THE SYSTEMATICS OF THE GENERA OF CARDIOCHILINAG (HYMENOPTERA: BRACONIDAE) WITH A REVISION OF AUSTRALASIAN SPECIES

CAMPUS

-1 APR 1996



PAUL C. DANGERFIELD B.Sc. (Adelaide)

Department of Crop Protection, Waite Campus, The University of Adelaide.

A thesis submitted for the Degree of Doctor of Philosophy in the Faculty of

Agricultural and Natural Resource Sciences at The

University of Adelaide.

August 1995

To my children, Anne-Marie and Michael

'that they may one day understand'

TABLE OF CONTENTS

Summary v
Declaration ix
Acknowledgments
Chapter 1: Introduction
1.1. General introduction and justification of project
1.2. Aims of project
Chapter 2: Review of Literature
2.1. Systematics of the Cardiochilinae
2.1.1. Subfamily status
2.1.2. Subfamily relationships
2.1.3. Taxonomy of genera and species 10
2.2. Distribution
2.3. Biology 14
Chapter 3: Materials and Methods
3.1. General methods
3.2. Collecting techniques
3.3. Scanning electron microscopy
3.4. Terminology
3.5. Institutional abbreviations
3.6. Phylogenetic analyses
3.6.1. Computers and programs
3.6.2. Morphometric data 23
3.6.3. Format for outgroup analysis
3.6.4. Brief discussion of theoretical phylogenetic methods
3.6.5. Methods for assessment of phylogenetic analyses
3.6.6. Discussion of PAUP features
3.6.7. Testing for significance of phylogenetic results

Chapter 4: Morphology of the Cardiochilinae
4.1. Introduction
4.2. Pupal cases
4.3. Larval morphology
4.4. General adult morphology
4.4.1. Head
4.4.2. Mesosoma
4.4.3. Wings
4.4.4. Legs
4.4.5. Metasoma
4.4.6. Female genitalia 40
4.4.7. Male genitalia 40
Figures 4.1 to 4.21
Chapter 5: Cladistics of Genera
5.1. Introduction
5.2. Taxa used in analyses 44
5.2.1. Selection of ingroup and outgroup taxa
5.2.2. Discussion of higher level hymenopteran taxonomy for
outgroup selection 47
5.3. Selection of characters
5.4. Character discussion: polarity and order assignment
5.4.1. Qualitative characters
5.4.2. Morphometric characters
5.5. PAUP analyses
5.5.1. Introduction
5.5.2. Comparison of different outgroups
5.5.3. Comparison of morphometric and qualitative data
5.6. Results of PAUP analyses and formation of a generic classification . 68
5.7. Testing for significance of results
5.8. Discussion of classification75
Figures 5.1 to 5.4

Chapter 6: Revision of Genera
6.1. Introduction
6.2. Key to world genera of the subfamily Cardiochilinae
6.3. Treatment of genera
6.3.1. Asiacardiochiles Telenga, stat. rev
6.3.2. Austerocardiochiles, gen. nov
6.3.3. Bohayella Belokobylskij 85
6.3.4. Brevicardiochiles, gen. nov
6.3.5. Cardiochiles Nees, sensu stricto
6.3.6. Circocardiochiles, gen. nov
6.3.7. Hartemita Cameron
6.3.8. Heteropteron Brullé
6.3.9. Hymenicis, gen. nov
6.3.10. Latitergum, gen. nov
6.3.11. Leptocardiochiles, gen. nov 100
6.3.12. Neocardiochiles Szépligeti 102
6.3.13. Polycardiochiles, gen. nov 103
6.3.14. Pseudcardiochilus Hedwig 106
6.3.15. Psilommiscus Enderlein, stat. rev 108
6.3.16. Retusigaster, gen. nov 109
6.3.17. Toxoneuron Say, stat. rev
6.3.18. Wesmaelella Spinola 114
6.4. Species incertae sedis 115
Figures 6.1 to 6.110 121
Chapter 7: Revision of Australasian Cardiochiline Species 122
7.1. Introduction to Australasian cardiochiline fauna 123
7.2. Key to Australasian species of Cardiochilinae 124
7.3. Treatment of Australasian Cardiochilinae 128
7.3.1. Austerocardiochiles callemondah 128
7.3.2. Aus. deetoo
7.3.3. Aus. exleyae
7.3.4. Aus. morulus
7.3.5. Aus. pollinator 137
7.3.6. Bohayella adina 140
7.3.7. Boh. toxopeusi
7.3.8. Cardiochiles evelinae144
7.3.9. Car. goosei 145
7.3.10. Car. iqbali 147

7.3.11. Car rasi 148
7.3.12. Car. rufator
7.3.13. Car. saeedi 152
7.3.14. Car. scotti
7.3.15. Car. uniformis 154
7.3.16. Car. verticalis 156
7.3.17. Circocardiochiles occidentalis160
7.3.18. Hymenicis bubbur
7.3.19. Hym. nockatungensis
7.3.20. Hym. noongarensis
7.3.21. Latitergum areyongensis
7.3.22. Lat. eremophilasturtiae172
7.3.23. Lat. turneri
7.3.24. Polycardiochiles dissimulator 176
7.3.25. Pol. fuscipennis 177
7.3.26. Pol. gwenae
7.3.27. Pol. philippensis
7.3.28. Pseudcardiochilus naumanni 185
7.4. Distribution patterns of Australasian fauna 188
7.5. Biology of Australasian fauna 189
Figures 7.1 to 7.49
Chapter 8: General Discussion 191
Appendices: A1 to A5 198
A1. 10 x10 matrix 199
A2. Morphometric data: Graphs showing discrete state divisions 200-213
A3. Morphometric data: Table of ordered means 214-217
A4. Data matrix of character states for the Cardiochilinae
A5. Dangerfield and Austin (1990) 219
References

SUMMARY

Members of the wasp subfamily Cardiochilinae (Hymenoptera: Braconidae) are endoparasitic in lepidopterous larvae and have proven and potential importance as biocontrol agents of agricultural pests. This project was initiated firstly to examine the taxonomy of species in the Australasian region, which was previously poorly studied, and secondly, to develop a phylogenetic framework for world genera based on cladistic methodology.

A brief literature review provides a background to the taxonomic, phylogenetic and biological knowledge of the subfamily and outlines the need for a revision based on the morphological diversity of the speciose genus *Cardiochiles* Nees ab Esenbeck, which contained 95% (170 described species) of the world fauna. A detailed treatment of the morphology of the Cardiochilinae provides a framework for the phylogenetic and taxonomic analyses conducted, and introduces new characters and terminology used in the revision.

The subfamily forms a monophyletic group based on the following combination of apomorphies: second submarginal cell of the fore wing broad, large and four-sided; first metasomal tergite with 'Y-shaped' groove; spiracle position on the first laterotergite of the metasoma; laterotergites only partially defined; axilla reduced to a vertical area of carinate lobe; and the form of larval mouthparts.

Prior to the cladistic analyses of genera and species, the higher phylogeny of the Hymenoptera is reviewed, specifically to select more distant outgroups to the sister group of the cardiochilines, the Microgastrinae. This section also reviews the choice of characters, the assignment of character states, and an assessment of polarity and order for the characters used. The program PAUP (Version 3.1.1) is employed to determine the most parsimonious solution to the data set, which was assembled using MacClade (Version 3.02). An assessment of the different parameters of the software is also presented. Statistical testing of the resultant phylogenies utilised both the PTP test to

v

analyse cladistic information and the T-PTP test to analyse cladistic structure of the trees obtained.

The types of Cardiochilinae from all previously recognised genera, exemplar species, and the new taxa identified in this study were used in the cladistic analyses. These analyses were undertaken using *Prasmadon* Nixon (Microgastrinae), *Epsilogaster* Whitfield (Mendesellinae) and a hypothetical ancestor as outgroups. In addition, the hypothetical ancestor was used with polarities and orders predetermined from a multiple outgroup comparison of characters. Results using these three outgroups yielded similar monophyletic groupings of species, however, the sister group relationships of these clades were not always well-defined, with basal clades changing position when different outgroups were employed. Tests for significance confirmed that the resultant trees contained significant cladistic information and structure, but the sister group relationships of some genera could not be elucidated due to the variation in the structure of the trees when different outgroups were used.

A generic classification from the Cardiochilinae is proposed based on the recognisable monophyletic groups from the analyses, representing eighteen genera. Eight of these genera are described as new, seven are redescribed, and three raised to generic level having previously been treated as junior synonyms of *Cardiochiles sensu lato*. The genera proposed are *Asiacardiochiles* Telenga, stat. rev. (1 species - Russian), *Austerocardiochiles* gen. nov. (6 species - Oriental, Australasian and African), *Bohayella* Belokobylskij (3 species - Oriental and Australasian), *Brevicardiochiles* gen. nov. (3 species - African and Philippine), *Cardiochiles* Nees *sensu stricto* (22 species - cosmopolitan), *Circocardiochiles* gen. nov. (1 species - Oriental and Australian), *Hartemita* Cameron (9 species - Oriental), *Heteropteron* Brullé (1 species - Neotropical), *Hymenicis* gen. nov. (3 species - Australian), *Latitergum* gen. nov. (3 species - Australian), *Leptocardiochiles* gen. nov. (1 species - Nearctic), *Neocardiochiles* Szépligeti (1 species - Neotropical), *Polycardiochiles* gen. nov. (10 species - cosmopolitan), *Pseudcardiochilus* Hedwig (3 species - Australian), *Psilommiscus* Enderlein, stat. rev. (1 species - Oriental), *Retusigaster* gen. nov. (6

vi

species - Nearctic and northern Neotropical), *Toxoneuron* Say, stat. rev. (12 species - Nearctic and northern Neotropical) and *Wesmaelella* Spinola (2 species - Neotropical). Sixty-six previously described species and the 21 species newly described here are placed within the revised generic classification, an illustrated key to genera is presented, and the relationships and distributions of genera are discussed. A survey of available host data revealed information for only five genera: Uraniidae have been recorded as hosts for *Bohayella*, Pyralidae and Noctuidae for *Cardiochiles*, Gelechiidae and Cosmopterigidae for *Leptocardiochiles*, Gelechiidae, Noctuidae and Tortricidae for *Polycardiochiles*, and Noctuidae for *Toxoneuron*. One hundred and four species are listed as species *incertae sedis*, because insufficient information was available due to their descriptions being too superficial to place them into the generic classification, and their holotypes were not available prior to the completion of this study.

Following the reclassification of genera, the subfamily is revised for the Australasian region, here defined as Australia, New Guinea, the Bismark Archipelago, Fiji and New Zealand, although no species are known from the latter two areas. Twenty-six species from eight genera are recorded from Australasia. Twenty-one species are described as new and five are redescribed: Austerocardiochiles callemondah sp. nov., Aus. deetoo sp. nov., Aus. exleyae sp. nov., Aus. morulus sp. nov., Aus. pollinator sp. nov., Bohayella toxopeusi sp. nov., Cardiochiles evelinae sp. nov., Car. goosei sp. nov., Car. iqbali sp. nov., Car. rasi sp. nov., Car. rufator Roman, Car. saeedi sp. nov., Car. scotti sp. nov., Car. uniformis Turner, Car. verticalis Turner, Circocardiochiles occidentalis sp. nov., Hymenicis bubbur sp. nov., Hym. nockatungensis sp. nov., Hym. noongarensis sp. nov., Latitergum areyongensis sp. nov., Lat. eremophilasturtiae sp. nov., Lat. turneri sp. nov., Polycardiochiles dissimulator (Turner), Pol. fuscipennis (Szépligeti), Pol. gwenae sp. nov., and Pseudcardiochilus naumanni sp. nov. One species from the Oriental region, Pol. philippensis (Ashmead), is redescribed due to its strong similarity to, and parapatric distribution with, Pol. fuscipennis. Boh. adina (Wilkinson), also from the Oriental region, is described and transferred from Cardiochiles sensu lato. Previously recognised species Car. assimilator Turner, Car. fasciatus Szépligeti, Car. piliventris Cameron, Car. similis Brues and Car. trichiosomus Cameron are synonymised with Pol. fuscipennis. An illustrated key to Australasian species based on females is presented, as are notes on their biology (where known), relationships and distribution.

Finally, the results of this study are discussed in the broad context of their influence on future research. They will hopefully serve as a base for further taxonomic revisions of specific zoogeographic regions. Clearly, many species are yet to be described given that the revision here of the Australasian fauna has resulted in a three-fold increase in known species, and other regions, particularly the Neotropical, Oriental and Ethiopian, are poorly studied. It is hoped that the resultant phylogenetic hypotheses will serve as a framework for future evolutionary studies on the host relationships and ecology of the subfamily, and also aid in ongoing phylogenetic work aimed at resolving the relationships among braconid subfamilies.

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 acknowledgment is made of any reference to work therein.

One published paper is included as part of this thesis written by P. C. Dangerfield and A. D. Austin. This work was proposed by A. D. Austin, but the research conducted towards it and writing of the manuscript was solely my responsibility.

August 1995

P. C. Dangerfield.

Acknowledgments

Six years can see a lot of changes in a person's life and the completion of this thesis sees me a completely different person from at the start. It has given me much, allowed me to challenge and defeat many of my inhibitions, and realise many future goals.

I thank my principal supervisor Andy Austin for being a 3D supervisor. He gave me the direction to continue this project to it's culmination, the discipline to knuckle down when it counted, and discussions that helped to stimulate many of the ideas presented. Thank you Andy for realising my potential and leading me into a stimulating career.

I wish to thank Jim Whitfield for discussion of characters and generic boundaries and for encouragement with my work; Stuart Maclure for his assistance with scanning electron microscopy and an undying wit; Bob Wharton for discussion, advice and collection of fresh material; Angelo Karakousos for his willingness to help by making computer time available to me; Ting Kui Qin for preliminary advice on significance testing of phylogenetic results; and John Truemann who helped me get the tests right. I would also like to thank the Curators or Collection Managers of the institutions from which material was obtained: David Wahl (AEIC); Ian Naumann (ANIC); Don Azuma (ANSP); Tom Huddleston (BMNH); Gordon Nishida (BPBM); W. Pulawski (CASC); John Huber (CNCI); Jeno Papp (HNHM); Michael Kelley (MCZC); Alice Wells (MNTD); Ken Walker (MVMA); Fredrik Rondquist (NHRS); Murray Fletcher (NSWA); John Donaldson (QDPI); C. van Achterberg (RMNH); Bob Wharton (TAMU); Margaret Schneider (UQBA); Gary Hevel (USNM); Terry Houston (WAMP); Kevin Richards (WADA); Sergey Belokobylskij (ZMAS); and Dr F. Kock (ZMHU).

Lastly I would like to thank my family and friends, particularly my parents for believing in me and for all their love and support through the hard times, and my kids for all their love and helping to keep my feet firmly on the ground. I would especially like to

х

thank Gwen Mayo for her love and understanding, as well as her comments and proof reading of this thesis. She was always there when I needed her with a shoulder to lean on and an ear to chew.

CHAPTER 1

Introduction

1.1 General introduction and justification of project

1.2 Aims of project

1.1. General introduction and justification of project

Parasitoid wasps lay their eggs in or on the body of an arthropod host following which the larvae consume and kill the host. This mode of life has undoubtedly led to the parasitic Hymenoptera being one of the most speciose groups of invertebrates (LaSalle and Gauld 1993). By consuming members of host populations they play a role in regulating numbers and, as such, have become important in agriculture as biological control agents of pest species. Since the first use of parasitic wasps and insect predators as biological control agents, many different species have been imported into different regions to control pest populations. Importation of natural enemies constitutes what is usually referred to as 'classical biological control'. However, in recent decades the augmentation of beneficial species, where they are naturally found, has received substantial study. Further, detailed work on parasitoid guilds of pest species has shown that individual pests may support 20 to 30 different parasitoid species, representing primary and hyperparasitoids, ecto and endoparasitoid species, idiobiont and koinobionts, and species that oviposit into egg, larval, pupal and rarely the adult stages of the host (Godfray 1993). Although these lifestyles are not mutually exclusive, they do show the biological diversity of species within a guild.

MARTE CALIFUS LIERIAN

CHAPTE

The first and most important step in any biological or ecological study on parasitoids is the accurate identification of the species involved. It is the most important because all subsequent work relies on the ability to recognise the species concerned. The consequences of poor taxonomy through misidentification are well documented and they are often very costly (Noyes and Hayat 1994). For example, following an unsuccessful attempt to control the introduced leaf-blister sawfly, *Phylacteophaga froggatti* Riek, in New Zealand, it was found that two species of parasitoid wasp, *Bracon phylacteophagus* Austin and Faulds and *B. confusus* Austin and Faulds, had been introduced rather than one (Austin and Faulds 1989; Faulds 1990). Not until their accurate identification, was control of the pest successful. A knowledge of the systematics (phylogenetic position) of parasitoid species and genera is also important, as this information provides the means to predict aspects about the biology and host relationships of a taxon.

The most important hymenopteran families used in biocontrol programs are the Braconidae, Encyrtidae and Aphelinidae. The Aphelinidae and Encyrtidae are either ecto or endoparasitoids mostly on members of the Sternorrhyca (Hemiptera), most notably the scale insects, and may have complex biologies (Naumann 1991). The speciose Encyrtidae are endoparasitic mostly on the Hemiptera but also exploit a wide variety of other insect larvae (Noyes and Hayat 1994). The Braconidae is also a speciose group of primarily endoparasitic koinobionts on a variety of insect larvae. Achterberg (1984) argued that ancestral braconids were probably ectoparasitoids of wood-boring coleopteran larvae and that endoparasitism may have arisen many times in the group.

There are about 29 braconid subfamilies but this number is presently under review due to ongoing phylogenetic work on the group (Achterberg 1990; Whitfield 1992; Whitfield and Mason 1994). The Cardiochilinae is a small but worldwide subfamily of braconid wasps comprising about 170 described species. The known hosts of these parasitoids are lepidopteran larvae of the families Cosmopterigidae, Gelechiidae, Pyralidae, Noctuidae and Uraniidae, some of which are major pests of agricultural crops.

The classification for the Cardiochilinae, previous to this study, had not been based on phylogenetic relationships and the majority of species were placed in a single genus, *Cardiochiles* Nees ab Esenbeck. This has been primarily due to the synonymy of several genera with *Cardiochiles* and, subsequently, most other species have been described in that genus. These synonymies were undertaken without a sound knowledge of the world fauna and were not cladistically based. Because of this the genus is referred to in the loose sense, i.e. *Cardiochiles sensu lato*.

The last revision of the Cardiochilinae for the Australasian region by Turner (1918) listed eight described species, and many still remain to be described, with an estimated 25 species for the region based on specimens examined in museum material. Description of new species will undoubtedly reflect a broader range of morphologies for the subfamily and further place in doubt the validity of the status of *Cardiochiles s. l.*

Much work is currently being undertaken on a sister group subfamily, the Microgastrinae, because it has yielded many species useful for the biological control of lepidopteran pests (Mason 1981; Austin and Dangerfield 1992, 1993). Understanding the range of morphologies and character states present in the sister group is important in being able to evaluate ingroup relationships.

1.2. Aims of project

The Cardiochilinae were chosen for detailed study because they are poorly known on a worldwide basis, they hold a critical position within the family as the sister group to the Microgastrinae, they harbour potential biological control agents themselves, and the Australasian fauna was virtually unstudied.

This project aimed to undertake a cladistic analysis of phylogenetic relationships for the Australasian fauna and critical extra-limital taxa, using a character matrix of data polarised against multiple outgroups. This analysis was used to test the phylogenetic status of *Cardiochiles s. l.* and determine the genera for the subfamily based on monophyletic groups from cladistic-based analyses.

To provide the most rigorous data set for the analysis, detailed studies focussed on documenting the host relationships of species, and resolving potentially new morphological characters. The constructed data set was analysed using a computer-based algorithm after detailed investigation of the different functions of that program, in order to determine the most parsimonious result for the data. Further, the resultant trees were tested using the most recently available statistical analyses to confirm the cladistic information and structure for the phylogeny proposed.

This study then aimed to revise the taxonomy of Australasian Cardiochilinae and to assess the relationships among these species and genera on a worldwide basis using cladistic-based phylogenetic techniques. Detailed morphological comparisons using light microscopy and Scanning Electron Microscopy (SEM) were undertaken to evaluate species' boundaries, the level of intraspecific variability, to describe new taxa, and to compile an illustrated key to species for this region. Where possible, biological

information including host data, and geographic information was also incorporated into these comparisons.

The ultimate aim of this study was to produce a natural (evolutionary-based) higher classification for the world Cardiochilinae and a knowledge of the Australasian species that could be used as a solid framework for future studies on the biology and ecology of the group, particularly for taxa with potential as biological control agents. Whether or not this has been achieved will depend on future research using the results of this study and testing the ideas and hypotheses that are presented in the following chapters.

Note: Because of the large number of figures in this work they have been grouped at the end of each Chapter.

CHAPTER 2

Review of Literature

- 2.1. Systematics of the Cardiochilinae
 - 2.1.1. Subfamily status
 - 2.1.2. Subfamily relationships
 - 2.1.3. Taxonomy of genera and species
- 2.2. Distribution
- 2.3. Biology

CHAPTER 2

2.1. Systematics of the Cardiochilinae

2.1.1. Subfamily status

The genus *Cardiochiles* was first described by Nees ab Esenbeck in 1818 but no species were included nor was the genus placed in a subfamily. *Ichneumon saltator* was subsequently designated as the type of the genus by Nees ab Esenbeck in 1834. Later in 1900, the subfamily Cardiochilinae was erected by Ashmead (1900) and it also included the previously designated Toxoneurinae Cresson (1887). The latter subfamily was synonymised with the Cardiochilinae at the same time that *Toxoneuron* Say (1836), the only included genus, was synonymised with *Cardiochiles*. Although Toxoneurinae is the older of the two taxon names, Cardiochilinae, by all subsequent authors, that informally validates the name. Strictly a submission should be made to ICZN to suppress the name Toxoneurinae, however the ICZN rules were not put in place until 1965 and the name Cardiochilinae was already in accepted use at that time. Toxoneuridae was described by Marshall (1901) to include the genus *Toxoneuron* Say (1836), however, this assignment post-dated the previous synonymy of the genus, and the family name was never adopted by later authors.

Szépligeti (1896, 1900) described species of *Cardiochiles* but placed the genus in the Microgasteroinae, and then subsequently referred them to the Cardiochilinae (Szépligeti 1902, 1904, 1908). Prior to this, numerous revisions of the subfamily classification of the Braconidae placed *Cardiochiles* in various groupings. The Cardiochilinae was given tribal status in the subfamily 'Polymorphinae' by de Gaulle (1907), now given major group status 'Polymorphes' by Shenefelt (1973). It was then placed in the Vipionidae by Viereck (1918), now a junior synonym of the Braconinae (Shenefelt 1973). Handlirsch (1925) treated the genus as a member of the Helconinae as did Watanabe (1934, 1937), Ceballos (1943) and Docavo Alberti (1960). Telenga (1955) described species of *Cardiochiles* and accommodated the genus in the tribe 'Microgasterini' and then treated the latter as a subfamily, Microgasterinae (Telenga 1955). Nixon (1965) maintained Telenga's classification of three tribes within the Microgasterinae, the Microgastrini, Cardiochilini and Acoeliini. The Cardiochilini sensu stricto Nixon (1965) was diagnosed by the following characters: fore wing with three cubital cells, the 2nd always much longer than wide; 2nd abscissa of the radius much longer than the first; 3rd abscissa of the radius at its base characteristically concave towards the wing-edge; antenna with at least 26 segments; notauli always welldeveloped; spiracles of the first metasomal tergite situated on the laterotergite; and inner spur of the hind tibia always longer than the length of the hind basitarsus. Mason (1981) raised these microgasterine tribes to subfamily rank, but maintained that they were closely related based on the spiracle of the first metasomal segment being situated on the laterotergite of T1. He also realised that this character was shared with the majority of symphytan families and concluded it to be plesiomorphic. Mason (1981) nominated several synapomorphies for the Cardiochilinae: dorsal pronotum flat or bulging without obvious modifications, except for a small transverse anterior groove (also seen in some sawflies); distal abscissa of the radius of the fore wing basally convex anteriorly; and fully grown larvae with porrect sclerotised 1-segmented palps. Mason also presented information for six larval characters in his reclassification of microgastrine genera. Those which refer specifically to cardiochilines are: larval antennae present; mandible with a long blade carrying a row of about 25 long teeth along the whole length; and palpi sclerotised and about as long as wide (in some Cardiochilinae). However, the range of species examined was not given and the extent to which these characters are representative for the subfamily as a whole is not known.

