoenus' macdonaldi**	0.63	0
*'Eufoenus' malkini**	0.70	1
*'Eufoenus' masneri**	0.68	0
*'Eufoenus' morganensis**	0.56	0
*'Eufoenus' nalbarraensis**	0.80	1
*'Eufoenus' schmidti**	0.50	0
*'Eufoenus' taylori**	0.62	0
Hyptiogaster arenicola	0.60	0
Hyptiogaster humeralis	1.00	1
Hyptiogaster kalbarrii	0.55	0
Hyptiogaster pinjarregaensis	0.70	1
Hyptiogaster rufus	0.60	0
Pseudofoenus crassipes	0.85	1
Pseudofoenus unguiculatus	0.93	1
Mean	0.73	
SD	0.18	

Appendix A2.7. Segment coding for character 64 - metasoma length : mesosoma length using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	2.10	1
Aulacofoenus deletangii	1.90	0
Aulacofoenus fallax	2.60	2
Aulacofoenus fletcheri	2.40	2
Aulacofoenus infumatus	1.90	0
Aulacofoenus kurmondi	2.50	2
Aulacofoenus marionae	2.50	2
Aulacofoenus perenjorii	2.60	2
Aulacofoenus thoracicus	2.30	1
Aulacofoenus whiani	2.70	3
Crassifoenus grossitarsis	1.80	0
Crassifoenus houstoni	2.00	0
Crassifoenus macronyx	2.10	1
Eufoenus antennalis	2.00	0
Eufoenus australis	2.23	1
Eufoenus crassitarsis	2.20	1
Eufoenus darwini	3.00	3
Eufoenus extraneus	2.00	0
Eufoenus ferrugineus	2.32	1
Eufoenus floricolus	2.05	0
Eufoenus inaequalis	2.60	2
Eufoenus minimus	2.00	0
Eufoenus patellatus	2.36	1
Eufoenus pilosus	2.50	2
Eufoenus rieki	2.59	2
Eufoenus ritae	1.92	0
Eufoenus spinitarsis	2.70	3
*'Eufoenus' beverlyae**	2.51	2
*'Eufoenus' cardaleae**	2.60	2
*'Eufoenus' collessi**	1.93	0
*'Eufoenus' coorowensis**	2.19	1
*'Eufoenus' crosskeyi**	2.25	1
*'Eufoenus' douglasi**	2.23	1
*'Eufoenus' ericae**	2.30	1
*'Eufoenus' feckneri**	1.94	0
*'Eufoenus' iqbali**	2.00	0
*'Eufoenus' karimuiensis**	2.42	2
*'Eufoenus' kelleri**	2.41	2
*'Eufoenus' macdonaldi**	2.00	0
*'Eufoenus' malkini**	2.34	1
*'Eufoenus' masneri**	2.52	2
*'Eufoenus' morganensis**	2.12	1
*'Eufoenus' nalbarraensis**	2.08	0
*'Eufoenus' schmidti**	2.01	0
*'Eufoenus' taylori**	2.43	2
Hyptiogaster arenicola	2.40	2
Hyptiogaster humeralis	2.10	1
Hyptiogaster kalbarrii	2.40	2
Hyptiogaster pinjarregaensis	2.30	1
Hyptiogaster rufus	2.50	2
Pseudofoenus crassipes	1.80	0
Pseudofoenus unguiculatus	1.80	0
Mean	2.26	
SD	0.28	