Walker *et al.* (1990) reassessed Mason's data and used the Cardiochilinae and Khoikhoiinae (described by Mason 1983) as an outgroup to the Miracinae and Microgastrinae. However, their analysis attempted to better resolve the generic relationships within the Microgastrinae, not those of related subfamilies.

Achterberg (1984) reinforced the subfamily status of the Cardiochilinae based on several additional characters: cephalic structures of the final larval instar including the mandibles, lacking the apomorphous condition of a differentiated base; adults having

SR1 of the fore wing strongly curved towards 1-R1; and the second submarginal cell of the fore wing being large.

Quicke and Achterberg (1990) used nine larval characters in their phylogenetic analysis of the braconid subfamilies, but like Mason (1981), neglected to refer to which cardiochiline species they had used to score characters. None of these characters were listed as polymorphic for the Cardiochilinae and so were assumed to be constant: *viz*. larval antennae papilliform; mandibles smooth and simple; epistome incomplete or absent; first thoracic spiracle in anterior part of second segment; post-ventral tracheal commisure absent; ventral abdominal tracheal commisures absent; and first instar caudal vesicle present. One character, the length of the larval mandible blade, had been assigned a state not described in the text. As for Mason (1981), these data must be treated with caution as they were undoubtedly scored for few species, given the scope of Quicke and Achterberg's study which treats 96 characters for all braconid subfamilies.

More recently, Achterberg (1993) has provided a key to braconid subfamilies with five characters to define the Cardiochilinae: vein 3-SR of fore wing being sclerotised and much longer than vein r; antenna with 20-51 segments; maxillary palp with 6 segments; vein 2r-m of hind wing absent; and scutellum with a more or less developed medio-posterior depression.

2.1.2. Subfamily relationships

The Cardiochilinae has been considered to be the sister group of the Khoikhoiinae + Microgastrinae + Miracinae (Achterberg 1984; Austin 1990; Walker *et al.* 1990), and together these subfamilies represent a monophyletic lineage. Achterberg (1988) presented a provisional cladistic analysis of braconid subfamilies that placed Microgastrinae + Khoikhoiinae as the sister group to the Cardiochilinae, based on the following synapomorphies: hypostomal carina absent; 1st metasomal spiracle in epipleural area; and fore spur 0.7-1.0 times fore basitarsus. In this analysis the Miracinae are placed some distance from the Khoikhoiinae + Microgastrinae, based on larval characters, venom apparatus and biology of the latter subfamily. Whitfield and Mason (1994) described a new

subfamily of Braconidae, the Mendesellinae, and included it in the 'microgastroid assemblage' (sensu Tobias 1967; Quicke and Achterberg 1990; Wharton et al. 1992), a group which includes the Adeliinae, Cardiochilinae, Cheloninae, Dirrhopinae, Ecnomiinae, Ichneutinae, Khoikhoiinae, Mendesellinae, Microgastrinae, Miracinae and Neoneurinae. Their provisional analysis placed the Cardiochilinae as the sister group to the Khoikhoiinae + Miracinae + Microgastrinae, with the Mendesellinae being the next removed (Whitfield and Mason 1994). Although some of the more basal family relationships were not resolved in their analysis, the authors suggest that sister group relationships within the 'microgastroid' assemblage are 'significant'. With this analysis and the analyses of other authors previously mentioned, the representative taxa evaluated to score characters were not given, casting doubt over the extent of knowledge of the subfamilies analysed. Also, suggesting that certain clades are significant can only be done with confidence from some kind of statistical testing and these were not conducted for the analyses undertaken by Whitfield and Mason (1994). However, the relationships given represent the most robust to date and were therefore utilised as a starting point for the relationships analysed in this study.

2.1.3. Taxonomy of genera and species

Prior to the present study the Cardiochilinae contained seven extant genera worldwide, *viz. Bohayella* Belokobylskij, *Hartemita* Cameron, *Heteropteron* Brullé, *Neocardiochiles* Szépligeti, *Pseudcardiochilus* Hedwig, *Wesmaelella* Spinola, and *Cardiochiles* Nees ab Esenbeck, however, the later genus contained the majority (95%) of the 170 described species. In this Section these genera are placed in an historical perspective, and as well comments are provided on the major revisions for zoogeographic regions and the defining synapomorphies for each genus.

Szépligeti (1902) revised the tropical Cardiochilinae and included four genera; *Cardiochiles* (four new species), *Toxoneuron* (one new species), *Oligoneurus* (one new species), and *Psilophthalmus* (one new species), with the latter two genera described as new. However, *Oligoneurus* is now considered to be a member of the Ichneutinae (see

Austin and Wharton 1992 for discussion). Enderlein (1905) revised the Indo-Australian and African Cardiochiles and included ten species, while Turner (1918) described five species of Cardiochiles from the Australasian region. Watanabe (1937) keyed the six known Japanese species, and Mao (1949) revised the Cardiochiles of north America and treated 30 species. One of these, Cardiochiles minutus (Cresson) (1873), transferred from Toxoneuron, predates Asiacardiochiles minutus Telenga (1955). Sharkey and Mason (1986) synonymised Asiacardiochiles with Cardiochiles but they did not rectify the nomenclatural problem created from the homonyms, *Car. minutus* (Cresson 1873) and Car. minutus (Telenga 1955). The Cardiochilinae of Russia have been reviewed by several authors (Abdinbekova 1975; Tobias and Alexeev 1977; Tobias et al. 1986; Belokobylskij 1987). Tobias et al.(1986) provided a key to the Russian fauna and recognised 28 species of *Cardiochiles* as well as *Asiacardiochiles minutus* Telenga. Bohayella Belokobylskij (1987) was described as a monotypic genus from Russia. Huddleston and Walker's (1988) revision of *Cardiochiles* spp. for the Sahel of Africa listed 34 species for the Afrotropical region. The Oriental genus Hartemita was brought out of synonymy from *Cardiochiles* by Dangerfield and Austin (1990) and nine species were recognised (Appendix A5).

Cardiochiles, based on the type *Ichneumon saltator* Fabricius, has had eight genera synonymised with it between 1899 and 1986, as outlined in Table 2.1.

Genus	Synonymy
Asiacardiochiles Telenga 1955	Sharkey and Mason 1986
Ditherus Cameron 1902	Morley 1909
Ernestiella Cameron 1905	Turner 1918
Psilommiscus Enderlein 1912	Muesebeck 1949
Schönlandella Cameron 1904	Szépligeti 1911
Tenthredoides Cresson 1865	Cresson 1873
Toxoneuron Say 1836	Ashmead (1899)1900

Table 2.1. Genera treated as junior synonyms of Cardiochiles s.l.

The genus *Cardiochiles s. l.* is morphologically diverse, and because of the large number of species relative to other genera within the Cardiochilinae, the diagnostic characters for the genus have often been synonymous with those for the subfamily. These include the fore wing vein 4-SRb being angled or curved medially, the presence of a 'Y'-shaped furrow on the first metasomal tergite, projecting mouthparts (labio-maxillary complex), and the anterior metasomal spiracles being located on the first laterotergites (Mao 1949; Mason 1981; Huddleston and Walker 1988).

Dangerfield and Austin (1990) recognised *Hartemita* Cameron as a valid genus to accommodate a distinctive group of Oriental species, primarily based on their equidimensional shaped discal cell, indistinct propodeal areola, flattened or laminate hind basitarsus, short and evenly sclerotised hypopygium, and the very short and evenly downcurved ovipositor.

Most other extant genera have been retained as separate to Cardiochiles because they contain one, or at most two, aberrant species that are easy to recognise. The recently described monotypic genus Bohayella (Belokobylskij 1987) from eastern Russia is highly distinctive because of its very narrow elongate first metasomal tergite, presence of a 'ball and socket'-like joint between the first and second tergites, equidimensional fore wing discal cell, presence of an epicnemial carina, and prominent medial keel on the Mason (1983) correctly placed the monotypic South American genus frons. Heteropteron Brullé 1846 in the Cardiochilinae, where previously the genus had been incorrectly listed as a member of the Braconinae (Shenefelt 1978). Neocardiochiles Szépligeti (1908) is a South American genus that is morphologically very similar to Wesmaelella and Heteropteron. Pseudcardiochilus Hedwig (1957) was described as monospecific including Pse. abnormipes Hedwig. It was synonymised with Cardiochiles s. l. by Tobias and Alexeev (1977), then was redescribed and returned to valid status by Achterberg (1980b). Pseudcardiochilus is defined by the wide and dorsally glabrous apex of the hind tibia (Hedwig 1957; Achterberg 1980b). Wesmaelella Spinola (1851) is a distinctive monotypic South American genus, and with its junior synonym Psilophthalmus (Szépligeti) (in Schulz 1911), contains two species W.

rubricollis Spinola (1851) and *W. nigripennis* (Szépligeti) (1902), the latter being the most aberrant cardiochiline known.

The fossil genus *Eocardiochiles* Brues (1933), based on *E. fritchii* Brues (1933), which is preserved in Baltic amber, was not included in this revision as Mason (1981) transferred it to the Microgastrinae based on the 18-segmented antennae.

2.2. Distribution

The Cardiochilinae are cosmopolitan in distribution but are more generally associated with tropical or arid habitats. Of the 150 species described prior to this study only seven had been described from the Australasian region (Szépligeti 1900; Roman 1915; Turner 1918), and no revisionary work had been undertaken for the region since that of Turner (1918). *Cardiochiles s. l.* is distributed world wide, while all other extant genera have restricted distributions as summarised in Table 2.2. *Psilommiscus* is known only from Sumatra, *Asiacardiochiles* from Kazakhstan, *Pseudcardiochilus* from Iran, *Bohayella* from south-east Eurasia, and *Hartemita* from south-east Asia, while the genera *Heteropteron*, *Neocardiochiles* are restricted to north and central South America. *Toxoneuron* and *Tenthredoides* are restricted to north and central America and northern South America, but has been introduced into the Philippines and Thailand.

Table 2.2.	Distribution	of extant	cardiochiline	genera	by	zoogeographic
	region (after	Wallace	1876).			

Genus	Zoogeographic regions
Cardiochiles	Afrotropical, Australian, Nearctic, Neotropical, Oriental, Palaearctic
Bohayella	Oriental
Heteropteron	Neotropical
Hartemita	Oriental
Neocardiochiles	Neotropical
Pseudcardiochilus	Palaearctic
Wesmaelella	Neotropical

2.3. Biology

The biology of *Cardiochiles s. l.* has been reviewed in detail by Huddleston and Walker (1988), but generally their review is based on information obtained from very few species, specifically *Cardiochiles nigriceps* Viereck associated with *Heliothis* and *Helicoverpa* spp. in North America. Members of the Cardiochilinae are all endoparasitoids of lepidopteran larvae. Of the 150 recognised species 25 have known host associations (Table 2.3). All hosts have concealed, nocturnal habits, and have been recorded from the families Cosmopterigidae, Gelechiidae, Noctuidae, Pyralidae and Uraniidae.

Cardiochilines generally develop as solitary parasitoids, and have associated polydnaviruses to disrupt the host's immune response (Stoltz and Whitfield 1992; Whitfield 1994). In forced host studies conducted for *Car. nigriceps* (Vinson 1975; Lynn and Vinson 1977; Vinson and Iwantsch 1980), this species will parasitise other hosts closely related to it's natural hosts, however, the eggs are encapsulated by the forced host. These authors, particularly Vinson, have conducted many behavioural, biochemical, morphological and microbiological studies on *Car. nigriceps*. Danks *et al.* (1979) conducted work on the physiology and behaviour of *Car. nigriceps* and examined larval stages, but did not refer to the morphology of the larvae under study.

Several *Cardiochiles* species are of importance in the biological control of lepidopteran pests. Most notably, *Car. nigriceps*, an important parasitoid of heliothine moths on cotton, has achieved high success with up to 80% parasitism in the field (Lewis *et al.* 1972). This species has also been used against pests of tobacco budworm in the Philippines (Gardner 1957) and Thailand (Messenger 1974), although there are no recorded results of the success of these biological control programs. *Car. diaphaniae* Marsh has been introduced into Florida from Colombia as a biological control agent of *Diaphania* spp. (Pyralidae) on melon crops (Marsh 1986), and its biology has been studied by Smith *et al.* (1994). *Car. hymeniae* Fischer and Parshad is a known parasitoid of *Hymenia recurvalis* (F.) (Pyralidae), a pest of leafy vegetables in India.

The biology of the group as a whole is scant, however, studies undertaken on *Car. nigriceps* provide a detailed account of the life history of an important parasitoid of pest species, and can be used to imply the potential of other species in the subfamily.

Table 2.3.Known host associations for Cardiochiles spp., adapted from
Huddleston and Walker (1988).

Hosts	Parasite
Cosmopterigidae	
Stilbosis sp.	Car. minutus (Cresson)
S. ostryaeella (Chambers)	Car. minutus (Cresson)
Calaabiidaa	
Eving prunifoliella Chambers	Car minutus (Cresson)
Phthorimaga operculalla (Zeller)	Car explorator (Say)
F hinorinaea opercutetta (Zenet)	Car insculatus Mao
	Car. insculptus Mao
Noctuidae	
Helicoverpa armigera (Hübner)	Car. nigricollis (Cameron)
	Car, nigromaculatus (Cameron)
	Car. variegatus Szépligeti
H. assulta (Guenée)	Car. nigriceps Viereck
Heliocheilus albipunctella (de Joannis)	Car. sahalensis Huddleston and Walker
Heliothis subflexa (Guenée)	Car. nigricens Viereck
H virescens (Fabricius)	Car nigricens Viereck
11. Virescens (Lubious)	Car tennessensis Mag
Schinia sp	Car magnus Mao
benna sp.	cur. magnas muo
Pyralidae	
Achyra rantalis (Guenée)	Car. explorator (Say)
A. similalis (Guenée)	Car. explorator (Say)
Adelphia petrella (Zeller)	Car. apicalis (Cresson)
Cnaphalocrocis medinalis (Guenée)	Car. philippensis Ashmead
Diaphania hyalinata (Linnaeus)	Car. diaphaniae Marsh
Epipaschia zelleri (Grote)	Car. floridanus (Ashmead)
Etiella zinckenella (Treitschke)	Car. brachialis Rondani
	Car. saltator (Fabricius)
Hedylepta indicata (Fabricius)	Car. fulvus Cameron
Hymenia recurvalis (Fabricius)	Car. fulvus Cameron
•	Car. hymeniae Fischer and Parshad
Loxostege sticitcalis (Linnaeus)	Car. brachialis Rondani
	Car. saltator (Fabricius)
	Car. katkowi Kokoujev
Marasmia suspicalis (Walker)	Cardiochiles sp.
Nephopterix celtidella (Hulst)	Car. tibiator (Say)
N. crassifaciella Ragonot	Car. tibiator (Say)
N. demmersi floridens Heinrich	Car. tibiator (Say)
N. sabcaesiella (Clemens)	Car. tibiator (Say)
N. subfuscella (Ragonot)	Car. tibiator (Say)
Phostria obscurata (Moore)	Car. phostriae De Saeger
Syllente lunalis (Guenée)	Car. fulvus Cameron
Ulophora sp.	Car. apicalis (Cresson)
Tortrioidae	
Tortrix sp	Car explorator (Sav)
ionna sp.	Cur. explorator (Say)
Uraniidae (Epiplemidae)	
Dirades theclata Guenée	Car. adina Wilkinson

CHAPTER 3

Materials and Methods

- 3.1. General methods
- 3.2. Collecting techniques
- 3.3. Scanning electron microscopy
- 3.4. Terminology
- 3.5. Institutional abbreviations
- 3.6. Phylogenetic analyses
 - 3.6.1. Computers and programs
 - 3.6.2. Morphometric data
 - 3.6.3. Format for outgroup analysis
 - 3.6.4. Brief discussion of theoretical phylogenetic methods
 - 3.6.5. Methods for assessment of phylogenetic results
 - 3.6.6. Discussion of PAUP features
 - 3.6.7. Testing for significance of phylogenetic results

CHAPTER 3

3.1. General methods

Representative specimens of all previously recognised genera, species groups and all Australasian material were borrowed from world collections as listed in Section 3.5. They were assigned colour coded labels to represent those institutions, and housed in a unit tray system in fire-proof metal cabinets. This material, in association with published information, provided relevant data on geographic distributions and host relationships. Detailed morphological studies were undertaken using both light microscopy and Scanning Electron Microscopy (SEM).

Fine dissection of internal structures, particularly male and female genitalia and mouthparts, were carried out in ethanol. Specimens were then cleared partially in warmed 10% KOH, washed in distilled water, then in xylene, and mounted on microscope slides in either Canada Balsam in neutral xylene or Berlese's mountant, for light microscope examination.

3.2. Collecting techniques

The two most productive techniques for collection of cardiochilines in the past have been sweeping of plants in flower and malaise trapping. For this project malaise traps were set up in sites close to swamps and plants in flower where possible, however no specimens were collected by malaise trap. Many hymenopteran specimens were collected, however, only one site yielded a single cardiochiline species. These specimens were collected by sweeping on *Eremophila sturtiae* in fresh flower. A malaise trap set up in the same area for seven days and did not collect any cardiochiline specimens. Wharton (*pers. comm.*) collected specimens of *Polycardiochiles fuscipennis* (Szépligeti) in small swarms around grasses at the edge of swampy areas in Brisbane and in Papua New Guinea. This species has been the most commonly collected cardiochiline in the Australasian region. Table 3.1. summarises the available collection data for *Pol. fuscipennis*. Data labels rarely give the method of collection (78%) and this represents a great loss of potential information about the insect and ultimately the species. Of those specimens that did have collection data, malaise trapping has been the most successful. Data labels supply crucial information to future collectors on potential collection methods from which interpretations can be made, for example, that adults of certain species are mobile fliers (malaise traps), or occur at flowers (sweeping), or are nocturnal (light trap).

Technique	Number of specimens (%)
Malaise trap	124 (19%)
Pan trap	0
Light trap	11 (2%)
Sweeping	7 (1%)
Unknown	506 (78%)
Reared	0

Table 3.1.Comparison of collecting techniques shown on data labels of
Polycardiochiles fuscipennis (Szépligeti).

3.3. Scanning electron microscopy

Specimens for SEM were cleaned in a diluted pure soap solution (5%), soaked and rinsed thoroughly in distilled water, dehydrated in an alcohol series to absolute ethanol, and either air dried or critical point dried with carbon dioxide in an Emscope CPD 750. They were then mounted on card points with seccotine glue (water based), and secured to SEM stubs with carbon based plasticine (Leitz-C-Plast). Finally, specimens were sputter-coated with 40 nm of gold at 0.08 Tor and 15 milliamps for 4 min (at 15 milliamps 1 min is equal to 10 nm of gold), and examined under a Cambridge Stereoscan 250 (Mk 3B) SEM using secondary electron imaging at 20 kv and varying spot sizes of 5-8 nm. Sputter coating in an Argon atmosphere was preferred to evaporative coating (EC) in air as an even coat was not possible using EC. Problems with specimens charging, from sputter coating, were often due to shape and pilosity and were overcome by double coating of specimens. Where possible specimens were orientated with the surface of the stub out of focus or with enough tilt to remove the stub from view, so that a black background could be obtained for micrographs. When type specimens of new species were examined (see Figs 7.35 - 7.37) they were left uncoated, mounted as described above and examined under an Electroscan ES2 Environmental SEM.

3.4. Terminology

Names for new species and genera were derived from listings in Brown (1954) and Reed (1981). Terms for wing venation are based on a modified Comstock-Needham system (see Eady 1974; Achterberg 1979) but with some modifications (compared to those used by Dangerfield and Austin (1990)) based on Wharton, Achterberg and Sharkey (pers. comm.) (Figs 4.13-4.16). Those for the morphology of body parts are detailed in Chapter 4, and follow Austin and Dangerfield (1992, 1993), while the terms for surface sculpturing follow Eady (1968) and Harris (1979). The term epicnemial carina is used instead of prepectal carina, as in Austin and Dangerfield (1992), because this carina is now considered to be associated with the epicnemium, not the prepectus. Also, the term sternaulus is used instead of precoxal groove, in line with other recent works on braconids. The first tergite of the metasoma (T1) in all cardiochilines has an inverted 'Y-shaped' furrow which varies in shape and size. The narrow basal part of this furrow is here referred to as the 'stem' and the apical swelling as the 'bulb' (Fig. 4.1). The 'malar carina' is the ventral part of the occipital carinae in the malar region and sometimes has the hypostomal carina branching from it (Fig. 6.16). Measurements taken for various parts of the body and wing venation are given in Figures 4.1 - 4.3.

3.5. Institutional abbreviations

Abbreviations used in the text for institutions follow Arnett *et al.* (1986) where possible. People responsible for institutional loans are given in the acknowledgments section.

AEIC: American Entomological Institute, Gainesville.

ANIC: Australian National Insect Collection, Canberra.

ANSP: Academy of Natural Sciences, Philadelphia.

- BMNH: The Natural History Museum, London.
- BPBM: Bernice P. Bishop Museum, Honolulu.
- CASC: California Academy of Sciences, San Francisco.
- CNCI: Canadian National Collection, Ottawa.
- HNHM: Hungarian Natural History Museum, Budapest.
- MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
- MNHN: National Collection of Insects, Museum National d'Historie naturelle, Paris.
- MNTD: Museum of Northern Territory, Darwin.
- MRSN: Spinola Collection, Museo Regionale Scienze Naturali, Torino.
- MVMA: Museum of Victoria, Melbourne.
- NHRS: Naturhistoriska Riksmusset, Stockholm.
- NSWA: New South Wales Department of Agriculture, Sydney.
- QDPI: Queensland Department of Primary Industries, Brisbane.
- RMNH: Rijksmuseum van Natuurlijke Historie, Leiden.
- SMNS: Statliches Museum fur Naturkunde, Stuttgart.
- TAMU: Texas A & M University, College Station.
- UQBA: Department of Entomology, The University of Queensland, Brisbane.
- USNM: U. S. National Museum of Natural History, Washington, D. C.
- WAMP: Western Australian Museum, Perth.
- WADA: Western Australian Department of Agriculture, Perth.
- WARI: Duncan Swan Insect Collection, The University of Adelaide, Adelaide.
- ZMAS: Zoological Museum, Academy of Sciences, Leningrad.
- ZMHU: Museum fur Naturkunde der Humbolt Universitat zu Berlin, Berlin.

Phylogenetic analyses 3.6.

3.6.1. **Computers and programs**

EXTRACTOR

The following applications and programs were used to carry out the phylogenetic and other analyses conducted during the study: Applications PAUP 3.1.1 (Swofford 1993) MS-BASIC (binary) 2.0 OUICK BASIC (binary). N.B. this application is faster than BASIC, but only able to be run on a Macintosh SE or Classic, due to Systems file incompatibility Microsoft EXCEL 4.0 (1985-1992) MacClade 3.02 (Maddison and Maddison 1992) Speedometer 3.23 (Berfield 1993) **RANDOMISER 3** Programs

The program PAUP 3.1.1 (Swofford 1993), used for all parsimony-based phylogenetic analyses undertaken during this study, was registered to Dr A. D. Austin (Department of Crop Protection, The University of Adelaide) as was MacClade 3.02 (Maddison and Maddison 1992). The latter program was used to input data in spreadsheet format, that was then converted to NEXUS format when opened in PAUP 3.1.1.

Five different Apple Macintosh computers were used for analyses, depending on the size of the matrix to be analysed, and availability of machines. Computer specifications (Table 3.2) and comparative performance analyses, as assessed by the program Speedometer 3.23 (Berfield 1993) (Table 3.3), provide a comparison of the time taken for each analysis. Due to the different RAM size of each computer (Table 3.2), the time taken to conduct analyses varied greatly. The slowest computer, the Classic, was rated at 1.0 and values for other computers were rated relative to the Classic. For example, the Quadra 840AV has a mathematical computation time 135 times faster than the classic (Table 3.3).

Table 3.4 summarises the time taken for the different computers used to undertake an 'exhaustive search' for a standard 10x10 matrix (Appendix A1) using PAUP 3.1.1. The matrix was constructed using the random fill option of MacClade 3.02, and tested on the factory default settings of PAUP 3.1.1. Significantly, the LCIII, Powerbook 145 and Quadra 840AV were substantially faster at analysing the matrix than the Classic, but the times taken were proportionally less than indicated by the Speedometer program.

Table 3.2. Specifications for Macintosh computers used for analyses during the study, showing the Central Processing Unit (CPU), Floating Point Unit (FPU), Memory Management Unit (MMU), Random Access Memory (RAM), and Read Only Memory (ROM) for each machine.

Specifications	Classic	LC	LCIII	PowerBook 145	Quadra 840AV
CPU	MC68000	MC68020	MC68030	MC68030	MC68040
FPU	a l	-	~	:=);	Integral FPU
MMU		MacIIAMU	MC68030MMU	MC68030MMU	Integral MMU
Physical RAM	4096K	10240K	8192K	8192K	32768K
Logical RAM	4096K	10236K	8185K	8190K	32727K
ROM Version	\$0276	\$067K	\$067C	\$067C	\$077D
ROM Size	256K	512K	1024K	1024K	2048K

Table 3.3. Relative performance ratings of computers used in this study, comparing speed of central processing unit (CPU), and a standard graphics and mathematical calculation provided by Speedometer (Berfield 1993).

Ratings	Classic (reference)	LC	LCIII	PowerBook 145	Quadra 840AV
CPU	0.995	3.559	6.811	6.455	21.36
Graphics	0.995	4.159	7.837	5.280	22.71
Math	0.994	4.085	9.988	7.877	135.13

Table 3.4. Time taken for PAUP 3.1.1 to undertake an 'exhaustive search' of a random 10 x 10 matrix constructed using the random fill option of MacClade 3.02.

	Classic	LC	LCIII	PowerBook 145	Ouadra 840AV
Time (min:sec)	46:38	21:26	8:26	9:26	1:21
x faster than Classic	1.0	2.18	5.53	4.94	34.5

3.6.2. Morphometric data

Morphometric data represents important information about morphological differences among taxa. However, it is continuous and needs to be assigned discrete states so that it may be incorporated into a phylogenetic analysis. Any form of grouping of continuous data into discrete states, however undertaken, will be based on arbitrarily, or subjectively, chosen points. Chappill (1989) outlines three different ways of assigning states to morphometric data. They are Simple gap-coding, Generalised gapcoding (Archie 1985) and Segment coding (Colless 1980; Thorpe 1984). These three methods were compared using real character sets from this study, chosen to give the largest and smallest ranges of data. A combination of gap coding, with gaps greater than 0.5 standard deviation (SD), and segment coding based on 1 SD segments either side of the mean (used as an arbitrary starting point for coding), was eventually employed here. This was the best method because it provided reasonable separation of groups of measurements. The majority of characters were coded on segment coding only, but in some cases, segments, by chance, contained only a few taxa that were separated by a large gap (i.e. the two groups of measurements were at the extremes of the segment). When these groups were separated by a gap greater than 0.5 SD they were recoded as different states (see Appendices A2.1 and A2.7). However, if one of these groups of measurements came within 0.15 SD of a measurement in an adjacent segment, then they were included in that segment rather than being coded separately, e.g. scutellar sulcus dimensions (character 37 - see Appendices A2.8 and A3) and stigmal dimensions (character 38 - see Appendices A2.9 and A3). Segments containing a single taxon were coded separately only as long as they were more than 0.15 SD away from an adjacent taxon, otherwise they were combined. Those groups that were separated by more than one or two SD segments were given their expected character assignment, assuming that the other segments were still valid. For example, for the ratio of ovipositor breadth to length (character 43 - see Appendices A2.14 and A3), Car. naumanni (coded 6) is separated by more than one standard deviation from the next taxon, Har. muirii (coded 4).
For some initial analyses the data set was analysed with morphometric characters excluded so as to assess the relative effect of the morphometric data versus discrete characters on the results obtained. This was done because such data may potentially weaken the final result due to the arbitrary or incorrect assignment of character states (Crowe 1994) (refer Section 5.5.2 and Appendices A2, A3).

3.6.3. Format for outgroup analysis

Choice of taxa and the format for outgroup analysis follow Wharton *et al.* (1992) and Watrous and Wheeler (1981). The outline of the format used was:

- 1) The most critical outgroup comparisons involved the sister-group of the taxa studied.
- 2) If the most immediate outgroup (see Table 5.3) was variable with respect to the character in question or had a state not found in the ingroup, then more distant taxa were surveyed to determine character polarity.
- 3) If relationships among the potential outgroups were extremely uncertain, parsimony arguments were not applied.
- Arguments for polarity were made explicitly with well-stated justifications when exceptions were made.
- 5) Decisions were consistent and explained thoroughly.
- Attention was paid to details in discussion of morphology, particularly for polymorphic character states.
- Reasons were stated for using particular terminology for morphology, especially for wing venation, where there are problems with homology (Wharton *et al.* 1992).
- 8) Polarity decisions were dependent upon which taxa were selected as outgroups. A review of outgroups and a discussion of their placement in the hymenopteran phylogeny was therefore prepared (see Section 5.2.2).
- The only valid absence was considered to be the loss of character (Pimental & Riggins 1987).

3.6.4. Brief discussion of theoretical phylogenetic methods

Farris (1970, 1979) was instrumental in the acceptance that the most parsimonious trees obtained for a data set provide the best estimate of phylogenetic relatedness. Trees are chosen based on their shortest length to satisfy the grounds of parsimony (i.e. trees that have the minimum number of character reversals), and a single shortest tree provides the most powerful result that can be obtained because there are no conflicting hypotheses. Where multiple most parsimonious trees are found (i.e. conflicting hypotheses), then a consensus tree provides a compromise for assigning taxonomic status to clades, as it takes into account all of the most parsimonious trees obtained (Anderberg and Tehler 1990). However, there is some controversy about using consensus information for erecting classifications (Miyamoto 1985; Carpenter 1988). The consensus tree (Kluge and Farris 1969) was the first measure used to summarise the information content of a character set. Goloboff (1991a, 1991b) discussed the importance of the Consistency Index (CI) as the most suitable measure for comparing homoplasy for different and similar sets of data, but showed that low values of CI do not necessarily imply that there is less information for choosing among trees. Goloboff (1991a) discussed, on theoretical grounds, the potential problems and the attributes of consensus, retention and rescaled retention indices, and defined the 'decisiveness' of a character set (i.e. "the information allowing a choice or a decision between different classifications"). This was based on the "sum of the steps of all possible fully resolved trees" that is "dependent only on the number of taxa and the number of characters showing apomorphy in different numbers of taxa present". Page (1992) discussed the relationships of information content and structure of trees, and their topology, to classifications by reviewing the work of Mickevick and Platnick (1989). The arguments presented by these authors highlight the ongoing debate over the significance and validity of the confidence of different measures of information and structure contained within data sets. Most efforts have been directed toward the use of 'permutation tail probability' (PTP) and 'topology dependent-PTP' (T-PTP) tests for assessing cladistic information and structure (Archie 1989; Faith 1991; Faith and Cranston 1991, 1992; Trueman 1993), and these tests are discussed and utilised in Sections 3.6.7 and 5.7.

3.6.5. Methods for assessment of phylogenetic results

This section introduces and discusses the indices and statistical methods employed to assess the results of phylogenetic analyses. One of the advantages of using PAUP 3.1.1 is that it evaluates and displays various types of diagnostic information that can be used to interpret the results of an analysis. The CI, mentioned above (Kluge and Farris 1969), and the Homoplasy Index (HI) represent a measure of homoplasy in a tree. They indicate how the data set fits the tree topology, yet vary with respect to the size of the data set (Archie 1989). The CI is a measure of m/s, where m is the minimum amount of change that the character may show on any conceivable tree, and s is the length or number of steps required by the character on the tree being evaluated (Swofford et al. 1993). It can be estimated for a single character on a tree or as an overall CI for a suite of characters or an entire tree. The HI becomes a direct measure of homoplasy, with a value of one representing maximum homoplasy. This is usually interpreted as 1-CI except when multistate characters are treated as polymorphic, because character changes are allowed within the terminal and m is variable. The Retention Index (RI) (Farris 1989, 1990a) becomes (g-s)/(g-m), where g is the maximum possible amount of change that a character could acquire on any conceivable tree. This can then become the Rescaled Consistency Index (RC) (Farris 1989, 1991a) defined as RI x CI (Swofford et al. 1993).

PAUP 3.1.1. has a method of reweighting characters based on CI, RI or RC, that has the effect of making those characters with high measures for these indices carry more weight in resultant or *a posteriori* analyses.

The f-ratio, introduced as the f-value by Farris (1972), is discussed further by Brooks *et al.* (1986) as a measure of distance matrices between the original data set and an inferred data set. It can be used to determine the best tree with the same CI (Brooks *et al.* 1986) as it is sensitive to the distribution of characters among taxa. The f-ratio is given as a value between 1 and 0, with the best tree having a value of 0.

Consensus trees are used to summarise the differences among trees when more than one most parsimonious tree is obtained from analysis of a particular data set. The two types of consensus trees employed here are strict and majority rule. A strict consensus shows only those nodes which agree in all trees, and collapses nodes which disagree to polytomies (inferring simultaneous divergence of multiple lineages). A majority rule tree shows those nodes which are supported by the highest percentage of the trees, and nodes are given a percentage which indicates the number of trees in agreement with that node. When large numbers of trees are obtained (≥ 20) a 90% majority rule will be taken as significant (e.g. when 18 out of 20 trees agree with that node).

Rohlf's Consensus Index (Rohlf 1982) is a measure of the overall agreement of all trees included in the consensus tree. It is automatically calculated by PAUP 3.1.1. and will be used as a measure of significance for the consensus trees obtained. Rohlf (1982) recommended that the strict consensus tree be used, rather than any other, as it is the only true measure of total agreement of all of the trees obtained in an analysis.

3.6.6. Discussion of PAUP features

A set of analyses was designed to gain the maximum potential from PAUP, i.e. to optimise the use of the program to find the most parsimonious result for the data set (Appendix A4) through an understanding of the different parameters of the Heuristic Search mode. In this Section specific parameters discussed are underlined. Tests of 'Option' parameters were conducted on an *a posteriori* basis, using *Epsilogaster* as the only outgroup (see Section 5.5.2) as it produced the shortest tree from the different combinations of outgroups with PAUP run on the factory default settings.

<u>ACCTRAN</u> or 'accelerated transformation' relates to character changes, or character-state optimisation on a tree within the assumption constraints of order and polarity. ACCTRAN takes into account the possibility of a single origin for a character followed by reversals higher up the tree. <u>DELTRAN</u> or 'delayed transformation' works in the converse way, in that it allows for two origins of a character state (i.e.

parallelisms). These differences are important when following the character state changes on a tree. In this study it was preferred that each character had a single origin rather than multiple ones so that any changes were due to reversals, therefore, ACCTRAN was used.

PAUP 3.1.1 has three search options; 'Heuristic', 'Branch and Bound', and 'Exhaustive'. The Exhaustive method evaluates every possible tree from the data matrix but is useful only for matrices with less than 11 taxa (Swofford et al. 1993), due to the excessive number of rearrangements needed to evaluate all trees. The Branch and Bound method suffers from the same problem and can not be used with large numbers of taxa and characters. The Heuristic option searches for local optima in the data rather than a global optimum, with an initial tree being generated by stepwise addition, and subsequent rearrangements based on different branch swapping algorithms. Due to the large number of taxa and characters incorporated into the matrix here, only the Heuristic search option could be used. For this search option, stepwise addition creates a starting tree by adding the taxa in a particular order or addition sequence, assessing which is the best terminal for the next taxon that gives the shortest resultant tree. The different addition sequences available are simple, which is based on the order of taxa in the matrix; closest, which evaluates all possible three taxon trees and then places the remaining taxa until the shortest length tree is found; asis, which adds taxa in the order presented in the data matrix; and random which obtains a specified number of permutations of the taxa to be used in an addition sequence. Swofford et al. (1993) indicates that no one method is best for any particular type of data set and all alternatives should be investigated.

The different <u>branch swapping</u> algorithms are listed in order of increasing effectiveness in Swofford *et al.* (1993). These different options, <u>TBR</u> (tree bisection-reconnection), <u>SPR</u> (subtree pruning-regrafting) and <u>NNI</u> (nearest neighbour interchanges) were tested on the 'simple', 'asis' and 'closest' stepwise addition options. TBR/simple gave the best results with SPR increasing tree length by one step and NNI increasing length by more than four steps. For the SPR option, the 'closest addition sequence' produced the shortest trees, however, this was not as good as TBR/simple

options. TBR assesses all possible bisections and pairwise reconnection's of two disjoint subtrees by bisecting along a branch of the tree. TBR/simple was used for most subsequent analyses (refer Section 5.5.2).

In all analyses undertaken here, multi-state taxa were interpreted as polymorphisms. After examining the effects of the various options offered by PAUP, discussed above, the rooting options were investigated and the option to make the ingroup monophyletic and the outgroup a monophyletic sister group. This option was used in all subsequent analyses as it prevents the outgroup being included unintentionally within the ingroup, a problem that was not encountered, but should be guarded against. When outgroups were defined, trees were rooted making the ingroup monophyletic and, if more than one outgroup taxon was defined, then these were made polyphyletic with respect to the ingroup.

It was useful to let the maximum number of trees increase to maximum memory capability otherwise a warning at 100 trees is shown and this slowed the time for analyses. Also, increasing the RAM to the maximum allowable for the computer, was necessary in order to save as many trees as possible for each analysis. <u>Stepmatrix</u> allowed assignment of states, not observed in terminal taxa, to internal nodes ("short-cut"), and only those states that can be identified as potential shortcuts by the "3+1" test. Stepmatrices options allow the internal nodes to be restricted to only the states found in the terminal taxa, or allow internal node transformations of non-terminal taxon states. Initial analyses were undertaken to test the different combinations of outgroups used (Section 5.5.2), uninformative characters were always excluded from the analysis, as the inclusion of these characters changes the consensus indices, thus making them difficult to compare.

The <u>MULPARS</u> and <u>COLLAPSE</u> options were always employed. MULPARS only saves minimal trees and COLLAPSE collapses zero length branches. Reweighting options based on retention, consistency and rescaled consistency indices were undertaken when more than one shortest tree was found, and these had the effect of changing the overall structure of the result.

3.6.7. Testing for significance of phylogenetic results

The worthiness of different significance tests for phylogenetic results have been discussed and reviewed by Carpenter (1992), Trueman (1993), Farris *et al.* (1994) and Faith *et al.* (1994). Ideally, different tests should be employed to examine the significance of cladistic information and structure within a tree or trees. However, the PTP test, first proposed by Archie (1989) and developed by Faith (1991), Faith and Cranston (1991, 1992) and Trueman (1993), is superior to other tests in a practical sense, because software developed by Trueman is available, which makes this test easier to undertake than others. Apart from the limitations outlined by Trueman (1993), PTP tests also provide a gauge of whether resultant trees may have arisen by chance or contain significant cladistic information, and thus they have some statistical validity.

The basic method behind PTP testing, which assesses cladistic information, involves evaluating 'randomised data' sets, in the same way as the 'actual data' set, and assessing the differences between minimum lengths trees derived from the two sets of data. If 5% or fewer of the trees derived from the randomised data have lengths equal to or less than the actual minimal tree length (PTP ≤ 0.05), then the analysis is accepted as being statistically significant and not generated by chance alone. Thus, the null hypothesis that the tree contains no cladistic information is rejected. If all trees obtained from the randomisations are longer than the trees derived from the actual data set then PTP = 0.01.

To evaluate the monophyly or non-monophyly of whole trees or clades, T-PTP testing has been proposed by Faith (1991b). This procedure is similar to PTP testing in that it analyses minimum length differences among trees, however taxa are constrained within selected groups to assess monophyly or non-monophyly of the branching patterns within a tree. The randomised data are evaluated under the constraint of the minimal tree topology, derived from the actual data set, and also under the converse of this, i.e. they do not conform to the constraint tree, and the 'differences' in lengths are assessed accordingly (Faith 1991). Therefore, the 'critical length difference' is the length of the

constrained tree, subtracted from the length of the most parsimonious of all trees constrained not to have any of the original groups.

The ultimate aim is to assess whether monophyletic clades represent better groupings than might be expected by chance, based on shorter length differences of the trees derived from the actual data set. As in PTP testing, if all randomised differences are greater than the actual difference then T-PTP = 0.01, while T-PTP ≤ 0.05 is the minimum value to accept that significant hierarchical or cladistic structure exists.

Faith and Ballard (1994) outline the distinctions between PTP and T-PTP tests, in that the former indicate the strength of the "hierarchical information" and the latter assess the significance of the specific "hierarchical structure" within trees.

Farris (1991) proposed a similar test to T-PTP testing, *viz.* 'Q' or Permutation Congruence Tail Probability. This is a measure of the probability that homoplasy for the actual matrix is less than that for a suite of randomisations of the actual matrix. It therefore provides a permutation-relative index of congruence. The hypothesis is accepted at the 95% limits, as are PTP and T-PTP tests, and results are given as log values with Q'(X) = 1.3 for 95% and Q'(X) = 2 for 99% significance levels.

CHAPTER 4

Morphology of the Cardiochilinae

- 4.1. Introduction
- 4.2. Pupal cases
- 4.3. Larval morphology
- 4.4. General adult morphology
 - 4.4.1. Head
 - 4.4.2. Mesosoma
 - 4.4.3. Wings
 - 4.4.4. Legs
 - 4.4.5. Metasoma
 - 4.4.6. Female genitalia
 - 4.4.7. Male genitalia
- Figures 4.1 to 4.21

CHAPTER 4

4.1. Introduction

This chapter provides an illustrated and detailed treatment of the general morphology of the Cardiochilinae. As well as describing morphological characters, information is presented on terms, measurements and abbreviations used throughout the following chapters. The abbreviations used are in brackets, with those for specific terms in lower case and those for measurements in upper case, and specific terminology is italicised. As for virtually all previous studies on braconid phylogeny and taxonomy, the work presented here relies on adult morphology as the primary source of taxonomic data because the larvae of most species are unknown. However, in an effort to facilitate the use of larval and other characters in future studies the morphology of non-adult stages are reviewed here, along with some adult characters such as male genitalia, that subsequently were not used because information was unavailable for many species. Those characters used in the cladistic analyses are discussed in detail in Section 5.4.

4.2. Pupal cases

Pupal cases were found associated with a few species, viz. Bohayella adina (Wilkinson), Cardiochiles sahalensis Huddleston & Walker, Psilommiscus sumatranus Enderlein and Toxoneuron nigriceps (Viereck). In general, pupal cases are buff to white in colour, elongate-oval in shape and sometimes flattened longitudinally. Often they have longitudinal ridges similar to those found in diapausing cocoons of Microplitis demolitor Wilkinson (Microgastrinae) (Austin and Dangerfield 1993), and have dark brown discolouration at the edges of the emergence hole. The size of the case usually reflects the size of the wasp that has emerged from it, with the exception of cases for Car. sahalensis which are slightly larger than the length and breadth of the specimen. Boh. adina has a case which is light yellow to buff in colour, stout, oval, about 1.5 x as long as broad, papery-fibrous in texture, and with a torn half moon-shaped sub-apical emergence hole. Car. sahalensis has a thick papery pupal case which is light brown in

colour with darker brown longitudinal stripes, about 1 cm in length, 2.3 x as long as broad, is longitudinally ridged, with the larval host head capsule incorporated into the cocoon at one end, and a roughly torn emergence hole at the other. From the pupal case of *Car. sahalensis* a larval mandible was extracted (presumably final instar larva) (Fig. 4.8). The case of a single specimen of *Psi. sumatranus* was found inside the host cocoon, the latter being enclosed within the curled leaf of the host' food plant. The parasitoid's cocoon is white, loosely woven, and laterally flattened. At the closed end of the case is a meconial mass with a roughly torn opening at the other end. The data label reads 'larvae fed on Cystus' (*Cistus* (Cistaceae) or 'rock rose' is an ornamental shrub used for scenting soaps or as a tea substitute in Asia and Indonesia). *Tox. nigriceps* has a smooth, papery case that is light buff in colour, oval, about 2.5 x as long as broad, and with a rough dirt encrusted circular apical emergence hole which completely truncates one end of the case.

4.3. Larval morphology

Quicke and Achterberg (1990) used nine larval characters in their phylogenetic analysis of braconid subfamilies, but they neglected to discuss the characters, or the species for which these characters were scored (see Chapter 2). Mason (1981) referred, generally, to the larvae of Cardiochilinae and *Cardiochiles* as an outgroup for his analysis of microgastrine relationships (see Chapter 2). The only cardiochiline named in his review was *Cardiochiles minutus* (author not stated, refer Section 2.1.3) for which the adult wings were figured. Mason (1981) also illustrated larval head, integument and mandibles for microgastrines, but not for cardiochilines.

The only larval character examined in this study was the form of the mandible, which was extracted from the cocoon of *Car. sahalensis* (see Section 4.2). It has a broad tapering conical base with four stout sub-apical hairs, and is slightly sclerotised and yellow. The blade of the mandible is tan in colour, evenly sclerotised and bidentate, with a long pointed leading tooth and a broad apically rounded basal tooth (Fig. 4.8).

4.4. General adult morphology

4.4.1. Head

The head of cardiochilines (Figs 4.1, 4.2) is generally broadly ovate in dorsal view with an excavate occipital region. In dorsal view, the occipital depth (OD) varies with respect to the length of the head (HL), and the length of the eye (EL) varies with respect to the length of the temple (TL). The eye pilosity varies considerably from long and dense (Fig. 4.9) through various stages of reduction (Figs 6.32, 6.87, 6.98, 6.101) to glabrous. The eyes are slightly emarginate at either side of the antennal sockets (Fig 4.2). The face is prominent anteriorly, often with a dorsal medial node, and varies in breadth (FB) and height (FH) (Fig. 4.2). The occelli form a compact triangle at the centre of the vertex, and the area enclosed by them is referred to as the *stemmaticum* (Achterberg 1979). The distance between the eyes and the ocelli is always equal to or larger than the width of the stemmaticum.

In anterior view, the antennal sockets are positioned on the upper one-quarter of the head, and the width between the sockets (AS) may be much broader or narrower than the width of a single socket (AW) (Fig. 4.2). In posterior view, the foramen magnum is bordered by the *foraminal carina* (fc) (Fig. 4.10). This carina is variably developed and shows different combinations of dorsal and lateral reduction.

The mouthparts are hypognathous and recessed into the *hypostoma* which is sometimes bordered by a *hypostomal carina* (hc) (Fig. 4.10). The hypostomal carina may be complete, reduced in the malar region, or absent. The *malar carina* (mc) (Fig. 6.8) refers to the ventral part of the occipital carina present only in the malar region, and it sometimes has the hypostomal carina branching from it. The maxillary palps (mp) can have six well-developed segments (Fig 4.5), or the basal segment may be either reduced to a small plate, or completely absent to leave five segments. The labial palps are four-segmented. The labrum is separate from the clypeus and often hidden beneath it. When visible, at least in part, it is either convex, straight or concave at the apex, about one-half to three-quarters as broad as the clypeus, and may have a fringe of setae along the apical margin (Fig. 6.71). The clypeus varies in height (CH) and breadth (CB) and may be

well-defined laterally or fused to the face (Fig. 4.2). The *galea* (ga) is variable in width and length (GL), and may be broad and rounded (Fig. 4.5) to elongate, narrow and pointed apically (Fig. 4.6). The *glossa* (gs) is short (Fig. 4.7) or extremely elongate (Fig. 6.x), and may be bilobed (Figs 4.6, 4.7) or rounded at the apex (Fig. 4.5).