Appendix A2.8. Segment coding for character 65 - ovipositor length : metasoma length using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	0.79	3
Aulacofoenus deletangii	0.00	0
Aulacofoenus fallax	0.00	0
Aulacofoenus fletcheri	0.00	0
Aulacofoenus infumatum	0.00	0
Aulacofoenus kurmondi	0.00	0
Aulacofoenus marionae	0.00	0
Aulacofoenus perenjorii	0.00	0
Aulacofoenus thoracicus	0.00	0
Aulacofoenus whiani	0.00	0
Crassifoenus grossitarsis	0.00	0
Crassifoenus houstoni	0.00	0
Crassifoenus macronyx	0.00	0
Eufoenus antennalis	0.00	0
Eufoenus australis	0.00	0
Eufoenus crassitarsis	0.00	0
Eufoenus darwinii	0.00	0
Eufoenus extraneus	0.00	0
Eufoenus ferrugineus	0.00	0
Eufoenus floricolus	0.00	0
Eufoenus inaequalis	0.00	0
Eufoenus minimus	0.00	0
Eufoenus nitidiusculus	0.00	0
Eufoenus patellatus	0.00	0
Eufoenus pilosus	0.00	0
Eufoenus reticulatus	0.00	0
Eufoenus rieki	0.00	0
Eufoenus ritae	0.00	0
Eufoenus spinitarsis	0.00	0
*'Eufoenus' beverlyae**	0.00	0
*'Eufoenus' cardaleae**	0.00	0
*'Eufoenus' collessi**	0.00	0
*'Eufoenus' coorowensis**	0.00	0
*'Eufoenus' crosskeyi**	0.00	0
*'Eufoenus' douglasi**	0.00	0
*'Eufoenus' ericae**	0.00	0
*'Eufoenus' feckneri**	0.00	0
*'Eufoenus' iqbali**	0.00	0
*'Eufoenus' karimuiensis**	0.00	0
*'Eufoenus' kelleri**	0.00	0
*'Eufoenus' macdonaldi**	0.00	0
*'Eufoenus' malkini**	0.00	0
*'Eufoenus' masneri**	0.00	0
*'Eufoenus' morganensis**	0.00	0
*'Eufoenus' nalbarraensis**	0.00	0
*'Eufoenus' schmidti**	0.00	0
*'Eufoenus' taylori**	0.00	0
Hyptiogaster arenicola	0.58	2
Hyptiogaster humeralis	0.25	1
Hyptiogaster kalbarrii	0.84	3
Hyptiogaster pinjarregaensis	0.75	3
Hyptiogaster rufus	0.90	3
Pseudofoenus crassipes	0.00	0
Pseudofoenus unguiculatus	0.00	0
Mean	0.08	
S.D.	0.23	

Appendix A2.9. Segment coding for character 66 - clypeal width : height using technique of Chappill (1989). Note: Several new species (*) have been assigned to _Eufoenus_ on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	2.9	4
Aulacofoenus deletangii	2.1	2
Aulacofoenus fallax	2.0	2
Aulacofoenus fletcheri	1.7	1
Aulacofoenus infumatum	1.8	1
Aulacofoenus kurmondi	1.5	0
Aulacofoenus marionae	1.5	0
Aulacofoenus perenjorii	1.8	1
Aulacofoenus thoracicus	2.5	3
Aulacofoenus whiani	1.6	1
Crassifoenus grossitarsis	1.6	1
Crassifoenus houstoni	1.5	0
Crassifoenus macronyx	1.5	0
Eufoenus antennalis	1.4	0
Eufoenus australis	1.7	1
Eufoenus crassitarsis	1.4	0
Eufoenus darwinii	2.2	2
Eufoenus extraneus	1.4	0
Eufoenus ferrugineus	1.6	1
Eufoenus floricolus	1.6	1
Eufoenus inaequalis	1.5	0
Eufoenus minimus	2.1	2
Eufoenus nitidiusculus	2.4	3
Eufoenus patellatus	1.8	1
Eufoenus pilosus	1.7	1
Eufoenus reticulatus	1.9	1
Eufoenus rieki	1.5	0
Eufoenus ritae	1.3	0
Eufoenus spinitarsis	2.3	2
'Eufoenus' beverlyae*	1.7	1
'Eufoenus' cardaleae*	2.0	2
'Eufoenus' collessi*	1.9	1
'Eufoenus' coorowensis*	1.2	0
'Eufoenus' crosskeyi*	2.1	2
'Eufoenus' douglasi*	1.7	1
'Eufoenus' ericae*	1.4	0
'Eufoenus' feckneri*	1.5	0
'Eufoenus' iqbali*	1.9	1
'Eufoenus' karimuiensis*	1.6	1
'Eufoenus' kelleri*	2.4	3
'Eufoenus' macdonaldi*	1.6	1
'Eufoenus' malkini*	1.2	0
'Eufoenus' masneri*	1.5	0
'Eufoenus' morganensis*	1.7	1
'Eufoenus' nalbarraensis*	2.0	2
'Eufoenus' schmidti*	1.7	1
'Eufoenus' taylori*	1.7	1
Hyptiogaster arenicola	1.5	0
Hyptiogaster humeralis	1.4	0
Hyptiogaster kalbarrii	1.7	1
Hyptiogaster pinjarregaensis	1.9	1
Hyptiogaster rufus	1.8	1
Pseudofoenus crassipes	2.2	2
Pseudofoenus unguiculatus	2.1	2
Mean	1.8	
S.D.	0.3	