4.4.2. Mesosoma

In dorsal view the mesosoma (Fig. 4.1) comprises the pronotum, tegulae, scutum, scutellum, metanotum and propodeum. The dorsal pronotum (dp) is broadly rectangular, smooth or longitudinally carinate, and emarginate or straight anteriorly. The medial scutum is separated from the lateral lobes of the scutum by the notauli (n). The medial scutum is smooth or has a medial longitudinal, sometimes carinate, ridge which is occasionally set into a furrow. The lateral lobes of the scutum sometimes possess parapsidal grooves (pg) which are broad and shallow in the posterior one-third, and parallel to the lateral margin. There may also be lateral carinae forming a raised outer border of the scutum. The notauli are smooth or crenulate, narrow or wide, and are usually well-defined. The posterior margin of the scutum has the faint impression of a transcutal suture (ts), which is defined laterally by a groove, is absent medially but discernible in yellow specimens by a faint internal line. Posterior of the transcutal suture, small axillae (ax) are defined either side of the rectangular scuto-scutellar sulcus. The axillae are reduced to a vertical area which have a lateral carinate lobe. The scuto-scutellar sulcus varies in length (SSL) and breadth (SSB), and may be fine or deep, smooth or crenulate. The scutellum is triangular in shape, variable in the length (SL) and breadth (SB), and may be bordered laterally by carinae, a smooth or rugulose area, or have an apical cup-like structure. The lateral scutellum may be smooth or crenulate, and the posterior band may be smooth or crenulate medially, and rounded or slightly emarginate at the medial apex. The metanotum is composed of the dorsellum (ds) medially, and the lateral metanotum. The dorsellum usually has a medial longitudinal carina, however this is sometimes absent. The lateral metanotum is closely abutted to the posterior band of the scutellum so that the phragma of the scutellum is never revealed. The lateral metanotum is variably setose, usually with at least antero-lateral setae. The propodeum is broadly trapezoidal in shape, broadest basally, and has the lateral spiracles positioned one-third to one-fifth from the anterior margin. The spiracles vary from circular or ovoid, to elongate and kidney-shaped. The sculpturing of the propodeum varies in shape from completely smooth (Fig. 6.106), to having a complete well-defined *areola* (ar) (Fig. 4.1). The areola may be oval- or diamond-shaped, reduced anteriorly to two posterior carinae diverging anteriorly, or reduced posteriorly with the anterior carinae forming prominent arches that reach to the *lateral carinae* (lc) of the propodeum.

In lateral view the mesonotum is composed of the propleuron, pronotum, mesopleuron and metapleuron. Several structures on the mesopleuron (*viz.* the *epicnemial carina* (ec), epicnemial furrow, *sternaulus* (st), pleural suture and epistomal scrobe) vary among species (Fig. 4.4). The epicnemial carina (formerly known as the prepectal carina - Austin and Dangerfield 1993) is a character that has been used at the generic level for several braconid subfamilies. Mason (1981) stated that the presence of an epicnemial carina is a plesiomorphic character and considered it o be of significance at the generic level in the Microgastrinae. For example, the microgastrine genera *Snellenius* Westwood and *Microplitis* Foerster have been distinguished on the presence or absence of an epicnemial carina (Mason 1981; Austin and Dangerfield 1993), with *Microplitis* lacking this character. In cardiochilines the sternaulus (formerly known as the precoxal groove - Austin and Dangerfield 1993) is smooth or crenulate.

In ventral view the mesonotum is composed of the propleuron, prosternum, mesosternum and the metasternum. The prosternum is small, diamond-shaped and mostly concealed by the fore coxae. The mesosternum is the region below the precoxal groove and has an epicnemial carina variably developed anteriorly. The metasternum is mostly concealed by the mid and hind coxae.

4.4.3. Wings

Terms for wing venation follow those proposed by Wharton, Achterberg and Sharkey (*pers. comm.*) to be used in their revision of New World genera, which is derived from the modified Comstock-Needham system (Eady 1974; Achterberg 1979). Wing venation and terminology are outlined in figures 4.13 to 4.16, and measurements taken of the wing are given in figure 4.3.

Conventions used here for venation are as follows: longitudinal veins are in capitals (e.g. <u>CU</u> instead of Cu); major sections of longitudinal veins intersected anteriorly by cross-veins have numbers to indicate divisions (e.g. <u>2</u>-M and <u>3</u>-M); major abscissae intersected posteriorly by cross-veins have lower case letters indicating divisions (e.g. 2-M<u>a</u> and 2-M<u>b</u>); cross veins have lower case letters (e.g. r-m), and names for cells follow the Comstock-Needham system.

Both fore and hind wings show variable patterns and intensity of infuscation. In the fore wing the stigma may be elongate or broad, measured as a ratio of stigmal length (STL) to stigmal width (STW). 2r arises half to two-thirds along the stigmal length and the length of 2r varies with respect to the height of the second submarginal cell (H2S). The discal cell can be elongate or short, measured as a ratio of discal length (DL) to discal width (DW), with veins 1-SR+M and 1-CUb variable in length. 1r may be absent or present as a short apical stump, dividing 2+3-SR into its component parts 2-SR and 3-SR. The second submarginal cell may be short or elongate with 4-SRa and 2-M being variable in length. 3r may be absent or present as a short apical stump dividing SR into 4-SRb and 5-SR. 1a and 1-2A+3A may be absent or present either spectrally, as pigmented lines or as complete veins.

The hind wing has a variable number of hamuli which may vary among species or between wings on the same specimen. 1-SRa may be absent or present between 1-SC+R and r-m (Fig. 4.15). 2-M is usually pigmented or rarely as a spectral trace. 2-1A may be absent, present as a stump, or complete and reaching the wing margin.

The most unusual venation for the subfamily is that of *Wesmaelella* (Fig. 4.16). The wings have dark infuscation without patterns and are evenly setose throughout. The fore wing has thick venation which is heavily sclerotised; 1r is long; 4-SRb has a basal break; and 3-M and 2-CUb are bifurcate at their apices. The most unusual vein found in the fore wing of *Wesmaelella* is the development of a basal stump of 1-2RS, which is unlike that of any other braconid. The hind wing has partial development of 2r-m, eight enlarged hamuli, 2-1A sinuate and reaching the wing margin, and 2-M as a heavily sclerotised vein.

4.4.4. Legs

The legs may be slender or moderately robust and have distinctive developments on the hind tibiae and basitarsi. The hind tibia may have a dorso-apical projection which may be either pointed or with a concavity at the apex (Figs 6.72, 6.73, 6.100). The hind basitarsus may be cylindrical or ovoid in cross-section, or laterally flattened and laminate with a dorso-apical extension (Fig. 6.29). The outer surface of the hind tibia usually has a group of club-tipped setae near the apex (Figs 6.16, 6.100), and the tibiae and tarsi often have stout spines among the pilosity. The tarsal claws may be simple or pectinate. Pectination varies in form from teeth of even width which are evenly spaced (Fig. 4.12), to claws with a broadened apical tooth (Fig. 6.63). Some have simple claws but with stout hairs that can be easily misinterpreted as pectination.

4.4.5. Metasoma

The tergites and pleurites of the metasoma are fused, as in the Microgastrinae, so that the pleurites are referred to as laterotergites. The first tergite of the metasoma (T1) has a medial field with an inverted 'Y-shaped' furrow (Fig. 4.1). The narrow basal part of this furrow is referred to as the *stem* and the apical swelling as the *bulb*. The ratio of the lengths of stem (S) and bulb (B) vary among species. The length of T1 (T1L) varies with respect to its breadth (T1B), as does the length (T2L) and breadth (T2B) of T2 (Fig. 4.1). The suture between T2 and T3 may be well-defined, or reduced and partially fused.

4.4.6. Female genitalia

The female genitalia are partly covered ventrally by sternite six, which is referred to as the sub-genital plate or hypopygium (h) (Figs 4.4, 4.11, 4.21). This sternite, which is 'U-shaped' in cross section, is variable in shape and degree of sclerotisation (see Section 5.4). Hypopygial desclerotisation may be of five different types. It may be evenly sclerotised throughout, or slightly desclerotised only along the medial line but not membranous, or wholly desclerotised along the medial line and folded fan-like (Fig. 4.21), or with an apical transverse desclerotised membranous area (Fig. 6.43). The shape and length of the ovipositor and sheaths varies greatly and may be correlated with the form of the hypopygium. The ovipositor may be as long or longer than the hind tibia; of even width and pointed at the apex; long but broadened and truncated at the apex; shorter than the length of hind tibia and with the apex variable in shape; or very short and down-curved with a very short hypopygium so that the ovipositor may be hidden by the hypopygium. Austin (1990) suggests that the most likely function of a medially membranous hypopygium in the Microgastrinae, is to allow the ovipositor to be directed forwards between the hind coxae without the rest of the hypopygium having to rotate to the same degree. In the case of some Cardiochilinae the hypopygium is membranous and expandable medially, yet has a solid inflexible bridge apically. This apical bridge would inhibit the forward direction of the ovipositor and may be used in a different way to that in microgastrines. The apex of the hypopygium sometimes has an apical fringe which extends onto the lateral hypopygium (Figs 6.66, 6.67). The ovipositor has circular sensillae which are often concentrated toward the apex (Fig. 6.69).

4.4.7. Male genitalia

The male genitalia are covered ventrally by sternite eight (S8), which is variable in shape. Sternite seven (S7) is emarginate apically and varies in length and breadth. S8 may be emarginate or convex postero-medially and have an antero-medial projection which varies in size (Figs. 4.17 - 4.19). The genitalia are of constant form in the few species examined (Fig. 4.20). The *adeagus* (ad) is membranous with apical nodules, and

has two basal *adeagal apodemes* (ada) which are about as long as the adeagus itself. The slightly-sclerotised *volsella* (vo) is composed of the *digitus* (di) which has stout apical spines, the much reduced *cuspis* (cu) which has apical nodules, and the basal *volsellar apodemes* (va) which extend to about the same length as the adeagal apodemes. The *parameres* (pa) are well-sclerotised and large, with long setae on the apical two-thirds, and basal arms which encircle the volsellar and adeagal apodemes. The two parameres are attached basally to the *gonocondyle* (gc).

CHAPTER 4

Figures 4.1 to 4.21

Figs 4.1-4.4. Adult of a generalised Cardiochilinae showing select morphological features and measurements taken for morphometric analyses (in upper case): 4.1, dorsal head, mesosoma, T1 and T2; 4.2, anterior head; 4.3, medial fore wing; 4.4, lateral habitus.

- propodeal areola ar: AS: antennal separation AW: width of antennal socket ax: axilla **B**: bulb of first tergite CB: clypeal breadth CH: clypeal height DL: discal cell length ds: dorsellum dorsal pronotum dp: DW: discal cell width EH: eye height EL: eye length epicnemial carina ec: facial breadth FB: fc: foraminal carina FH: facial height galea ga: GL: galeal length glossa gs: H2S height of the second submarginal cell h: hypopygium hc: hypostomal carina HL: head length lc: lateral carinae of the propodeum
- malar carina mc: maxillary palps mp: n: notauli OD: occipital depth parapsidal groove pg: S: stem of first tergite S7: sternite seven S8: sternite eight SB: scutellum breadth SL: scutellum length SSB: scutellar sulcus breadth SSL: scutellar sulcus length sternaulus st: STL: stigmal length STW: stigmal width TIB: breadth of first tergite of metasoma T1L: length of first tergite of metasoma breadth of second tergite of T2B: the metasoma T2L: length of second tergite of the metasoma TL: temple length transcutal suture ts:









Figs 4.5-4.7. Mouthparts of adult cardiochilines showing galea (ga), glossa (gs) and maxillary palps (mp): 4.5, *Hymenicis noongarensis* sp. nov.; 4.6, *Cardiochiles rufator* Roman; 4.7, *Austerocardiochiles pollinator* sp. nov. **Fig. 4.8.** Larval mandible (late stage instar) of *Cardiochiles sahalensis* Huddleston and Walker. Scale lines: 4.5-4.7, 0.5 mm; 4.8, 0.25 mm.



Fig. 4.9. Ventral view of head of *Cardiochiles s. str.* sp. **Fig. 4.10.** Posterior head of *Retusigaster* sp. showing foramenal carina (fc) and hypostomal carina (hc). **Fig. 4.11.** Ventro-lateral view of apical metasoma of *Cardiochiles s. str.* sp. showing hypopygium (h). **Fig. 4.12.** Hind tarsal claw of *Cardiochiles s. str.* sp. Scale lines: *4.9-4.10*, 1mm; *4.12*, 0.1 mm.



Figs 4.13 - 4.15. Wings of a generalised Cardiochilinae: 4.13, fore wing; 4.14, hind wing; 4.15, medial hind wing. **Fig. 4.16.** Fore and hind wing of Wesmaelella *rubricollis* Spinola. Terminology for wing venation is a modified Comstock-Needham system (see text for further details).



Figs 4.17 - 4.19. Sternites 7 (S7) and 8 (S8) of male: 4.17, Hymenicis noongarensis sp. nov.; 4.18, Cardiochiles verticalis Turner; 4.19, Austerocardiochiles pollinator sp. nov. Fig. 4.20. Dissected male genitalia of Hymenicis noongarensis sp. nov. showing adeagus (ad), adeagal apodemes (ada), cuspis (cu), digitus (di), gonocondyle (gc), parameres (pa), volsella (vo), and volsellar apodeme (va).. Fig. 4.21. Ventral apical sternites of female Polycardiochiles fuscipennis (Szépligeti) showing hypopygium (h) with medially desclerotised and folded membranous region with sclerotised bridge. Scale lines = 0.5mm.



CHAPTER 5

Cladistics of Genera

- 5.1. Introduction
- 5.2. Taxa used in the analyses
 - 5.2.1. Selection of ingroup and outgroup taxa
 - 5.2.2. Discussion of higher level hymenopteran taxonomy for outgroup selection
- 5.3. Selection of characters
- 5.4. Character discussion: polarity and order assignment
 - 5.4.1. Qualitative characters
 - 5.4.2. Morphometric characters
- 5.5. PAUP analyses
 - 5.5.1. Introduction
 - 5.5.2. Comparison of different outgroups
 - 5.5.3. Comparison of morphometric and qualitative data
- 5.6. Results of PAUP analyses and formation of a generic classification
- 5.7. Testing for significance of results
- 5.8. Discussion of classification

Figures 5.1 to 5.4.

CHAPTER 5

5.1. Introduction

This chapter examines the phylogeny of the Cardiochilinae by cladistic analysis and constructs a generic classification for them based on the cladistic relationships among 60 select taxa. It details the species and characters used for the analysis, and discusses the assignment of character states, and their polarity and order, where possible. The resultant data set is analysed by the method of maximum parsimony using the computer program PAUP 3.1.1. The relationships derived from these analyses are discussed and the information and structure of trees are tested using the currently accepted statistical tests for significance. Finally, a preliminary classification is proposed from these data for the genera of the world.

5.2. Taxa used in the analyses

5.2.1. Selection of ingroup and outgroup Taxa

In-group taxa were selected to include all Australasian species described in the taxonomic revision for this region (see Chapter 7), type species of all extant genera and those previously synonymised (Table 5.1), and selected species from zoogeographic regions that were otherwise not represented. The ingroup taxa chosen for analysis are given in Table 5.2 and are arranged to show the genera from which they were originally described and the zoogeographic regions in which they occur.

No single outgroup was found which possessed morphological characters with constant states, i.e. each potential outgroup possessed some polymorphic characters. It was therefore necessary to include multiple outgroups in order to polarise characters for the phylogenetic analysis. The format for outgroup analysis has been outlined in Chapter 3.6.3. A detailed review of characters and character state changes was undertaken for the Braconidae and a wide range of hymenopteran families because the states found for some characters in the ingroup, for example, the presence of 1r in the forewing, were not

found in any of the sister groups or near outgroups but were represented in more distant families within the Symphyta and Sphecoidea.

Genus	Type species	Type depository	
Extant			
Bohayella Belokobylskij 1987	Boh. tobiasi	ZMAS	
Cardiochiles Nees	Car. saltator	Lost	
Hartemita Cameron 1910	Har. latipes ZMHU		
Heteropteron Brullé 1846	Het. macula	a Possibly in MNHN	
Neocardiochiles Szépligeti 1908	Neo. fasciipennis	HNHM	
Pseudcardiochilus Hedwig 1957	Pse. abnormipes	SMNS	
Wesmaelella Spinola 1853	Wes. rubricollis	MRSN	
Synonymised			
Asiacardiochiles Telenga 1955	Car. minutus	ZMAS	
Ditherus Cameron 1902	Car. ruficollis	BMNH	
Ernestiella Cameron 1905	Car. nigromaculatus	BMNH	
Laminitarsus Fullaway 1919	Har. muirii	BPBM	
Psilommiscus Enderlein 1912	Car. sumatranus	Unknown, cotypes BMNH	
Psilophthalmus Szépligeti 1902	Wes. nigripennis	HNHM	
Schönlandella Cameron 1904	Car. nigromaculata	BMNH	
Tenthredoides Cresson 1865	Car. seminiger	ANSP	
Toxoneuron Say 1836	Car. viator	Lost	

Table 5.1. Extant and synonymised genera of Cardiochilinae showing type species and type depository

Australian	Ethiopian	Nearctic	Neotropical	Oriental	Palaearctic
Cardiochiles dissimulator Car. fuscipennis Car. rufator Car. uniformis Car. verticalis New Species areyongensis bubbur callemondah deetoo eremophilasturtiae evelinae exleyae goosei gwenae iqbali morulus naumanni nockatungensis noongarensis occidentalis pollinator rasi saeedi scotti toxopeusi turneri	Car. enderleini Car. hymeniae Schönlandella nigromaculata	Car. diaphaniae Car. dilatus Car. explorator Car. magnus Car. mexicanus Car. rubicundus Car. rubicundus Car. rubidus Tenthredoides nigriceps Ten. seminiger Toxoneuron bicolor Tox. viator	Heteropteron macula Neocardiochiles fasciipennis Psilophthalmus nigripennis Wesmaellela rubricollis	Car. atricornis Car. pedis Car. philippensis Car. subflavus Hartemita latipes Laminitarsus muirii Psilommiscus sumatranus	Asiacardiochiles minutus Bohayella tobiasi Car. acutus Car. saltator Car. sp indet. Ditherus ruficollis Pseudcardiochilus abnormipes

 Table 5.2. Ingroup taxa used in the phylogenetic analysis of the Cardiochilinae and their corresponding zoogeographic regions. Species are listed according to their original generic placement, except for the new species described here in Chapter 7 (see Chapter 6 for authorship of species).

5.2.2. Discussion of higher level hymenopteran taxonomy for outgroup selection

The Hymenoptera are considered to be a monophyletic group with the sistergroup being the Mecopterida (Mecoptera + Siphonaptera + Diptera + Trichoptera + Lepidoptera) (Hennig 1981). The earliest hymenopteran fossils belong to the family Xyelidae and their wing venation is the best representation of a ground plan within the Hymenoptera (Rasnitsyn 1969). The Symphyta are considered to be basal within the Hymenoptera but they form a paraphyletic assemblage (Gibson 1985; Johnson 1988; Rasnitsyn 1988; Whitfield et al. 1989; Dowton and Austin, in press). Recently Gibson (1985) and Whitfield (1992) consider the Orussidae to be the sister group of the Apocrita and the Xiphydriidae the sister group of the Orussidae + Apocrita, but this has been questioned by Dowton and Austin (in press). Whitfield (1992) proposes a tentative composite hypothesis in which the Stephanidae are the basal group within the Apocrita and this has been confirmed by Dowton and Austin (in press) based on DNA sequence data. The remaining Apocrita have been divided into four major lineages, the Ichneumonomorpha, Vespomorpha (= Aculeata), Proctotrupomorpha, and Evaniomorpha (Rasnitsyn 1988, Whitfield 1992), but the last of these has not been supported by molecular evidence (Dowton and Austin 1994). The Ichneumonomorpha is divided into two major groups, the Ichneumonidae and the Braconidae, based on wing venation and the structure of the metasoma (Rasnitsyn 1980, 1988; Wahl 1986). The most likely outgroups outside of the Braconidae, to be used for character analysis of the Cardiochilinae should therefore be, in ascending order, the Xyelidae, Xiphydriidae, Orussidae, Stephanidae and Ichneumonidae. The relationships and supporting synapomorphies and plesiomorphies of these groups are discussed in the following section.

The synapomorphy that has been used to define the Xyeloidea as a monophyletic group, is the modified antennae with the third segment long and stout, followed by a filament of nine or more slender segments (Königsmann 1977). However, the Xyelidae have also been considered as a paraphyletic basal group in the

Hymenoptera, with the two major groups, the Macroxyelinae, that are presumed to have given rise to the Tenthredinoidea, and the Xyelinae + Madygellinae having given rise to all other Hymenoptera (Rasnitsyn 1969, 1988; Gauld and Bolton 1988). The placement of the Xyelidae remained unclear after an analysis of the structure of the metapostnotum undertaken by Whitfield *et al.* (1989), as the family possesses only plesiomorphic characters compared with the Tenthredinoidea. The synapomorphy for the Xyelinae is the position of the larval eye below the level of the antennae (Rasnitsyn 1988). In the present study *Xyela julii* (Brebisson) was used as a representative xyelid due to the availability of a specimen and its use in discussions on hymenopteran phylogeny by Gauld and Bolton (1988) and Naumann (1991).

The Xiphidriidae are supported by the following synapomorphies (Rasnitsyn 1988): pronotum with dorsal part very short except laterally; propleurae elongated; and larvae feeding on angiosperm wood. In the present study *Xiphydria camelus* (L.) was used as a representative xyphidriid. *Xiphydria* sp. has been illustrated in Gauld and Bolton (1988) and some character states could be checked directly from their figure of this genus.

Gibson (1985) and Whitfield *et al.* (1989) support the sister-group relationship of the Orussidae and the Apocrita based on the metapostnotum and associated structures and, in turn, found no evidence for a relationship between the Apocrita and Cephidae, as previously postulated by Rasnitsyn (1980). The Orussidae are well supported as a monophyletic group by the following synapomorphies: head with teeth in ring around median ocellus; female profurca with arms sessile and apart to house internal loop of ovipositor; ovipositor internal, and bent in long loop reaching prothorax (Rasnitsyn 1988). No published phylogeny is available for the Orussidae and so determining the basal genus was problematic. Orussid characters were assessed using *Guiglia sericata* Mocsary, as figured in Naumann (1991) and Gauld and Bolton (1988), and a specimen of *Guiglia schauinslandi* Ashmead which was available for examination in the WARI collection.

The systematics of the Ichneumonidae has been reviewed by Wahl (1986, 1988, 1990, 1991). In these revisions relationships among families are investigated and referred to without any concept of the family as a whole. Hand constructed phylogenies are proposed for tribal and generic classifications within subfamilies but the relationships among subfamilies are only eluded to on the whole. Gauld (1983) and Gauld & Holloway (1986) discuss the placement of the Labeninae which appears to be an ancient group and unique among ichneumonid subfamilies in having a Gondwanic distribution. The more basal tribes within this subfamily, Labenini and Groteini, are both well represented in the Australian and Neotropical regions (Gauld 1983). The genera Labena, Labium and Certonotus are common to both areas suggesting they arose prior to the separation of South America and Australia (Gauld 1983). Structurally, labenines exhibit many plesiomorphic features of ichneumonids, i.e. lack of specialised adult features and a primitive form of the final instar larvae (Gauld & Holloway 1986). Biologically they also show many of the so-called primitive features of ichneumonids, viz. they are ectoparasitoids and many are known to parasitise wood-boring hosts (Gauld & Holloway 1986). Due to their southern distribution, apparent basal position within the Ichneumonidae, and accessibility of specimens of apparently basal genera (Gauld 1983), the following taxa were used here for assessment: Certonotus tasmaniensis Turner, C. humueus Kriechbaumer, Labium longiceps (Cameron) and L. pilosum Turner and Wtrst.

Quicke and Achterberg (1990) have completed the most comprehensive and recent analysis of braconid subfamily relationships, although, there are significant problems with their work, as outlined by Wharton *et al.* (1992). The list of characters used in Quicke and Achterberg (1990), however, reflect the most extensive to date and provides a useful guide to characters and their states, if modified following Wharton *et al.* (1992).

Quicke and Achterberg (1990) place the Cardiochilinae as the sister group to the Khoikhoiinae, and the Cardiochilinae + Khoikhoiinae as the sister-group to the Microgastrinae. The groups basal to this (for the most consistent tree without weights)
are: Miracinae, Neoneurinae, Muesebeckiini, Ichneutinae, Aphidiinae, Mesostoinae + Ypistocerinae, Alysiinae + Opiinae, Rogadinae, Gnaptodontinae, Braconinae + Telengaiinae + Vaepellinae, Exothecinae + Hormiini, Apozyginae + Doryctinae, Betylobraconinae, Rhyssalinae, and Histeromerinae. Even though many problems are evident in this scheme, there is little dispute as to which are the more basal subfamilies. As outlined by Wharton et al. (1992), Quicke and Achterberg (1990) neglected to define a cyclostome lineage even though it was discussed in the text. The cyclostome subfamilies were defined as Doryctinae, Rogadinae, Braconinae, Telengaiinae, Ypistocerinae, Mesostoinae, Histeromerinae, and probably the Betylobraconinae, all of which are well basal to Cardiochilinae (Quicke and Achterberg 1990). Wharton et al. (1992) found it likely that the cyclostomes are a monophyletic assemblage even though the results of Quicke and Achterberg (1990) and Whitfield (1992) suggested this may not be the case. Whitfield (1992) discussed the phylogeny of the cyclostome groups based on both morphological and biological characters, but neglected to fully reference or discuss the reasoning for the outgroups chosen, even though the ichneumonids selected were chosen to represent putative basal taxa within the family. The taxa chosen by Whitfield did not coincide with the ideas presented by Gauld (1983). In this light, Whitfield (1992) did not reassess the character polarities of Quicke and Achterberg (1990) for characters 2, 5, 6, 9, 11, 14, 15, 19, 23, 25, 26, 27, 34 and 35 and these must be regarded as dubious. For outgroup comparison within the Braconidae, but outside the microgastroid complex of subfamilies the subfamilies used are listed in Table 5.3.

Within the microgastroid complex Whitfield and Mason (1994) described a new subfamily, the Mendesellinae, and placed it as the sister group to the Cardiochilinae + Microgastrinae + Khoikhoiinae based on a preliminary phylogenetic analysis. From the Mendesellinae two species of *Epsilogaster* Whitfield, *E. panama* Whitfield and *E. bicolor* Whitfield, were used hereto polarise characters, and they were combined as a representative outgroup taxon for some analyses.

The Microgastrinae, being the sister-group to Cardiochilinae + Khoikhoiinae, is

the most critical outgroup for determining the polarity of characters. This genera of this subfamily for Australasia was examined in detail by Austin and Dangerfield (1992) and this was used to assess in-group variability for microgastrines. Within the microgastrines *Prasmadon* Nixon has been postulated as the basal genus (Walker *et al.* 1990) and an undetermined species from Ecuador was available for study. *Microplitis demolitor* Wilkinson was also used because of it's medial placement within the microgastrines (Walker *et al.* 1990). The microgastrines are characterised by having 16 flagellomere segments and reduced distal wing venation by Austin and Dangerfield (1992), and Goulet and Huber (1993) use the following characters in their diagnosis of the subfamily for the world: fore wing with last abscissa of Rs not tubular; T1 with spiracle on laterotergite; occipital carina absent; antenna with 16 flagellomeres; apical margin of clypeus concave.

Braconidae	Microgastrinae	Prasmadon sp., (WARI)
		Xenogaster insolens (Wilkinson)
		Microplitis demolitor Wilkinson
	Mendesellinae	Epsilogaster panama Whitfield & Mason
		E. bicolor Whitfield & Mason
	Ichneutinae	Proterops nigripennis Wesmael, (male)
	Braconinae	Hybogaster australiensis (Ashmead)
Ichneumonidae	Labeninae	Ceratonotus tasmaniensis Turner
		C. humueus Kriechbaumer
		Labium longiceps (Cameron)
		L. pilosum Turner & Wtrst.
Orussidae		Guiglia sericata Mocsary
		G. schauinslandi Ashmead
Xiphydriidae		Xiphydria camelus (L.)
Xyelidae		Xyela julii (Brebisson)

 Table 5.3. Taxa used for multiple outgroup analysis represented in descending order of importance starting with the Microgastrinae.

5.3. Selection of characters

From a suite of 80 potential morphological characters 43 were chosen for the analysis of generic relationships. Thirty-six characters were excluded as they were too variable at species level, difficult to define as discrete states, were autapomorphic, or were identical across all ingroup species. Of the 43 'useful' characters, 29 were qualitative, and 14 were quantified as morphometric characters. The continuous data generated for morphometric characters, was assessed and assigned discrete states as outlined in Section 3.6.2 and Appendices A2 and A3. They were variously incorporated or excluded from the phylogenetic analysis in order to assess their effect on the resultant trees obtained. Characters 6 (glossal dimensions) and 7 (galeae dimensions) were initially included as morphometric characters but no reasonable way was found to quantify them and they were subsequently treated qualitatively.

5.4. Character discussion: polarity and order assignment

The character polarities and orders determined below by outgroup comparison were used to construct a hypothetical ancestor for the Cardiochilinae. Characters were employed in analyses using these polarities and orders, but they were also analysed unordered and unpolarised, and with polarities determined *a posteriori*, outgroup rooting of trees. A hypothetical ancestor was created based on multiple outgroup comparison for qualitative characters (see Table 5.4.1). Those characters not able to be ordered were left uncoded for the hypothetical ancestor. Morphometric data were assessed for the three nominated outgroups included in analyses. If the morphometric data for the two microgastrines fell within the same segment, this was used as the ancestral state. If the microgastrines conflicted, then the state for *Epsilogaster* was used as the ancestral state.

5.4.1. Qualitative characters

1. *Eyes pilosity.* Three character states are present in the cardiochilines a) long prominent eye setae, b) short sparse setae, and c) glabrous eyes. Outgroup comparisons

show that Xyelidae, Xiphydriidae, Orussidae, Ichneumonidae (Labeninae), and Braconidae (Braconinae) have glabrous eyes, and helconines have very reduced setae sparsely distributed between the ommatidia, as is the case in some cardiochiline species. Microgastrines have fully setose eyes along with the majority of cardiochiline species, however, Wesmaelella species have glabrous eyes. Achterberg (1988) used 'eyes often setose' as a synapomorphy defining the Cheloninae + Neoneurinae + Cardiochilinae + Khoikhoiinae + Microgastrinae. However, apparent reduction from very setose to sparsely setose eyes in some taxa show that this character is not as simple as indicated by Achterberg (1988). The Mendesellinae have eye setae present and conspicuous (Whitfield and Mason 1994). There are two potential ways of treating the presence or absence of eye setae; 1, absent (plesiomorphic) to present (apomorphic) with all the reductional variations considered as present, or 2, a transformation series from absent (glabrous) to sparse minute hairs increasing to long dense pilosity. The latter option was chosen for this study and coded as follows: pilosity absent (0), with minute sparse interommatidial setae (Figs 6.86, 6.87, 6.98, 6.101) (1), pilosity long and conspicuous (Figs 4.9, 7.35) (2).

2. Clypeal margin shape. The clypeal margin is mostly convex in the ingroup while microgastrines have the margin concave. Gauld (1985) examined this character for ichneumonids and considered that the weakly convex condition in many Ophioninae, Campoleginae and Cremastinae was plesiomorphic and any other development was apomorphic. However, due to the constant state found in the sister group this character was coded and polarised as: clypeal margin concave (0), convex(1).

3. Clypeal tubercles. Clypeal tubercles in cardiochilines are tooth-like structures on the medial clypeal margin, often occurring as a pair of teeth medially (Fig. 6.62). They occur in many species of Cardiochiles s. l. and Hartemita but not in any of the outgroups examined. Further, some ingroup taxa have the clypeal margin with the development of a central point or beak. This character was therefore coded as: clypeal margin without tubercles (0), with two tubercles or beak (1).

4. Malar carina. The malar carina is here referred to as the ventral part of the occipital carina in the malar region (Fig. 6.8). The occipital carina defines the outer part of the occipital region from the vertex and temples, and it being presence in the Braconidae is plesiomorphic as supported by outgroup comparison (Achterberg 1988; Quicke and Achterberg 1990). The majority of cardiochilines have the malar carina absent but some species have it present and joining the hypostomal carina. No cardiochilines possess the malar carina fully-developed as an occipital carina and so the reduced state is here regarded as plesiomorphic and its absence as apomorphic. Because of the reduced or absent condition of this character in some cardiochilines its derivation from either the occipital or hypostomal carina was difficult to determine. Wharton et al. (1992) point out the errors in Quicke and Achterberg's (1990) discussion regarding their coding of this character for subfamilies. Further the presence or absence of the hypostomal carina appears not to have been fully surveyed as Quicke and Achterberg (1990) code it as absent for the Cardiochilinae, whereas it is present in all of the species reviewed here. The mendesellines have no occipital carina, yet have a welldeveloped crenulate hypostomal carina. This character was therefore treated as unordered due to the uncertainty of its origin. Malar carina present (0), absent (1).

5. Shape of glossa. The apex of the glossa may be rounded (Fig. 4.5) or bilobed (Figs 4.6, 4.7). Wharton *et al.* (1992) suggest that they represent unrelated states based on the differing forms of glossal development in braconids and ichneumonids, and that the deeply bilobed form of the glossa is usually associated with elongated mouthparts. However, this character appears to be independent for cardiochilines as species with elongated mouthparts may have shallowly bilobed glossae, while others with small mouthparts may have the same bilobed state. The bilobed state may become more exaggerated with elongation of the mouthpart but not necessarily, as seen in *Asiacardiochiles minutus* Telenga which has an extremely elongate but shallowly bilobed glossa (Fig. 6.1). Quicke and Achterberg (1990) suggest that a distally rounded glossa is plesiomorphic and the bilobed state is apomorphic. Compared with the figures in Quicke and Achterberg (1990), the condition seen in cardiochilines is not bilobed in

the same way, but is cleft medially. Some cardiochilines have the glossa rounded to flat medially and this may be considered as a reversal of the bilobed state or the original plesiomorphic state. Mendesellines have what appears to be two layers that comprise the glossa, with the ventral layer rounded, and the dorsal layer with a medial cleft giving it a bilobed appearance. Gauld and Bolton (1988) state that the glossa is deeply bilobed when it is elongate in vespoids and some sphecids. The ichneumonids examined here have the glossa weakly bilobed. Therefore, in braconids the weakly bilobed state should be considered plesiomorphic and the rounded and deeply bilobed states treated as separate apomorphic states. Glossa weakly bilobed (Figs 6.1, 6.48, 6.81) (0), rounded (Fig. 4.5) (1), deeply bilobed (Fig. 4.6) (2).

6. Glossal elongation. Cardiochilines which have elongated galeae also have elongate glossae, except for Asi. minutus which has short galeae and an extremely elongate glossa (Fig. 6.1). Microgastrines and mendesellines have short glossae. This character was difficult to assess as a morphometric character as it would require dissection in order to fully measure its length. The glossa was coded as either short or long based on external examination. If it was hidden by or just visible below the mandibles it was considered to be short. If the glossa was visible by more than its breadth then it was coded as long. Outgroup comparison indicates that the elongate state is derived. Unfortunately the degree of 'shortness' could not be assessed as the glossae could not be dissected for many critical but rare specimens. Glossa short (Figs 4.5, 4.7, 6.22)(0), long (Figs 6.1, 6.14, 6.20) (1).

7. Galeae dimensions. Cardiochilines with elongate glossae may also have elongate galeae (Figs 4.6, 6.20). Hartemita have short mouthparts but very broad stout galeae. Mendesellines also have short broad galeae. Asi. minutus has an elongate glossa but short narrow galeae (Fig. 6.1). As for the glossae, dissection of the mouthparts is the only sure way of determining the length and width of the galea. Outgroup comparison shows this character is variable in all groups. In most species of cardiochilines they are either short (about as long as wide) but there appears to be two other states. The galeae may be either broadened but short, or lengthened. This

character will therefore be treated as unordered. Galeae short and narrow (Fig. 4.7) (0), short and broad (Fig. 4.5) (1), elongate (Fig. 4.6) (2).

8. Maxillary palp segmentation. Reduction in the number of maxillary palp segments from six, as in cardiochilines, to five and four has been considered to be the putative apomorphic trend within braconids (Mason 1981; Walker *et al.* 1990). Microgastrines have five-segmented palps (Mason 1981), all other braconid outgroups have six segments, while ichneumonids have five segments (Gauld 1985). In this study six segments was considered as plesiomorphic. Although outgroup comparisons here would suggest five segments as the plesiomorphic state, the larger number in most cardiochilines can logically be considered as more plesiomorphic. There are two possible ways that reduction from six to five may occur, either by fusion of segments five and six or by loss of a segment. In cardiochilines some species of *Tenthredoides sensu* Say have the fifth segment reduced to a plate, while *Bohayella* species have five segments and it is not known whether the sixth segment has been fused or lost. Maxillary palps 6 (Figs 4.5 - 4.6) (0), 5 (1).

9. Mandibular dentation. The majority of cardiochilines examined have bidentate mandibles (Fig. 4.9) while microgastrines have the mandibles unidentate or bidentate. Ichneumonids have bidentate mandibles (Gauld 1984, 1985) but show variation in tooth length. Bohayella appear to have unidentate mandibles although potentially this condition might be the result of mandibular wear. However, no unusual scarring was evident on the mandibles of such species suggesting that they are truly unidentate. Mandibles bidentate (0), unidentate (1).

10. Notauli. The notauli in cardiochilines are variable in size, depth, shape and sculpturing, as they are in all outgroups. Due to the complexity of different states possible only sculpturing was considered at generic level in this study. Notauli smooth (Fig. 6.2) (0), sculptured (Fig. 6.6) (1).

11. Scutal medial carina. Most cardiochilines have the medial scutum smooth (Figs 6.57, 6.65). One group of Australasian species have a medial longitudinal carina set in a furrow which is distinct and sometimes crenulate (Figs 7.1, 7.2, 7.5, 7.6). This

character was not found in any of the outgroups examined and its presence is considered to be apomorphic. Medial scutum carina absent (0), carina present (1).

12. Apical scutellar cup. A transverse carina and depression at the apex of the dorsal scutellum, anterior to the medial posterior band, forms a cup-shape in some cardiochilines (Fig. 6.80). Several microgastrines also have a similar development of the apical scutellum. This character was not found in any of the other outgroups and was considered to be apomorphic. Apical scutellum smooth (Fig. 6.64) (0), with cup-shaped depression (Fig. 6.80) (1).

13. Propodeal areola. Cardiochilines have the propodeal areola present and well-defined, variously reduced, to completely absent. Hartemita has only posterior diverging carinae (Figs 6.27, 6.31), while Wesmaelella, Neocardiochiles and Heteropteron have the areola completely absent and a relatively smooth propodeum (Figs 6.34, 6.50, 6.106). Some Australasian cardiochilines show slight reduction of the areola anteriorly (Figs 6.44, 7.30). The presence of a fully areolated propodeum is considered to be the plesiomorphic state as it is for microgastrines (Mason 1982, Walker *et al.* 1990, Austin and Dangerfield 1992) and the various reductional stages as a transitional series. Propodeal areola present ($\mathbf{0}$), slightly reduced anteriorly ($\mathbf{1}$), reduced to two posterior diverging carinae ($\mathbf{2}$), completely absent ($\mathbf{3}$).

14. Medial longitudinal furrow of propodeum. Cardiochilines that lack a propodeal areola have a further development of the propodeum: a propodeal furrow is present in *Heteropteron* and *Neocardiochiles* (Figs 6.34, 6.50) but not in any other cardiochiline genera. A similar character is also found in the Ophioninae (Ichneumonidae) where it was considered to be apomorphic (Gauld 1985). Propodeal medial longitudinal groove absent (0), present (1).

15. Epicnemial carina. Wharton et al. (1992) renamed the prepectal carina as the epicnemium on the basis that it is not related to the prepectus of symphytans or chalcidoids. These authors refer to Gauld (1985) who uses the term epicnemial carina, with the epicnemium being the region anterior to this carina. Mason (1981) treated the presence of this character as plesiomorphic and a trend of various reductional stages to

absent as apomorphic. Cardiochilines have the epicnemial carina either present or absent, while mendesellines do not possess such a carina. Microgastrines are variable for this character, and notably two closely related genera, *Microplitis* Wilkinson and *Snellenius* Westwood, have been separated on the presence or absence of this character (Austin and Dangerfield 1994). Walker *et al.* (1990) suggested that this character needed further examination. Gauld (1985) stated that the presence of a complete carina is plesiomorphic for ichneumonids and that in a number of taxa the lateral portion of the carina has been lost. Epicnemial carina present (0), absent (1).

16. Hind tibial apical projection. Pseudcardiochilus abnormipes Hedwig and Cardiochiles viator (Say) possess an apico-dorsal projection on the hind tibia which terminates in a concave cup-like truncation (Fig. 6.100). This character was not seen in any of the outgroups and is here considered to be apomorphic. Hind tibia without a projection (0), projection present (1).

17. Hind basitarsus flattening. The majority of ingroup and outgroup taxa have cylindrical hind basitarsi that are slightly flattened at the tibial tarsal joint (Figs 6.60, 6.76). Development of a slight dorsal ridge on the dorso-basal basitarsus is common in some ingroup and outgroup species. A completely flattened and laminate hind basitarsus is given as a synapomorphy for *Hartemita* (Figs 6.29, 6.33) (Dangerfield and Austin 1990). However, varying degrees of flattening are also found in several other cardiochilines which, otherwise, are very different to *Hartemita*. *Hartemita* represents the extreme form of the basal flattening observed in many other braconid subfamilies, and so this character can be polarised with the basitarsus cylindrical to ovoid in cross-section as the plesiomorphic state. Hind basitarsus cylindrical to ovoid (0), flattened and laminate (1).

18. Tarsal claw pectination. Mason (1981) considered simple claws to be the apomorphic state as found in most genera of microgastrines. Ichneumonids examined all possess pectinate tarsal claws. Some cardiochilines have pectinate tarsal claws but the apical tooth is broad and spatulate (Fig. 6.63). This state was not found in any ichneumonids or other braconid subfamilies examined and is here considered to be

apomorphic. Mendesellines have a broad lobe on the basal tarsal claw but otherwise they are not pectinate. This character is therefore treated unordered with evenly pectinate claws as the plesiomorphic state, as follows: tarsal claws evenly pectinate (Fig. 4.12) (0), pectinate with broad apical tooth (Fig. 6.63) (1), simple (2).

19. Presence of 1r in fore wing. Cardiochilines may have up to three radial cross veins (Fig. 4.13). Eady (1974 after Ross 1936) showed a hypothetical fore and hind wing for the Hymenoptera as having 1r and 2r present. Wesmaelella and some *Toxoneuron sensu* Say have a remnant part of 1r arising from 2-SR and 2r (commonly referred to as r) between 2-SRb and 3-SR, and extending to the pterostigma. Mendesellines have only 2r present. None of the designated outgroups have 1r present but Goulet and Huber (1993) showed that some symphytans (Megalodontidae, Siricidae, Tenthredinidae) and sphecids have 1r and 2r present. The sister group, Microgastrinae, have 1r absent indicating that this is the plesiomorphic state for the ingroup. But, by reference to the symphytan groups given in Goulet and Huber (1993), and by the methods outlined in Section 3.6.3 part 9, this character will be treated as: 1r present (0), absent (1).

20. Presence of 3r in fore wing. Some cardiochilines have a spectral vein arising from SR1 which is presumed to be homologous to 3r (Fig. 4.13). This vein is not found in any other groups examined and therefore must be considered to be apomorphic. 3r absent (0), present (1).

21. Discal cell elongation. In microgastrines the discal cell is 'equidimensional' in shape as it is in the mendesellines, i.e. the cell is not skewed along its width as often seen in the Cardiochilinae (Fig. 4.13). The Khoikhoiinae and members of other braconid subfamilies have the discal cell of varying shape. The elongation of this cell is the state found in the majority of cardiochilines, and depends on the lengths of 1-M+R and CU1b; it is peculiar to them and is therefore considered to be apomorphic. Discal cell equidimensional (0), elongate (1).

22. Bend in Rs of fore wing. This character has been used by past authors to define the Cardiochilinae (Mason 1981). However, it varies substantially in form

within the subfamily. For instance *Wesmaelella* has a brake in Rs and a sharp angle near its base (Fig. 4.16). Microgastrines have Rs straight and so the character is treated as: Rs straight (Fig. 6.4) (0), curved near base (Figs 6.7, 6.25) (1), or angled near base (Fig. 6.24) (2).

23. 2r-m in hind wing. Wesmaelella has the anterior half of 2r-m present in the hind wing, and it is the only genus in the ingroup to have this character (Fig. 4.16). Mendesellines and khoikhoiines show no sign of 2r-m, while the great majority of microgastrines (except *Miropotes* and *Austrocotesia*, Austin and Dangerfield 1992) have the vein present but completely spectral. Other braconids and ichneumonids examined have this vein absent. Absent (0), present in part and spectral (1), present in full, spectral or pigmented (2).

24. 2-1A in hind wing. This vein is either completely absent, present as a stump, present and extending half way to the wing margin, or reaching the wing margin. In mendesellines and microgastrines it is absent while in khoikhoiines it is either present or absent. Outgroup analysis therefore indicates the following states: absent or represented only as a stump (Figs 7.22, 7.24) (0), present in part (Fig. 4.14) (1), complete to wing margin (Fig. 4.16) (2).

25. Setosity of the ovipositor sheath. The ovipositor sheaths can be smooth and shining without hairs, evenly setose, or with setation only at the apex. This character varies greatly in the outgroups examined and could not be polarised. Sheaths evenly setose (0), setation apically (1), smooth or hairless (2).

26. Medial sclerotisation of the hypopygium. Some cardiochilines possess an evenly sclerotised hypopygium while others have it variably desclerotised. In species where the medially desclerotised and membranous part runs longitudinally along the hypopygium there is always an apical sclerotised bridge (Fig. 4.21) (refer Chapter 3). In microgastrines (e.g. Apanteles s. str. and Miropotes - see Austin 1990) this medial desclerotisation is different in form to that found in cardiochilines, as they have the apical point desclerotised as well. Therefore, superficially, this character appears to be convergently evolved in some members of the Cardiochilinae, Microgastrinae and

Acaelinae. Desclerotisation of the hypopygium has been discussed in detail by Austin (1990) where a medially desclerotised hypopygium is proposed to be apomorphic and the evenly sclerotised condition plesiomorphic. This is the reverse of that proposed by Mason (1981). Two degrees of desclerotisation occur in the cardiochilines. Both types have an apical sclerotised bridge while one has the ventral mid-line desclerotised (infolded in dried specimens) but the membranous part is not extensive enough to be folded fan-like in repose. In the other type the hypopygium is extensively desclerotised and membranous so that it appears to be folded fan-like (Figs 4.11, 6.68). These two states are sometimes difficult to discern but will be coded differently as follows: Hypopygium medially evenly sclerotised throughout (0), medially desclerotised and infolded but not membranous and folded fan-like medially (1), medially desclerotised, membranous and folded fan-like (2).

27. Apical sclerotisation of the hypopygium. Some Australasian cardiochilines have the apical third of the hypopygium desclerotised and membranous (Fig. 6.43), distinct from the form discussed in character 26. The hypopygium of *Khoikhoia townesi* Mason has slight medio-apical desclerotisation but not in the same way as that found in the cardiochilines. This apical desclerotisation was, therefore, considered to be apomorphic and treated as follows: the apex of hypopygium evenly sclerotised or with sclerotised bridge (0), apical border desclerotised and membranous (1).

28. Apical shape of the hypopygium. The apex of the hypopygium in cardiochilines can be either acutely pointed or truncate (right angled) to obtuse. Mendesellines have an acutely pointed apical hypopygium that may sometimes be truncated at the tip (Whitfield and Mason 1994). Microgastrines exhibit all states of this character. A short truncate hypopygium appears to associated with a short downcurved ovipositor and will be considered as apomorphic. Hypopygium pointed (Fig. 6.60) (0), pointed but truncate (Figs 6.105, 6.107) (1), square or obtuse (Figs 6.12, 6.28) (2).