Appendix A2.10. Segment coding for character 67 - length of fore wing vein 1-M : length 1-Rs using technique of Chappill (1989). Note: Several new species (*) have been assigned to *Eufoenus* on the basis of the generic descriptions and key to genera in Crosskey (1962).

Species	Mean	1 x SD
Gasteruption sp. 1	0.00	0
Aulacofoenus deletangii	1.08	1
Aulacofoenus fallax	1.92	2
Aulacofoenus fletcheri	1.92	2
Aulacofoenus infumatum	1.25	1
Aulacofoenus kurmondi	1.38	1
Aulacofoenus marionae	1.57	2
Aulacofoenus perenjorii	1.17	1
Aulacofoenus thoracicus	1.57	2
Aulacofoenus whiani	1.82	2
Crassifoenus grossitarsis	1.89	2
Crassifoenus houstoni	2.26	3
Crassifoenus macronyx	2.00	2
Eufoenus antennalis	2.00	2
Eufoenus australis	1.94	2
Eufoenus crassitarsis	1.98	2
Eufoenus darwinii	0.90	1
Eufoenus extraneus	1.93	2
Eufoenus ferrugineus	1.50	2
Eufoenus floricolus	1.29	1
Eufoenus inaequalis	1.83	2
Eufoenus minimus	1.04	1
Eufoenus nitidiusculus	1.47	2
Eufoenus patellatus	1.91	2
Eufoenus pilosus	1.90	2
Eufoenus reticulatus	0.87	1
Eufoenus rieki	1.36	1
Eufoenus ritae	1.22	1
Eufoenus spinitarsis	1.00	1
*'Eufoenus' beverlyae**	1.20	1
*'Eufoenus' cardaleae**	1.05	1
*'Eufoenus' collessi**	0.79	1
*'Eufoenus' coorowensis**	1.88	2
*'Eufoenus' crosskeyi**	1.00	1
*'Eufoenus' douglasi**	1.19	1
*'Eufoenus' ericae**	1.32	1
*'Eufoenus' feckneri**	1.38	1
*'Eufoenus' iqbali**	1.06	1
*'Eufoenus' karimuiensis**	1.08	1
*'Eufoenus' kelleri**	0.93	1
*'Eufoenus' macdonaldi**	1.51	2
*'Eufoenus' malkini**	1.74	2
*'Eufoenus' masneri**	1.93	2
*'Eufoenus' morganensis**	1.83	2
*'Eufoenus' nalbarraensis**	0.82	1
*'Eufoenus' schmidti**	1.34	1
*'Eufoenus' taylori**	1.00	1
Hyptiogaster arenicola	3.10	4
Hyptiogaster humeralis	2.55	3
Hyptiogaster kalbarrii	2.97	4
Hyptiogaster pinjarregaensis	3.40	4
Hyptiogaster rufus	2.60	3
Pseudofoenus crassipes	0.00	0
Pseudofoenus unguiculatus	0.00	0
Mean	1.51	
S.D.	0.69	

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