29. Ovipositor curvature. The ovipositor and sheaths may be straight or downturned towards the apex, with the latter state often being associated with the ovipositor being extremely short. This character is variable in most outgroups examined, apart from the orussids which are moderately long and straight, and will be treated unordered and unpolarised. The degree of curvature was not measured and discrete states were assigned as: straight or gently curved (Figs 6.17, 6.23, 6.105) (0), strongly downcurved (Figs 6.12, 6.28, 6.82) (1).

5.4.2. Morphometric characters

Section 3.6.2 presents the method used to assess morphometric data and the method used for assigning discrete states, while figures 4.1 to 4.3 show how the measurements were taken. Appendix A2 gives the graphical representations of characters state assignment and appendix A3 is a table of means of morphometric data for each taxon.

30. Clypeal dimensions. The ratio of clypeal breadth to height varies so that the clypeus can be either broad (Fig. 7.32) or narrow (Fig. 7.7). Of the seven character states assigned here, six were equal to one standard deviation, and with the seventh state (state 6 below) having a gap greater than 0.5 standard deviation, isolating *Car. magnus* as autapomorphic (Appendix A2.1). Clypeal breadth to height: 0.99-1.41 (0), 1.42-1.84 (1), 1.85-2.27 (2), 2.28-2.70 (3), 2.71-3.13 (4), 3.14-3.35 (5), 3.36-3.57 (6).

31. Facial dimensions. The ratio of facial breadth to height varies so that the face can be either broad (Fig. 6.42)or narrow (Fig. 6.14). Eight segments were assigned with three unoccupied segments of 1 standard deviation (Appendix A2.2). Facial breadth to height: 0.87-1.36 (0), 1.37-1.86 (1), 1.87-2.36 (2), 2.37-2.86 (3), 4.37-4.86 (7).

32. Eye to temple ratio. In dorsal view the ratio of the length of the eye to the length of the temple from the eye varies so that the temples may be long (Fig. 6.95) or short (Fig. 6.77). All segments were of one standard deviation size (Appendix A2.3). Eye to temple ratio: 0.46-0.64 (0), 0.65-0.82 (1), 0.83-1.01 (2), 1.02-1.19 (3), 1.2-1.38 (4), 1.39-1.56 (5).

33. Occipital depth. The depth of the occipital excavation in dorsal view varies with respect to the length of the head. All segments were of one standard deviation size

(Appendix A2.4). Occipital depth to length of dorsal head: 0.07-0.18 (0), 0.19-0.30 (1), 0.31-0.42 (2), 0.43-0.54 (3), 0.55-0.66 (4), 0.67-0.79 (5).

34. Scape dimensions. The ratio of length to breadth of the scape varies considerably so that the scape may be elongate or short and broad. All segments were of one standard deviation size (Appendix A2.5). Scape length to breadth: 0.56-0.81 (0), 0.82-1.07 (1), 1.08-1.33 (2), 1.34-1.59 (3), 1.6-1.85 (4), 1.86-2.12 (5).

35. Antennal separation. This is defined as the width between the antennal sockets divided by the width of a single socket and it varies so that the sockets are widely separated (Fig. 6.75) or close together (Fig. 6.20). All segments were of one standard deviation size (Appendix A2.6). Antennal separation: 0.13-0.43 (0), 0.44-0.74 (1), 0.75-1.05 (2), 1.06-1.35 (3), 1.36-1.68 (4), 1.68-1.99 (5).

36. Antennal segmentation. The number of antennal segments is variable for cardiochilines, but fixed for the microgastrine which have 18 segments. All segments were of one standard deviation, with one unoccupied segment separating the microgastrines from the cardiochilines (Appendix A2.7). Antennal segmentation: 18 (0), 26-29 (2), 33-37 (3), 38-44 (4), 45-48 (5), 52 (6).

37. Scutellar sulcus dimensions. The scutellar sulcus can be broad and short (Fig. 6.70) or narrow and long (Fig. 6.77), but the width to length of the sulcus varies in cardiochilines and all outgroups. Character states (2) and (3) are of uneven size and incorporate outlying taxa separated by > 0.5 standard deviation from the other taxa (Appendix A2.8). Scutellar sulcus width to length: 1.9-3.3 (0), 3.4-4.8 (1), 4.9-6.5 (2), 6.6-7.6 (3), 7.7-8.3 (4), 8.4-9.9 (5).

38. Stigmal dimensions. The stigma of the fore wing varies in width to length making it either narrow (Fig. 6.109) or broad (Fig. 6.46). Segment (2) was extended to incorporate outlying extremes separated by > 0.5 standard deviation from the other taxon in segment (3) (Appendix A2.9). Stigmal width to length: 2.0-2.71 (0), 2.72-3.43,(1) 3.44-4.2 (2), 4.21-4.87 (3), 4.88-5.5 (4), 5.6-6.3 (5).

39. *Hamuli number.* The number of hamuli on the fore wing was coded differently to all other morphometric characters. With only a limited range of discrete

whole values, it was easier to code this character as separate numbers. However, some specimens examined were polymorphic, i.e. hamuli number varied between wings, and so states were grouped together to deal with this variation (Appendix A2.10). Hamuli number: 3(0), 4, 5(1), 6(2), 7, 8(3), 9(4).

40. Shape of T1. Most cardiochilines have the same basic form of the first metasomal tergite T1, with a basal stem and an apical bulb forming a Y-shaped groove (see Section 4.4.5), but this may vary from long and narrow (Fig. 6.10) to short and broad (Fig. 6.44). Khoikhoiines have a percurrent medial longitudinal groove. Bohayella have T1 elongate and very narrow with indistinct lateral margins (similar to the microgastrine, Wilkinsonellus Mason and are unlike any other cardiochilines examined. Heteropteron also has an elongate T1 but it is broadened apically. All segments were of one standard deviation size (Appendix A2.11). T1 length to width 0.1-0.9 (0), 1.0-1.8 (1), 1.9-2.7 (2), 2.8-3.6 (3), 3.7-4.5 (4), 4.6-5.4 (5), 5.5-6.4 (6).

41. Median field of T2. The length to width of the second metasomal tergite varies greatly in the ingroup (Figs 6.44, 6.49). Character state segments (3) and (4) are of uneven size due to > 0.5 standard deviation gap in segment (4), so the lower extreme taxa in this segment were incorporated into segment (3) (Appendix A2.12). Median field of T2 length to width: 0.07-0.29 (0), 0.3-0.52 (1), 0.53-.75 (2), 0.76-1.0 (3), 1.01-1.22 (4).

42. Ovipositor sheath length. Mason (1981) stated that elongate ovipositor sheaths (i.e. as long as hind tibia) are plesiomorphic and that much shorter or much longer sheaths are apomorphic states. The ichneumonids examined have the sheaths long and subequal to or slightly longer than the hind tibial length. However, in several subfamilies the sheaths are much reduced in length (Gauld 1984). Some cardiochilines have short sheaths but none have them greatly elongate. Masons polarity is adopted here based on the mendeselline form being as long as the hind tibia. All segments were of one standard deviation size (Appendix A2.13). Ovipositor sheath length to hind tibial length: 0-0.21 (0) 0.22-0.51 (1), 0.52-0.81 (2), 0.82-1.11 (3), 1.12-1.42 (4).

43. Ovipositor sheath dimensions. The dimensions of the ovipositor sheaths can

be quantified as a ratio of their length to maximum breadth. This character does not vary in the same way as the length of the sheaths with respect to the hind tibial length, and appears to be an independent character. All segments were of one standard deviation size (Appendix A2.14). Ovipositor sheath breadth to length: 0.01-0.10 (0), 0.11-0.27 (1), 0.28-0.44 (2), 0.45-0.61 (3), 0.62-0.78 (4), 0.79-0.95 (5), 0.96-1.13 (6).

Table 5.4.1. Summary of character orders (X) and ancestral states (Y), where known, derived from the multiple outgroup analysis conducted in Section 5.3. Unordered characters (u) and ordered characters (0).

	123456789	1111111111 0123456789	222222222222 0123456789	. 3 3 3 3 3 3 3 3 3 3 3 4 4 4 4 0 1 2 3 4 5 6 7 8 9 0 1 2 3
x	0?0 0000?0	1000000000	00000020000	021102101001?30
Y	0000000000	u 0 0 0 0 0 0 0 0 0 0) 0 0 0 0 0 u 0 0 u u	. u u u u u u u u u u u u u u u u u u u

5.5. PAUP analyses

5.5.1. Introduction

The data matrix (Appendix A4) of character states for the Cardiochilinae, outlined in Section 5.4, was coded for the taxa given in Table 5.2. This section introduces the analyses discussed in Section 5.6, used in the construction of the generic classification for the Cardiochilinae, and investigates the effects of the morphometric data (see Section 5.4.2) on the analyses.

5.5.2. Comparison of different outgroups

Initial analyses were conducted to determine the effects of different combinations of outgroups, and assess the lengths and number of trees obtained for each combination. Tree length refers to the number of character state changes in the tree. Three outgroups were used: *Epsilogaster* Whitfield (Mendesellinae), *Prasmadon* Nixon (Microgastrinae), and *Microplitis demolitor* Wilkinson (Microgastrinae). When conducting analyses in PAUP, a reference taxon must be specified as a starting point for the addition sequence. For the outgroups used here one was always designated as the

reference taxon. Results for the various combinations of outgroups showing the lengths of the most parsimonious trees are given in Table 5.5.1, along with the number of trees retained for each analysis.

These results show that *Epsilogaster* defined as the only outgroup provided a single most parsimonious tree (length 374), that was shorter than all other solutions using other outgroups or combinations of outgroups. The format used in this analysis is referred to hereafter as 'Analysis A'. The next most parsimonious result was obtained using *Prasmadon* as the only outgroup defined (length 376) (referred to as 'Analysis B'), followed by *Microplitis* and the various combinations of these outgroups (lengths 384 to 397).

Table 5.5.1. Summary of selected phylogenetic results showing different combinations of outgroups (reference taxon underlined) tested in preliminary analyses, giving tree length (L) and number of trees retained (N).

Outgroup(s)		L	N
<u>Epsilogaster</u> + Prasmadon + Microplitis demolitor		397	12
<u>Prasmadon</u> + M. demolitor		387	183
<u>Epsilogaster</u> + Prasmadon		386	3
Microplitis demolitor		384	4
<u>Epsilogaster</u> ('Analysis A')		374	1
<u>Prasmadon</u> ('Analysis B')	ě.	376	28

The initial analyses conducted utilised the 'factory' default settings of PAUP 3.1.1, however, Swofford (1993a) has provided a number of different addition sequences for this version of the program and states that no one strategy works best for all data sets, and that the best approach is to try as many alternatives as possible (see Section 3.6.6). Three addition sequences were tested for Analysis A with 'simple' producing a single tree of length 374, 'closest' producing 288 trees of length 375, and 'asis' producing 4505 trees of length 375, indicating that the simple addition sequence was the best for this data set.

These addition sequences affected the structure of the starting tree and, subsequently, also the structure of the final trees obtained, while using the same branch swapping algorithm (TBR). Ideally, different addition sequences should be tested each time the data matrix is altered in some way, e.g. when different outgroups are deleted or included. Also, this should be taken into account when assessing the results of PTP and T-PTP tests (see Section 5.7).

Further analyses were conducted with all outgroups removed. These defaulted the first taxon in the matrix, *Bohayella toxopeusi* sp. nov., as the reference taxon, and the relationships for this species were, therefore, not clearly resolved (see 'simple addition sequence' Section 3.6.6). This resulted in 16 shorter trees of length 365 (less than Analysis A due to the smaller number of taxa), the strict consensus of which had a Rohlf Consensus Index (RCI) of 0.158, indicating that there was little agreement between the shortest trees found. In order to overcome the problem of defaulting to an ingroup as the reference taxon, the states for the hypothetical ancestor outlined in Table 5.4.1 were used as the reference taxon. This analysis was of a different format and the 'simple', 'closest' and 'asis' options were retested. The asis option yielded the most parsimonious solution of 405 trees of length 377. The analysis using the hypothetical ancestor with *a posteriori* nominated character polarities and orders gave 168 trees of length 391, and hereafter is referred to as 'Analysis C'.

5.5.3. Comparison of morphometric and qualitative data

Qualitative and morphometric characters were analysed separately for Analysis A in order to illustrate the way each affects the resultant trees, as discussed in Section 3.6.2. When the qualitative and morphometric data were analysed independently the results were inconclusive, producing a 'tree-buffer overflow' (Swofford 1993a) for each. That is the number of trees exceeded the maximum number able to be saved in memory and the effectiveness of the search was diminished. When this maximum trees limit was reached, no shorter trees were found so the number of trees (N) simply reflects the limit reached, i.e. 3000 in each case. When the qualitative and morphometric data sets

were combined the result was significantly different in that only one shortest tree was found, indicating that there is substantial support between the two sets of data (see Table 5.5.2).

Table 5.5.2. Results of qualitative and morphometric data analysed
separately and together for Analysis A, showing length (L) and
number of shortest trees (N).

Analysis A	L	N	
Qualitative	116	3000	
Morphometric	212	3000	
All Characters	374	1	

5.6. Results of PAUP analyses and formation of a generic classification

Following the various analyses to find the most parsimonious tree for the available data, three are here discussed in detail. These analyses were selected to represent: 1, the shortest trees obtained, which used *Epsilogaster* defined as the outgroup with characters unordered and unpolarised, i.e. Analysis A (Fig. 5.1); 2, the shortest trees obtained from an outgroup representing the sister group to the Cardiochilinae, the Microgastrinae, which was found with *Prasmadon* defined as the outgroup with characters unordered and unpolarised, i.e. Analysis B (Fig. 5.2); and 3, the result obtained when polarities and orders were enforced using the hypothetical ancestor as the reference taxon (see Table 5.4.1), i.e. Analysis C (Fig. 5.3).

The results for these analyses are given in Table 5.6.1 and figures 5.1 - 5.3, and the indices listed can be used in combination to infer the amount of homoplasy in the resultant trees and which result is statistically better (see Section 3.6.5).

Comparison of tree length shows that using *Epsilogaster* as the only outgroup (Analysis A), produces the shortest tree of length 374, as stated above (Fig. 5.1), followed by *Prasmadon* as the only outgroup defined (Analysis B) with 28 trees of length 375 (Fig. 5.2), and the hypothetical ancestor with polarity and order enforced (Analysis C) with 168 trees of length 391 (Fig. 5.3).

Yeates (1992) suggested that autapomorphies should be included in analyses and are often removed without warrant. The inclusion of autapomorphies in this data set was a result of the removal of outgroup taxa from the matrix. Autapomorphies effect the calculation of homoplasy in a cladogram by adding extra steps required for the same topological result (Colless 1981; Brooks *et al.* 1986). So, if characters were uninformative (i.e. autapomorphic) they were excluded from the analysis (see Section 5.2). Analyses A and C rendered characters 2 and 6 uninformative and they were therefore excluded. For Analysis B only character 6 was excluded leaving one extra character than in Analyses A and C. However, Analysis B, with character 6 deleted still gave 28 trees but of length 373, 2 steps shorter than with character 6 included and one step shorter than Analysis A for the same character set. Also, the consensus tree topology remained unchanged with the deletion of character 6. If uninformative characters were not excluded from the analyses, Analysis A still produced one tree of length 375, while Analysis B had 28 trees of length 376. Thus, characters 2 and 6 have no effect on the tree topology.

Table 5.6.1. Summary of results obtained for analyses A, B and C showing shortest length (L), number of most parsimonious trees (N), homoplasy index (HI), retention index (RI), rescaled consistency index (RC), f-ratio and Rohlf's consensus index (Rohlf's CI).

Analysis	L	N	Щ	RI	RC	f-ratio	Rohlf's CI
А	374	1	0.733	0.611	0.165	0.3984	-
В	375	28	-	-	÷	-	с÷
B: strict consensus	380	2	0.726	0.609	0.168	0.5842	0.917
B: majority rule	375	-	0.723	0.616	0.172	0.5842	0.998
С	391	168			L.	UR.	72
C: strict consensus	391	2	0.742	0.588	0.153	0.6634	0.815
C: majority rule	380	-	0.734	0.605	0.162	0.5967	0.990

Significantly many of the same monophyletic groups appear in all three analyses, only their relationships to each other change. Those genera which remained monophyletic in all analyses conducted were *Bohayella*, *Cardiochiles s. str.*, *Hartemita*, *Hymenicis* gen. nov., *Toxoneuron* and *Wesmaelella* (Figs 5.1 - 5.3). It should also be noted that Hauser and Presch (1991) discussed the functions of ordered characters and stated that the practice of ordering multistate characters may be inappropriate when congruence between characters is used to assess character evolution. From this data set the unordered hierarchy of the cladogram disagrees with the *a priori* hypothesis of order based on multiple outgroup comparison. Therefore, the ordering of characters, as in Analysis C, would be inappropriate based on the ideas presented by Hauser and Presch (1991).

When the hypothetical ancestor with predetermined character polarities and orders was used as the only outgroup (Analysis C), the effect on overall tree topology was quite dramatic with respect to the results of Analyses A and B. In particular a number of clades are seen to have shifted position relative to each other (e.g. compare placements of *Wesmaelella*, *Hymenicis* and *Toxoneuron* - Figs 5.1 - 5.3), but significantly, this involved nodes that were unimportant for the recognition of these genera as monophyletic groups. Further, compared to Analyses A and B, the shortest trees generated from Analysis C showed less resolution in some of the terminal groups (e.g. polytomy for *Toxoneuron* and unresolved relationship between *Neocardiochiles* and *Heteropteron*). The monophyly of *Pseudcardiochilus*, *Austerocardiochiles* gen. nov. and *Polycardiochiles* gen. nov. that is fixed in Analyses A and B is lost in Analysis C (Fig. 5.3).

In Analysis A, most clades are well supported, and these correspond to most of the extant and several previously synonymised genera (Fig. 5.1), viz. Bohayella, Cardiochiles s. str., Hartemita, Pseudcardiochilus, Toxoneuron and Wesmaelella. Other extant or synonymised genera are recognised only by single species on the tree, viz. Asiacardiochiles, Heteropteron, Neocardiochiles and Psilommiscus and these remain valid in that they are separated from Cardiochiles s. str., but their monophyly remains untested with respect to the species they contain. Significantly, species of Tenthredoides included in the analysis fall out within the clade which includes all of the

Toxoneuron species, while the only Psilophthalmus species comes out with Wesmaelella. Eight clades do not correspond to any previously recognised genera. Three of these are represented by single species (described in Chapter 6 as Brevicardiochiles gen. nov., Circocardiochiles gen. nov., and Leptocardiochiles gen. nov.); four represented by groups of species (viz. Austerocardiochiles, Hymenicis, Polycardiochiles and Retusigaster gen. nov.); while three basal species form a These three species (viz. areyongensis, turneri and paraphyletic group. eremophilasturtiae) appear superficially to be similar morphologically and are endemic to Australia. They can be constrained together with a two step increase in tree length and the resultant clade is supported by the following characters: short broad stigma (2.0 - 2.7 times as long as wide - character 38), and shallow eye:temple ratio (0.46 - 0.64 times as deep as length of head - character 33). One other character that supports this clade is the form of T1 (character 40), in that all species have a similar length to width (0.8 - 1.1 times as long as wide). These taxa were separated in Analysis A by only two morphometric characters, i.e. the ratios of T1 length to width and facial height to width. However, the arbitrary nature of assigning discrete states to these characters has meant that they fall into different groups, even though they are very similar for the three species. Because several characters rendered these species easily identifiable from all others in the analysis a new genus, Latitergum gen. nov. is proposed to accommodate them (see Section 6.3.10), rather than describe them as three separate new genera. However, it should be noted that these species never form a monophyletic group in any of the analyses conducted and pending further investigation of new characters, they should be treated tentatively as a basal paraphyletic holding genus.

The exclusion of the monotypic Circocardiochiles from *Cardiochiles s. str.*, its sister group, is based on the former having shortened mouthparts and broad ovipositor sheaths unlike *Cardiochiles s. str.*

It should be noted that all trees have high levels of homoplasy and low levels of rescaled consistency (Table 5.6.1) as is generally the case for matrices with large numbers of taxa and fewer characters than taxa. The low f-ratio of Analysis A also

indicates that this is the better result of the three.

Based on¢ these results the tree which defined *Epsilogaster* as the outgroup (Analysis A), was used as the basis for the classification proposed for the genera of Cardiochilinae. The generic classification in figure 5.5, was obtained from including the type species of the proposed genera, for the one tree obtained in Analysis A. Figure 5.5 is a phylogram generated by PAUP 3.1.1, showing relative lengths of branches which gives the staggered form of the tree.

5.7. Testing for significance of results

As stated above and indicated by the indices given in Table 5.6.1, minimum length trees derived from the present analyses have high levels of homoplasy. Therefore, testing for significance of the cladistic or hierarchical structure and information was imperative. Both PTP and T-PTP tests were employed as it is possible to have significant cladistic information (indicated by PTP) and have no definitive topology implied by the data (indicated by T-PTP) (Faith and Ballard 1994).

PTP tests were undertaken on the data sets used for analyses A, B and C. Analyses for only twenty randomisations were undertaken due to the large amount of time required for each analysis (Table 5.7.1). All analyses have 'Q' = 1.32 and PTP < 0.05 (see Table 5.7.1), indicating that there is significant information in each of the data sets, and that the trees derived from each analysis were not capable of being generated by chance alone.

Analyses	Actual L	Random L	РТР	'Q'	Time
А	374	520-562	0.01	1.32	216:59:38.6
В	375	529-546	0.01	1.32	223:21:42.3
С	391	557-575	0.01	1.32	123:42:11.7

Table 5.7.1. Summary of PTP results.

T-PTP testing was first undertaken as an "all-groups" test (Faith and Ballard 1994) for Analysis A as this had generated the shortest tree and had the best consistency indices (Table 5.6.1). Secondly, the clade (node 105 in Fig. 5.1) containing the type species for *Cardiochiles*, *Car. saltator* (Fabricius) was tested to determine the monophyly of the genus in the strict sense.

The 'allgroups' test was used to determine how many nodes were supported by the data based on the number of steps taken to change the constraints tree and test the null hypothesis that 'the structure of each and every grouping contained in the constraint tree from Analysis A appear by chance alone'. This test used the constraint tree, given for the most parsimonious result from Analysis A, with all of the internal structure preserved. Fifty replicates were undertaken for this analysis and the results (Table 5.7.2) show the null hypothesis should be rejected ('Q' = 1.708, T-PTP < 0.05), indicating that at least one node somewhere in the tree (critical length difference = 1) is supported by these data. This test confirms, again, that there is significant hierarchical information in the tree as did the PTP test. It also indicates that the relationships of the resultant monophyletic groups proposed to represent genera in figure 5.4 cannot be clearly defined for the whole tree. Because the data matrix contained more taxa than characters (61 taxa and 43 characters), there was insufficient information to resolve all parts of the tree and some nodes were of zero or near-zero length.

Table 5.7.2.Summary of T-PTP results for 'allgroups' analysis which
constrained all of the structure in the single most parsimonious
tree from Analysis A, and Cardiochiles s. str. which was
constrained without internal structure.

Analysis	Critical Difference	Random Difference	'Q'	T-PTP	Time taken Hrs:Min:Sec
'all-groups'	1	129-171	1.708	0.02	286:34:15.5
Cardiochiles s. str. (node 105)	. 1	9-37	1.32	0.01	314:31:58.5

Node 105 (in Fig. 5.1), which represents the genus Cardiochiles s. str., was

tested for significant structure. This tested the null hypothesis that 'the tree containing the constraint defining *Cardiochiles s. str.* appears by chance alone'. Twenty replicates were undertaken for this analysis and the results (Table 5.7.2) show that the null hypothesis should be rejected ('Q' = 1.32, T-PTP < 0.05), indicating that the monophyly of this group is significantly supported by the data matrix.

Nodes, other than *Cardiochiles s. str.*, were also tested to determine the number of steps needed to remove the structure of their constraint as a monophyletic group. Ideally, T-PTP tests should be undertaken to do this, but, the excessive amount of computer time required for even one analysis precluded them from being undertaken in this study. Testing for critical length differences takes much less time and allows confidence of nodes to be tested based on length differences between constraint and non-constraint. The nodes examined are shown in Figure 5.1 and the results of these tests are summarised in Table 5.7.4 for each group being constrained together without any internal structure specified.

Table 5.7.4. Comparison of critical length differences for specific nodes fromAnalysis A which represent the critical groups containing the typespecies for genera, constrained without internal structure.

Node tested	Critical Group	Critical Length difference
62 63 67 70 78 85 94 115	Bohayella Hartemita Hymenicis Pseudcardiochilus Toxoneuron Austerocardiochiles Polycardiochiles South American group	1 4 2 1 2 1 1 1 2
116 79	All genera reduced eye setae	-2 1

A critical length with a positive difference indicate that a longer tree will change that group constrained to be monophyletic. However, those with negative length differences indicate that there are more parsimonious solutions than that proposed and, in such cases, the shorter trees were examined. Significantly, the genera proposed by nodes 62, 63, 67, 70, 78, 85 and 94, the clade defined by reduced eye setae (node 79), and the South American group of genera (node 115), gave positive results with critical length differences from 1 to 4 (Table 5.7.4), suggesting that these groups with greater critical length differences have support. The only negative result obtained was from constraining all proposed generic groups without internal structure (node 116). This reflects the number of steps needed to constrain the proposed polyphyletic holding genus of three Australian species, *Latitergum* (see Sections 5.6 and 6.3.10). The tree from the analysis which constrains *Latitergum* as a monophyletic group, keeps all other groups together as in Analysis A, and has a length of 376.

5.8. Discussion of classification

Wiley *et al.* (1991) outlined three rules for erecting classifications based on phylogenetic results. These are: only monophyletic groups should be considered; the classifications should be logically consistent with phylogenetic hypotheses; and each classification must express sister-group relationships among taxa. Although logical, these rules could not be applied here because the results of several analyses were used to develop a generic level classification (Fig. 5.4), and the position of several clades differed between the analyses. Although the majority of genera proposed represent monophyletic groups, these groups were chosen at different levels within the cladogram (see nodes numbered in Fig. 5.1). This was done for the practical reason of wanting to retain as many of the currently and previously recognised genera as possible, so that a minimum number of taxonomic changes would be invoked. The pragmatic decision to describe a paraphyletic holding genus, *Latitergum*, was based on the need for further investigation of character states and a re-evaluation of morphometric data.

CHAPTER 5

Figures 5.1 to 5.4

Fig. 5.1. The single shortest tree of length 374 produced from Analysis A (see Section 5.5.2), which used *Epsilogaster* sp. (Mendesellinae) as the defined outgroup. All character were treated unpolarised and unordered. Proposed genera are bracketed on the right and the nodes numbered were those tested for significance in Section 5.7. The abbreviations refer to the species, *nigriceps* and *seminiger* originally described in *Tenthredoides* (*Ten.*), and *nigripennis* originally described in *Psilophthalmus* (*P.*). For tree statistics see Table 5.6.1.



Fig. 5.2. Strict consensus of 28 trees of length 376 produced from Analysis B (see Section 5.5.2), which used *Prasmadon* sp (Microgastrinae) as the defined outgroup. All character were treated unpolarised and unordered. Proposed genera are bracketed on the right. The abbreviations refer to the species, *nigriceps* and *seminiger* originally described in *Tenthredoides* (*Ten.*), and *nigripennis* originally described in *Psilophthalmus* (*P.*). For tree statistics see Table 5.6.1.



Fig. 5.3. Strict consensus of 168 trees of length 391 produced from Analysis C (see Section 5.5.2), which used the character states, orders and polarities for the hypothetical ancestor (see Table 5.4.1) derived from multiple outgroup comparison (see Section 5.4). The abbreviations refer to the species, *nigriceps* and *seminiger* originally described in *Tenthredoides (Ten.)*, and *nigripennis* originally described in *Psilophthalmus (P.)*. Proposed genera are bracketed on the right. For tree statistics see Table 5.6.1.



Fig. 5.4. Generic classification for the Cardiochilinae based on analysis A. This phylogram was derived from the type species of the proposed genera and outlines the polyphyletic nature of the endemic Australian genus *Latitergum*, gen. nov.



CHAPTER 6

Revision of Genera

6.1	Introduction to generic revision
6.2	Key to world genera of the subfamily Cardiochilinae
6.3	 Treatment of genera with included world species 6.3.1. Asiacardiochiles Telenga, stat. rev. 6.3.2. Austerocardiochiles, gen. nov. 6.3.3. Bohayella Belokobylskij 6.3.4. Brevicardiochiles, gen. nov. 6.3.5. Cardiochiles Nees, sensu stricto 6.3.6. Circocardiochiles, gen. nov. 6.3.7. Hartemita Cameron 6.3.8. Heteropteron Brullé 6.3.9. Hymenicis, gen. nov. 6.3.10. Latitergum, gen. nov. 6.3.11. Leptocardiochiles, gen. nov. 6.3.12. Neocardiochiles Szépligeti 6.3.13. Polycardiochiles, gen. nov. 6.3.14. Pseudcardiochiles, gen. nov. 6.3.15. Psilommiscus Enderlein, stat. rev. 6.3.17. Toxoneuron Say, stat. rev. 6.3.18. Wesmaelella Spinola
6.4	Species incertae sedis
Figure	es 6.1 to 6.110.
CHAPTER 6

6.1. Introduction

The genera treated in this chapter are the results of the phylogenetic analyses conducted in Chapter 5. Distribution and known host information has been included as well as the world species included for each genus and species *incertae sedis*.

5.2. Key to world genera of the subfamily Cardiochilinae (Based on females)

present, in part, in fore wing (Fig. 6.109); propodeum smooth, without	2(1).
medial furrow (Fig. 6.106) Wesmaelella Spinola	
absent in fore wing; propodeum with medial furrow at least anteriorly	
(Figs 6.34, 6.50)	

with 1a absent (Fig. 6.38); hid tibial claws simple Heteropteron Brullé

4(1) T1 short and broad at apex, < 1.1 x as long as apically broad (Fig. 6.44);
 stigma of fore wing broad < 2.6 x as long as broad (Fig. 6.46); scutum,
 scutellum and notauli smooth; median field of T2 poorly-defined,

rectangular, 0.3-0.5 x as long as broad (Fig. 6.44); 4 hamuli on hind wing; ovipositor long > 0.7 x length of hind tibia; 28-29-segmented antennae; body small with orange and black pattern (< 4.5 mm length) Latitergum, gen. nov.

- - 7(6).

	with cup-like projection at apex, if projection slight then ovipositor sheaths
	smooth and polished Toxoneuron Say, stat. rev.
8(7).	Hind tarsal claws usually simple, if pectinate then T1 about 2.5 x as long as
	broad (Fig. 6.39)9
	Hind tarsal claws pectinate; T1 narrow and long, $> 3 x$ as long as broad (Fig.
	6.10) 11
9(8).	Hypopygium apically desclerotised and membranous (Fig. 6.43); glossa
	weakly bilobed at apex Hymenicis, gen. nov.
	Hypopygium evenly sclerotised throughout; glossa usually rounded at apex,
	if weakly bilobed then dorsal scutellum with apical cup-like pit (Fig. 6.80)
10 (9).	Dorsal scutellum with apical cup-like pit (Fig. 6.80); apex of hind tibia with
	slightly broad and flat projection (Fig. 6.83); hind basitarsus flattened in
	cross-section Retusigaster, gen. nov.
	Dorsal scutellum smooth, apex without cup-like pit (Fig. 6.70); apex of hind
	tibia variably produced, from extremely long and narrowing to a cup-like
	apex to slightly produced and pointed (Figs 6.72, 7.73, 6.76); hind
	basitarsus oval in cross-section Pseudcardiochilus Hedwig, stat. rev.
11(9).	Epicnemial carina present (Fig. 6.12); propodeal areola strongly-defined,
	carinate (Fig. 6.10) Bohayella Belokobylskij
	Epicnemial carina absent; propodeal areola present, at least in part, but not
	strongly carinate 12
12(11).	Hind basitarsus mostly cylindrical never laminate; propodeal areola complete;
	clypeal margin with two tubercles Brevicardiochiles, gen. nov.
	Hind basitarsus flattened and laminate (Figs 6.29, 6.33); propodeal areola
	reduced anteriorly (Figs 6.27, 6.31); clypeal margin pointed, convex or
	concave medially, without well-defined tubercles Hartemita Cameron
13(5).	Scutum with medial longitudinal carina present (Fig. 6.6); malar carina
	present (Fig. 6.8); occiput deeply excavate (Fig. 6.6); median field of T2

transverse lens-shaped (Fig. 6.6); hypopygium with medial longitudina
desclerotised and folded membranous area
Austerocardiochiles, gen. nov.
Scutum medially smooth; malar carina mostly absent (except in gwenae and
tibiator); occiput not deeply excavated; median field of T2 transverse bu
not lens-shaped; hypopygium either medially membranous or evenly
sclerotised 14
14(13). Glossa deeply bilobed at apex (Fig. 4.6); galea slightly elongate, visible 2 x
its breadth past mandibles (Fig. 6.20) Cardiochiles Nees, sensu stricted
Glossa only weakly bilobed at apex (Fig. 4.7); galea just visible beneath
mandibles
15(14). Glossa extremely elongated, reaching past fore coxae (Fig. 6.1); eye setae
sparse (Fig. 6.2) Asiacardiochiles Telenga, stat. rev
Glossa not elongated, only just visible below mandibles in anterior view; eye
setae dense 16
16(15) Hypopygium with medial longitudinal desclerotised area which may be eithe
infolded (but not wholly membranous), or membranous and folded fanlike
in repose (Fig. 6.68) Polycardiochiles, gen. nov
Hypopygium evenly sclerotised throughout 17
17(16). Ovipositor sheaths broadening to very broad apex, 0.3×10^{-10} x as broad as long
(Fig. 6.23) Circocardiochiles, gen. nov.
Ovipositor sheaths long but not broadened, $<0.2 \text{ x}$ as broad as long; body
very small and black in colour (Figs 6.48, 6.49)
Leptocardiochiles, gen. nov

6.3 Treatment of Genera

6.3.1. Genus Asiacardiochiles Telenga, stat. rev.

(Figs 6.1 - 6.5)

Asiacardiochiles Telenga 1955 Fauna SSR 5 (4): 236. [Type species, by monotypy, Asiacardiochiles minutus Telenga] Transferred from Cardiochiles sensu lato. Synonymised with Cardiochiles sensu lato by Sharkey and Mason, 1986: 300.

Diagnosis

Body small and predominantly black in colour; eyes with conspicuous sparse pilosity; galea visible past mandibles, as long as basally wide, blunt at apex; glossa extremely elongate reaching past fore coxae, 4-5 x as long as height of eye, apex slightly bilobed; clypeal margin with two well-developed tubercles; occiput in dorsal view shallowly excavated; malar carina absent; notauli strongly indented, smooth, meeting posteriorly; scutellar sulcus narrow; sternaulus smooth and shallow; propodeum about 2 x as broad as long, areola moderately well-defined, may be weak anteriorly, spiracles circular; second submarginal cell short; tarsal claws pectinate with three broad teeth and long apical tooth; T1 2.0 x as long as apically broad; median field of T2 not defined; hypopygium pointed at apex, evenly sclerotised throughout; ovipositor sheaths long, sub-equal to length of hind tibia, obliquely truncate at apex, setose in apical two-thirds.

Host

Unknown.

Distribution

Few specimens are known for this genus all of which have been collected in Kazakhstan and Turkmenistan in the plains of the south central Palaearctic region east of the Caspian Sea.

Comments

This genus is here brought out of synonymy with *Cardiochiles* based on the characters outlined in the diagnosis and the results of the cladistic analyses. Its relationships with other genera are unresolved given the inconclusive position of the genus in the cladistic analyses outlined in Chapter 5. *Asi. minutus* changed position when different outgroups are employed however it remained associated with *Latitergum*, the paraphyletic genus from Australia, and is probably related to this. *Asiacardiochiles* is only known from the type species.

World species included in Asiacardiochiles

Asi. minutus Telenga, 1955: 5. Distribution: Kazakhstan, Turkmenistan.

6.3.2. Genus Austerocardiochiles, gen. nov.

(Figs 6.6 - 6.9, 7.1 - 7.7)

Type species: Austerocardiochiles pollinator sp. nov.

Description

Body. Medium-sized, stout or robust, either black or yellow to orange and black, well-sculptured, often with infuscate patterned wings.

Head. Eyes conspicuously pilose; two clypeal tubercles present; clypeus 1.85 - 2.7 x as broad as high; face 1.37 - 1.86 x as broad as high; eye:temple ratio 1:0.65 - 1:1.19; malar carina present; glossa short, weakly bilobed at apex; galea short, sometimes broad; maxillary palps six-segmented; mandibles bidentate; occiput 0.31 - 0.79 x as deep as length of head; antennae separated by 0.5 - 1.0 x width of antennal socket; antennae with 33 - 48 segments; scape 1.1 - 2.0 x as long as broad.

Mesosoma. Notauli crenulate, well-defined, meeting posteriorly; scutum with medial longitudinal carina set in a furrow; scutellar sulcus variable in shape, 3.4 - 9.9 x as broad as long; apical scutellar cup mostly absent, sometimes present; propodeal areola

complete; propodeum without medial longitudinal furrow; epicnemial carina present at least ventrally.

Legs. Hind tibia without apical projection; hind basitarsus may be slightly flattened but mostly cylindrical in cross-section; tarsal claws pectinate.

Wings. Fore wing with 1r absent, 3r mostly absent, discal cell elongate, stigma 2.7 - 4.2 x as long as wide, Rs curved or angled but never straight; hind wing with 2r-m absent, 2-1A, 3 - 7 hamuli present.

Metasoma. T1 1.0 - 3.6 x as long as broad; median field of T2 0.07 - 0.52 x as long as broad, lens-shaped; ovipositor sheaths evenly setose, 0.2 - 0.8 x as long as hind tibia, 0.1 - 0.4 x as broad as long, straight along length; hypopygium pointed at apex, medially desclerotised and membranous, with apically sclerotised bridge.

Host

Unknown.

Distribution

This genus is widely distributed and most predominant in the southern hemisphere. It is known from Australia, Japan, Philippines, Laos and Africa and is restricted in Australia to remnant sub-tropical rainforest regions.

Comments

Austerocardiochiles is a distinctive genus, most notably because of the longitudinal carina set in a furrow on the medial scutum and the presence of a malar carina. It also has the epicnemial carina developed and the medial hypopygium longitudinally desclerotised. Its relationships are generally unclear (see Chapter 5). Though not confined to Australia, it is most speciose in the Australasian region. Aus. rufithorax Enderlein from Gambia is tentatively included in this genus but does not have the same prominent development of the malar carina as in other species. Three undescribed species are known from Japan (BMNH), Laos (BPBM) and the Philippines

(BMNH). It is named because of its sculptured or rough, harsh appearance from the Latin 'austerus'.

World species included in Austerocardiochiles

Aus. callemondah, sp. nov.

Aus. deetoo sp. nov.

Aus. exleyae, sp. nov.

Aus. morulus, sp. nov.

Aus. pollinator, sp. nov.

Aus. rufithorax Enderlein. Distribution: Africa- Gambia, Guinea, Nigeria, Sierra Leone. Host: unknown.

6.3.3. Genus Bohayella Belokobylskij

(Figs 6.10 - 6.12, 7.8 - 7.13)

Bohayella Belokobylskij, 1987: 302. [Type species, by original designation,Bohayella tobiasi Belokobylskij, 1987.]

Diagnosis

Small, black or black and yellow-orange with lightly to moderately infuscate apex of fore wing; eye pilosity conspicuously present or reduced to short sparse interommatidial setae; clypeal tubercles absent; malar carina absent; glossa short, weakly bilobed at apex; galea short and broad; maxillary palps reduced to 5 segments; mandibles either bi or unidentate; notauli deep, broad and crenulate; scutum with medial carina absent; scutellar sulcus broad and deep; apex of scutellum without cup- shaped carina; propodeal areola complete; epicnemial carina present and well-defined; hind tibia without apical projection; hind basitarsus cylindrical; hind tarsal claws pectinate with the first tooth broad; fore wing with 1r and 3r absent, discal cell shortened, Rs curved, stigma 2.7 - 3.4 x as long as deep; hind wing with 2-1A absent; T1 elongate, 4.6 - 6.3 x as long as broad, with medial raised node at base forming a socket for ball like projection of T2; T2 with medial ball-like projection at base, joined to socket of T1; ovipositor sheaths short, < 0.2 x as long as hind tibia, evenly setose, down-turned along length; hypopygium evenly sclerotised throughout, square or obtusely angled at apex.

Host

Boh. adina has been reared from larvae of Dirades theclata Guenée (Uraniidae: Epipleminae) from New Forest, India (Beeson and Chatterjee 1935).

Distribution

The genus is distributed from the southern central Palaearctic region to the Oriental region. There is no recorded overlap of species. *Boh. adina* occurs in India and Malaysia, *Boh. tobiasi* occurs in Russia and *Boh. toxopeusi* is known from only one specimen from New Guinea.

Comments

This genus is closely related to *Hartemita* and *Brevicardiochiles* but can be easily distinguished from them by the well-developed epicnemial carina, maxillary palps reduced to 5 segments and the shorter broader stigma of the fore wing. It can also be distinguished from *Hartemita* by the fully-developed propodeal areola, cylindrical hind basitarsus, and pectinate tarsal claws. This is the only genus in which some species show reduction of the mandibular teeth. An undescribed species from the Philippines has the mandibles meeting medially as blunt unidentate stumps. Some undescribed species from Borneo and the Philippines (BPBM), not included in the phylogenetic analysis (Chapter 5), have reduced eye pilosity but are identical to other *Bohayella* in all other respects. These species could not be placed into *Bohayella* but may either represent a close sister-group or eventually extend the limits of the genus based on the more conspicuous eye pilosity.

World species included in Bohayella

Boh. tobiasi Belokobylskij 1987: 302. Distribution: Russia. Host: unknown. Boh. toxopeusi, sp. nov. Distribution: New Guinea. Host: unknown. Boh. adina (Wilkinson), 1930: 486. Comb. nov. Transferred from Cardiochiles s.1. Distribution: India and Malaysia. Host: Dirades theclata Guenée(Uraniidae).

6.3.4. Genus Brevicardiochiles, gen. nov.

(Fig. 6.13)

Type species: Cardiochiles exiguurus Huddleston and Walker, 1988.

Description

Body. Small, yellow-orange and black in colour.

Head. Eye pilosity reduced to sparse short inter-ommatidial setae; two clypeal tubercles present; clypeus 1.8 - 2.3 x as broad as high; face 1.8 - 2.4 x as broad as high; eye:temple ratio 1:0.8 - 1:1.0; malar carina absent; glossa short, weakly bilobed at apex; galea broad and short; maxillary palps six-segmented; mandibles bidentate; occiput 0.2 - 0.3 x as deep as length of head; antennae separated by 1.3 - 1.7 x width of antennal socket; antennae with 38 - 44 segments; scape 1.3 - 1.6 x as long as broad.

Mesosoma. Notauli broad and crenulate; scutum with medial carina absent; scutellar sulcus 3.5 - 5.0 x as broad as long; apical scutellar cup absent; propodeal areola complete; propodeum without medial longitudinal furrow; epicnemial carina present.

Legs. Hind tibia without apical projection; hind basitarsus cylindrical in cross-section; tarsal claws pectinate.

Wings. Fore wing with 1r and 3r absent in fore wing, discal cell elongate; stigma 2.7 - 3.5 x as long as wide, Rs curved; hind wing with 2r-m and 2-1A absent.

Metasoma. T1 long, 2.8 - 3.6 x as long as broad; median field of T2 0.75 - 1.0 x as long as broad; ovipositor sheaths setose, < 0.2 x as long as hind tibia, 0.45 - 0.6 x as broad as long, down-turned along length; hypopygium evenly sclerotised throughout, with truncate to square angle at apex.

87

Host

Bre. exiguurus has been reared from the citrus looper Neocleora tulbaghata (Felder and Rogenhofer) (Geometridae) from the Transvaal, Africa in 1955 (BMNH - new record).

Distribution

Brevicardiochiles has described species distributed in Africa and the Philippines.

Comments

This genus is closely related to *Hartemita* and *Bohayella* and can be distinguished from these by the presence of two clypeal tubercles and the elongated discal cell. Further it differs from *Hartemita* by its sparse reduced eye setae, complete propodeal areola, presence of epicnemial carina and the form of hind tibia and basitarsus, and from *Bohayella* by its 6-segmented maxillary palps, pectinate hind tarsal claws with fine teeth, and narrower median field of T2. It is named after it shortened or abbreviated hypopygium.

World species included in Brevicardiochiles

Bre. exiguurus (Huddleston and Walker), 1988: 446. Comb. nov. Transferred from *Cardiochiles* s. l. Distribution: Ivory Coast, Sierra Leone, Transvaal. Host: *Neocleora tulbaghata* (Felder and Rogenhofer) (Geometridae).

Bre. nixoni (Huddleston and Walker), 1988: 448. Comb. nov. Transferred from Cardiochiles s. 1. Distribution: Burkina Faso, Sahel, Africa. Host: unknown.

Bre. subflavus (Mao), 1944: 102. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Luzon, Philippines. Host: unknown.

6.3.5. Genus Cardiochiles Nees, sensu stricto

(Figs 4.6, 4.9, 4.11, 4.12, 4.18, 6.14 - 6.20, 7.14 - 7.28)

Cardiochiles Nees ab Esenbeck, 1818: 307. [Type species, by subsequent designation, *Ichneumon saltator* Fabricius, by Nees ab Esenbeck, 1834.]

Genera removed from synonymy Asiacardiochiles Telenga; Pseudcardiochilus Hedwig; Psilommiscus Enderlein; Tenthredoides Cresson (transferred to Toxoneuron); Toxoneuron Say.

Diagnosis

Eyes conspicuously pilose; clypeus with two well-defined tubercles; malar carina absent; glossa elongate visible 2 x basal width past apex of mandibles; galea elongate, deeply bilobed at apex; maxillary palps six-segmented; mandibles bidentate; antennae 33 - 44-segmented; notauli variably sculptured; scutum with medial carina absent; scutellar apex smooth without cup-like carina; propodeal areola complete; epicnemial carina absent; apex of hind tibia not produced; hind basitarsus cylindrical in cross-section; tarsal claws pectinate; fore wing with 1r absent, 3r mostly present, discal cell elongate, Rs mostly angled sometimes curved, stigma 2.7 - 4.2 x as long as wide; T1 1.0 - 2.0 x as long as broad; median field of T2 0.3 - 0.75 x as long as broad; ovipositor sheaths > 0.3 x length of hind tibia; hypopygium pointed at apex, either evenly sclerotised throughout or medially desclerotised but not membranous; ovipositor sheaths straight along length.

Host

Cardiochiles sensu stricto have been reared from Pyralidae and Noctuidae. Pyralid hosts are Diaphania hyalinata (L.) for Car. diaphaniae Marsh, Hymenia recurvalis Fabricius for Car. hymeniae Fischer and Parshad, Crocidolomia binotalis for Car. goosei sp. nov., and Etiella zinckenella (Treitschke) and Loxostege sticticalis Linnaeaus for Car saltator. Noctuid hosts are Helicoverpa armigera (Hübner) for Car. nigromaculatus (Cameron) and Car. variegatus Szépligeti, Heliocheilus albipunctella (de Joannis) for Car. sahalensis Huddleston and Walker, and Helicoverpa sp for Car. uniformis Turner. These host records are presented in Table 2.3 adapted from Huddleston and Walker (1988).

Distribution

Cosmopolitan.

Comments

The type species for *Cardiochiles*, *Ichneumon saltator* is placed basally in the genus relative to other species (see Chapter 5) and it has a number of distinguishing characteristics. Most importantly this species has the hypopygium medially desclerotised and a large number of hamuli, unlike most other species in the genus.

Cardiochiles (Ditherus) *ruficollis* Szépligeti had been regarded as a junior synonym of *Car. saltator* by Cameron (1904). Although the type specimens of each species examined are similar in many ways they differ in that *Car ruficollis* has the following characters different from *Car. saltator*: face with medial longitudinal ridge; temples not visible around eyes in dorsal view; notauli reaching to scutellar sulcus; dorsellum and propodeal areola relatively larger; T1 longer than broad and stem broader with medial furrow. Based on these differences *Car. ruficollis* is here given species status

Cardiochiles sensu lato contained about 95% of the world species prior to the phylogenetic revision. Even though all of the described species have not yet been placed in the new generic revision, from the proportion that have, 22% are now contained in *Cardiochiles sensu stricto*.

World species included in Cardiochiles sensu stricto.

(see Chapter 7 for details of new species).

- Car. atricornis (Ashmead) 1894: 132. Distribution: Neotropical St Vincent, Grenada. Host: unknown.
- Car. coelofrons Huddleston and Walker 1988: 444. Distribution: Africa. Host: unknown.
- Car. diaphaniae Marsh 1986: 132. Distribution: Neotropical. Host: Diaphania hyalinata (L.) (Pyralidae).
- Car. evelinae sp. nov.
- Car. goosei sp. nov.

Car. hymeniae Fischer and Parshad 1968: 807. Distribution: India. Host: Hymenia recurvalis (Fabricius) (Pyralidae).

Car. iqbali sp. nov.

Car. niger Szépligeti 1914: 221. Distribution: Africa - Cameroon, Angola, Zaire, Equatorial Guinea. Host: unknown.

Car. nigromaculatus (Cameron) 1905: 170. Distribution: Oriental, Afrotropical. Host: Helicoverpa armigera (Hübner) (Noctuidae).

Car. pulchripes Szépligeti 1914: 221. Distribution: Africa - Equitorial Guinea, Sierra Leone, Cameroun. Host: unknown.

Car. punctatus Szépligeti 1913: 603. Distribution: Africa. Host: unknown. Car. rasi sp. nov.

Car. ruficollis (Cameron) 1902: 435. Distribution: Himalaya. Host: unknown.

Car. rufator Roman 1915: 798. Distribution: Australia. Host: unknown.

Car. saeedi sp. nov.

- Car. sahalensis Huddleston and Walker, 1988. Distribution: Africa- Senegal, Niger. Host: Heliocheilus albipunctella (de Joannis) (Noctuidae).
- Car. saltator (Fabricius) 1781: 433. Car. brachialis Rondani 1876: 63, synonymised by Tobias et al. 1986. Car. katkowi Kokoujev 1895: 370, synonymised by Tobias et al. 1986. Car. sibiricus Telenga 1955: 231, synonymised by Tobias et al. 1986. Distribution: Palaearctic England to Korea, and Oriental India. Host: Etiella zinckenella (Treitschke) (Pyralidae), Loxostege sticticalis Linnaeaus (Pyralidae).

Car. scotti sp. nov.

- *Car. testaceus* Kriechbaumer 1894: 63. Distribution: Africa Senegal, Mali, Niger, Upper Volta, Ivory Coast, Sierra Leone, Cameroon. Host: unknown.
- Car. uniformis Turner 1918: 803 Distribution: Australia. Host: Helicoverpa sp (Noctuidae).
- Car. variegatus Szépligeti 1913: 603. Distribution: Africa Senegal, Gambia, Niger, Nigeria, Tanzania. Host: *Helicoverpa armigera* (Hübner) (Noctuidae).
- Car. verticalis Turner 1918: 803 Distribution: Australia and Indonesia. Host: unknown.

6.3.6. Genus Circocardiochiles, gen. nov.

(Figs 6.21 - 6.24)

Type species Circocardiochiles occidentalis sp. nov.

Description

Body. Medium to small in size, orange and black in colour, with apically infuscate wings.

Head. Eyes conspicuously pilose; two clypeal tubercles present; clypeus 1.8 - 2.3 x as broad as high; face 1.8 - 2.4 x as broad as high; eye:temple ratio 1:0.65 - 1:0.8; malar carina absent; glossa short, weakly bilobed at apex; galea short; maxillary palps six-segmented; mandibles bidentate; occiput 0.2 - 0.3 x as deep as length of head; antennae separated by 0.75 - 1.0 x width of antennal socket; antennae with 33 - 37 segments; scape 1.3 - 1.6 x as long as broad.

Mesosoma. Notauli smooth; scutum with medial carina absent; scutellar sulcus 6.3 x as broad as long; apical scutellar cup absent; propodeal areola complete, well-defined; propodeum with medial longitudinal furrow; epicnemial carina absent.

Legs. Hind tibia without apical projection; hind basitarsus cylindrical in cross-section; tarsal claws pectinate.

Wings. Fore wing with 1r and 3r absent, discal cell elongate, stigma 3.4 - 4.2 x as long as wide, Rs curved; hind wing with 2r-m and 2-1A absent.

Metasoma. T1 1.0 - 1.8 x as long as broad; median field of T2 0.3 - 0.5 x as long as broad; ovipositor sheaths setose, 0.5 - 0.8 x as long as hind tibia, 0.3 - 0.4 x as broad as long, straight and broadening along length; hypopygium evenly sclerotised throughout, pointed at apex.

Hosts

Unknown.

Distribution

Australia and Sri Lanka.

Comments

The relationships of *Circocardiochiles* are not well-defined in the phylogenetic analyses (see Chapter 5), although the genus can be easily recognised by its apically broadened ovipositor sheaths and broadened clypeus. Apart from the type species an undescribed species is also known from Sri Lanka (CASC). These species differ in the sculpturing of the propodeum, size and colour pattern. It is named because of its changing placement in the phylogenetic analyses presented in Chapter 5.

World species included in Circocardiochiles.

Cir. occidentalis sp. nov. (see Chapter 7 for details).

6.3.7. Genus Hartemita Cameron

(Figs 6.25 - 6.33)

Hartemita Cameron, 1910: 99. [Type species, by monotypy, Hartemita latipes Cameron, 1910.] Dangerfield and Austin (1990)

Laminitarsus Fullaway, 1919: 57. [Type species, by monotypy, Laminitarsus muirii Fullaway, 1919.] Synonymised by De Saeger 1948.

Diagnosis

Small in size, yellow-orange and black patterned with lightly to moderately infuscate apex of fore wing; eye pilosity reduced to sparse interommatidial setae; clypeal tubercles absent, medial clypeal margin pointed convex or concave; malar carina absent; glossa short, weakly bilobed at apex; galea short and broad; maxillary palps six-segments; mandibles either bidentate; notauli crenulate; scutum with medial carina absent; scutellar sulcus broad and deep; apex of scutellum without cup- shaped carina; propodeal areola mostly reduced to short posterior diverging carinae, sometimes weakly defined amongst carinate sculpturing of propodeum; epicnemial carina absent; hind tibia widening to apex but not with dorsal projection; hind basitarsus enlarged elongate and laterally flattened, sometimes broadly laminate and much wider than distal tibia; hind tarsal claws pectinate; fore wing with 1r and 3r absent, discal cell shortened, Rs curved

or angled at base, stigma 2.7 - 3.4 x as long as deep; hind wing with 2-1A absent; T1 elongate, 2.8 - 6.3 x as long as broad; T2 with rectangular to square median field; ovipositor sheaths short, < 0.2 x as long as hind tibia, evenly setose, down-turned along length; hypopygium evenly sclerotised throughout, obtusely angled at apex.

Host

Unknown.

Distribution

This genus has a broad Oriental distribution occurring in India, Laos, Malaysia, Nepal, the Philippines and Taiwan.

Comments

This genus is related to *Bohayella* and *Brevicardiochiles* based on the weakly bilobed glossa, broad deep crenulate notauli, absence of 2-1A in the hind wing, shortened ovipositor and sheaths, truncate hypopygium, broad short galea, and the elongate T1. It can be distinguished from both genera by the propodeal areola being reduced to two posterior diverging carinae, absence of epicnemial carina, form of the hind tibial apex, laminate hind basitarsus and the ovipositor setae being absent at the base. Further *Hartemita* can be distinguished from *Bohayella* by the reduction of eye setae, six-segmented maxillary palps, and the even-sized tarsal claw teeth, and from *Brevicardiochiles* by the absence of clypeal tubercles, and the shortened discal cell of the fore wing. Specimens have mostly been collected using malaise traps in forested mountainous regions.

World species included in Hartemita.

- Har. basilaris Dangerfield and Austin 1990: 151. Distribution: N. Sumatra. Host: unknown.
- Har. bruneiensis Dangerfield and Austin 1990: 154. Distribution: Brunei. Host: unknown.

- Har. chapini (Mao) 1945: 189. Distribution: the Philippines, W. Malaysia and S. E. Sabah. Host: unknown.
- Har. latipes Cameron 1910: 99. Distribution: Nepal, Sumatra and Taiwan. Host: unknown.

Har. muirii (Fullaway) 1919: 57. Distribution: the Philippines. Host: unknown.

Har. rhadinotarsa Dangerfield and Austin 1990: 156. Distribution: south India, west Java and Nepal. Host: unknown.

Har. rudis (Mao) 1945: 190. Distribution: the Philippines. Host: unknown.

Har. singaporensis (Mao) 1945: 190. Distribution: Singapore, W. Malaysia, Sabah and Laos. Host: unknown.

Har. townesi Dangerfield and Austin 1990: 150. Distribution: Taiwan and Nepal. Host: unknown.

6.3.8. Genus Heteropteron Brullé

(Figs 6.34 - 6.38)

Heteropteron Brullé, 1846: 472. [Type species, by monotypy, Heteropteron macula Brullé, 1846.]

Heteropterum Schulz 1906: 138, emendation.

Diagnosis

Body large in size, smooth, orange and black in colour with strongly infuscate wings patterned with two yellow spots; eyes glabrous; clypeal tubercles absent, lateral clypeus poorly-defined; malar carina absent; glossa short, weakly bilobed at apex; galea short and broad; maxillary palps six-segmented; mandibles bidentate; antennae 45 - 48-segmented, scape short and rounded; antennal sockets close together, separated by 0.45 - 0.75 x width of antennal socket; notauli smooth, defined anteriorly, not meeting posteriorly; scutum smooth; scutellar sulcus smooth and shallow; scutellum without apical cup-like carina, but posterior band with medial cleft; dorsellum without medial or lateral carinae; propodeum smooth, without areola, with medio-apical pit present; epicnemial carina absent; apex of hind tibia not produced; hind basitarsus cylindrical; tarsal claws simple; fore wing with 1r and 3r absent, discal cell shortened, 1CUa reduced to a spot, stigma long and narrow, 5.6 - 6.3 x as long as wide, second

submarginal cell elongate, Rs of fore wing evenly curved along length; hind wing with 2r-m absent, 2-1A present half way to wing margin, with 6 - 7 hamuli; T1 large and broadening to apex; T2 with lateral nodes medio-apically and transverse medio-posterior ridge; ovipositor sheaths sinuate, elongate, 1.1 - 1.4 x as long as hind tibia, 0.1 x as broad as long; hypopygium evenly sclerotised throughout, pointed at apex.

Host

Unknown.

Distribution

South America, Brazil.

Comments

Heteropteron had been incorrectly placed in the subfamily Braconinae by Shenefelt (1978) but correctly belongs in the Cardiochilinae. The three South American genera *Heteropteron*, *Neocardiochiles* and *Wesmaelella* are closely related and form a basal monophyletic group within the cardiochilines (see Chapter 5). They are characterised by the following: eyes glabrous, propodeum smooth with areola completely absent, reduced occipital depth and large body size. *Heteropteron* can be distinguished from *Neocardiochiles* and *Wesmaelella* by the long fine sinuate ovipositor and sheaths, basal pit on propodeum, Rs of fore wing evenly curved along its length, narrow antennal separation, and the elongate T1. It is distinguished from *Neocardiochiles* by the simple tarsal claws, the shortened discal cell, and from *Wesmaelella* by the absence of 2r-m in the hind wing, the presence of 2-1A in the hind wing, the evenly pointed apex of the hypopygium, narrower clypeus, and the narrower stigma.

World species included in Heteropteron.

Het. macula Brullé 1846: 472. Distribution: Brazil. Host: unknown.

6.3.9. Genus Hymenicis, gen. nov.

(Figs 4.5, 4.17, 6.39 - 6.43, 7.29 - 7.31)

Type species Hymenicis noongarensis sp. nov.

Description

Body. Medium to small in size, orange or yellow in colour with black markings.

Head. Eye pilosity reduced to minute sparse interommatidial setae; clypeal tubercles absent; clypeus 2.7 - 3.3 x as broad as high; face 1.9 - 2.8 x as broad as high; eye:temple ratio 1:0.65 - 1:1.0; malar carina absent; glossa short, weakly bilobed at apex; galea broad and short; maxillary palps six-segmented; mandibles bidentate; occiput shallow in dorsal view, 0.2 - 0.3 x as deep as head; antennae broadly separated by 1.1 - 1.9 x width of antennal socket; antennae with 38 - 52 segments; scape 0.8 - 1.3 x as long as broad.

Mesosoma. Notauli either smooth or crenulate; scutum with medial carina absent; scutellar sulcus long, 1.9 - 4.8 x as broad as long; scutellum smooth, apical scutellar cup absent; propodeal areola either weak or absent anteriorly, well-defined in posterior half; propodeum without medial longitudinal furrow; epicnemial carina absent.

Legs. Hind tibia without apical projection; hind basitarsus cylindrical in cross-section; tarsal claws simple.

Wings. Fore wing with 1r and 3r absent, discal cell elongate, stigma broad 2.0 - 3.4 x as long as wide, Rs curved or angled at base; hind wing with 2r-m absent, 2-1A present in basal half, with 6 or 7 hamuli.

Metasoma. T1 1.9 - 2.7 x as long as broad; median field of T2 narrow, roughly equidimensional, 0.8 - 1.2 x as long as broad; ovipositor sheaths short, 0.1 - 0.2 x as long as hind tibia, 0.45 - 0.6 x as broad as long, down-turned along length, with long setae; hypopygium evenly sclerotised medially, but with apical one-quarter membranous and collapsible, sclerotised basal part truncate with membranous part pointed at apex.

Host

Unknown.

Distribution

This genus has only been recorded from Australia from the subtropical rainforests of Townsville to the arid desert region of central Australia and the western coastal region of Carnarvon.

Comments

Hymenicis is characterised by the apical desclerotisation of the hypopygium with pointed membranous fold at the apex. All species known for this genus are here described as new in the species revision (see Chapter 7). *Hymenicis* is closely related to *Retusigaster* and *Pseudcardiochilus* (see Chapter 5) but can be easily distinguished from these by the hypopygial desclerotisation and the absence of a hind tibial apical projection.

World species included in Hymenicis.

(see Chapter 7 for full details). Hym. bubbur sp. nov. Hym. noongarensis sp. nov. Hym. nockatungensis sp. nov.

6.3.10. Genus Latitergum, gen. nov.

(Figs 6.44 - 6.47, 7.35 - 7.41)

Type species Latitergum areyongensis sp. nov.

Description

Body. Small to medium in size, orange and black in colour.

Head. Eye pilosity either long and sparse or reduced to short sparse interommatidial setae; two medial clypeal tubercles present or absent; clypeus 1.4 - 2.7 x as broad as high; face 1.3 - 2.3 x as broad as high; eyes large, eye:temple ratio 1:0.46 -

1:0.6; malar carina absent; glossa short, weakly bilobed at apex; galea short to short and broad; maxillary palps six-segmented; mandibles bidentate; occiput 0.2 - 0.4 x as deep as head; antennae separated by 1 - 1.3 x width of antennal socket; antennae with 26 - 30 segments; scape 0.8 - 1.6 x as long as broad.

Mesosoma. Notauli smooth; scutum with medial carina absent; scutellar sulcus 5.0 - 6.5 x as broad as long; scutellum smooth without apical scutellar cup; propodeal areola either complete or reduced in anterior one-quarter; propodeum without medial longitudinal furrow; epicnemial carina absent.

Legs. Hind tibia without apical projection; hind basitarsus cylindrical in cross-section; tarsal claws either simple or pectinate.

Wings. Fore wing with 1r and 3r absent, discal cell elongate, stigma broad 2.0 - 2.7 x as long as wide, Rs evenly curved to apex; hind wing with 2r-m absent, 2-1A present as either a stump or reaching half way to wing margin.

Metasoma. T1 sort and broad at apex, 0.7 - 1.1 x as long as broad; median field of T2 rectangular, 0.3 - 0.45 x as long as broad; ovipositor sheaths evenly setose, elongate, 0.7 - 0.9 x as long as hind tibia, 0.15 - 0.25 x as broad as long, straight along length; hypopygium evenly sclerotised throughout (though sometimes collapsed in dry specimens), pointed at apex.

Host

Unknown.

Distribution

Latitergum is described only from Australia.

Comments

Latitergum is a paraphyletic genus described to accommodate three Australian species, which are, nonetheless, all similar morphologically (see Chapter 7). Although the phylogenetic analysis in Chapter 5 placed the three species distinct from each other

99

this result is based, in part, on trivial characters such as length of eye setae, and morphometric characters assigned arbitrary states. However, they share a number of distinctive characters which have been used here to define the genus: T1 short and broad at the apex, eye setae sparse but either long or short, and the restricted to the Australian mainland. It is named after the short first tergite of the metasoma after the Latin 'latitudo' meaning breadth or width and 'tergum' referring to T1.

World species included in Latitergum.

(see Chapter 7 for full details). Lat. areyongensis sp. nov. Lat. turneri sp. nov. Lat. eremophilasturtiae sp. nov.

6.3.11. Genus Leptocardiochiles, gen. nov.

(Figs 6.48, 6.49)

Leptocardiochiles, gen. nov.. [Type species, by monotypy, Cardiochiles minutus Cresson, 1873: 67.]

Description

Body. Small in size, black in colour.

Head. Eye pilosity long, moderately dense; two clypeal tubercles present; clypeus 1.9 - 2.2 x as broad as high; face 1.5 - 1.7 x as broad as high; eye:temple ratio 1:0.8 - 1:0.9; malar carina absent; glossa short, weakly bilobed at apex; galea short; maxillary palps six-segmented; mandibles bidentate; occiput 0.25 - 0.3 x as deep as length of head; antennae separated by about width of antennal socket; antennae with 38 - 44 segments; scape 1.7 - 1.8 x as long as broad.

Mesosoma. Notauli crenulate; scutum with medial carina absent; scutellar sulcus narrow, 6.5 x as broad as long; scutellum smooth, without apical scutellar cup; propodeal areola complete, diamond-shaped; propodeum without medial longitudinal furrow; epicnemial carina absent.

ALL DESCRIPTION OF A DE

Legs. Hind tibia without apical projection; hind basitarsus cylindrical to ovoid in cross-section; tarsal claws pectinate.

Wings. Fore wing with 1r absent, 3r present, discal cell elongate, stigma broad 2.6 x as long as wide, Rs angled in basal fifth; hind wing with 2r-m and 2-1A absent, with 3 hamuli.

Metasoma. T1 1.8 x as long as broad; median field of T2 0.5 - 0.6 x as long as broad; ovipositor sheaths setose, 0.4 - 0.5 x as long as hind tibia, 0.1 - 0.2 x as broad as long, relatively straight along length; hypopygium with medial longitudinal desclerotisation but with apical sclerotised bridge, pointed at apex.

Host

All available host records indicate that this genus parasitises leaf-mining or leafrolling lepidopteran larvae. *Lep. minutus* has been reared from the leafminer *Stilbosis ostryaella* (Chambers) (Gelechioidea: Cosmopterigidae) on *Ostrya virginiana* (Mill.) the 'eastern hop-hornbeam tree' (pers. comm. Jim Whitfield). There are also reports of *Lep. minutus* from *Evippe prunifoliella* (Chambers) (Gelechioidea: Gelechiidae) (Dalla Torre 1898, Riley and Howard 1890, Ashmead 1894)

Distribution

Nearctic.

Comments

This genus is closely related to *Polycardiochiles* and becomes the sister group of the latter. It can be distinguished from *Polycardiochiles* by the absence of carinae on the medial scutum, malar region and epicnemium and its unusual host group. The genus is so far known only from the type species, and is here named after its small body size, based on the Greek word 'leptos'.

101

World species included in Leptocardiochiles.

Lep. minutus (Cresson), 1873: 67. Distribution: Nearctic. Host: Stilbosis ostryaella (Chambers) (Gelechioidea: Cosmopterigidae); Evippe prunifoliella (Chambers) (Gelechioidea: Gelechiidae).

6.3.12. Genus Neocardiochiles Szépligeti

(Figs 6.50 - 6.56)

Neocardiochiles Szépligeti, 1908: 472. [Type species, by monotypy, Neocardiochiles Szépligeti, 1908.]

Diagnosis

Moderately large in size, black and orange in colour, yellow wings with infuscate patterns; eyes glabrous; clypeal tubercles absent; clypeus 2 x as broad as high; face 2 x as broad as high; occiput shallow in dorsal view; malar carina absent; glossa short, weakly bilobed at apex; galea short and broad; maxillary palps six-segmented; antennal sockets separated by 0.7 - 0.8 x width of antennal socket; antennae with 39 segments; notauli smooth; scutum with medial carina absent; scutellar sulcus smooth and narrow; scutellum smooth; propodeum smooth, without an areola, percurrent medial longitudinal furrow present, with two poorly-defined lateral basal pits; epicnemial carina absent; hind tibia without apical projection; hind basitarsus cylindrical to ovoid in cross-section; tarsal claws with uneven pectination; fore wing with 1-r and 3-r absent;, discal cell elongate, stigma narrow and elongate 6 x as long as wide, Rs angled in basal onequarter; hind wing with 2r-m absent, 2-1A present basally, reaching half way to wing margin; T1 broadening to apex with medio-apical furrow longitudinally; T2 with large rectangular median field; ovipositor sheaths long, about as long as hind tibia, 0.1 x as broad as long, straight along length, setose in apical four-fifths; hypopygium appearing evenly sclerotised throughout but with faint basal desclerotisation and associated lighter colour, evenly pointed at apex.

Host

Unknown.

Distribution

Neocardiochiles is restricted to the northern Neotropical regions of Brazil, Suriname and Venezuela.

Comments

Neocardiochiles is closely related to the other two South American genera, *Heteropteron* and *Wesmaelella*. Differences between these genera are given in the comments under the diagnosis for *Heteropteron*. *Neocardiochiles* is distinct from all other genera in that it has a medial percurrent longitudinal furrow on the propodeum. An undescribed species (AEIC) from Brazil differs in the stronger definition of the medial propodeal furrow, the greater development of the basal hypopygium medial desclerotisation, infuscation of the wings and colour pattern of the body, and another from Venezuela (AEIC) differs in the form of the hind tibia and colour pattern of the body.

World species included in Neocardiochiles.

Neo. fasciipennis Szépligeti 1908: 423. Distribution: northern Neotropical -Surinam. Host: unknown.

6.3.13. Genus Polycardiochiles, gen. nov.

(Figs 4.7, 4.21, 6.57 - 6.69, 7.42 - 7.45, 7.49)

Type species Cardiochiles fuscipennis Szépligeti, 1900: 60.

Description

Body. Moderate in size, mostly black with white or yellow patches a few species orange with black areas.

Head. Eye pilosity mostly long and moderately dense but sometimes sparse and short (as in *Pol. pedis*); mostly with two clypeal tubercles present (absent in *Pol. tibiator*); clypeus 1.4 - 3.3 x as broad as high; face 1.3 - 2.3 x as broad as high; eye:temple ratio 1:0.5 - 1:1.0; malar carina mostly absent but sometimes weakly present; glossa short, weakly bilobed at apex; galea short; maxillary palps six-segmented; mandibles bidentate; occiput 0.2 - 0.5 x as deep as head; antennae separated by 0.4 - 1.3 x width of antennal socket; antennae with 33 - 44 segments; scape 1.0 - 1.85 x as long as broad.

Mesosoma. Notauli smooth or crenulate; scutum with medial carina absent; scutellar sulcus 3.5 - 8.0 x as broad as long; scutellum smooth mostly without apical scutellar cup (present in *Pol. pedis*); propodeal areola complete, oval- to diamond-shaped; propodeum without medial longitudinal furrow; epicnemial carina mostly absent (present in *Pol. pedis*).

Legs. Hind tibia without apical projection; hind basitarsus cylindrical to ovoid in cross-section; tarsal claws pectinate, some with broad apical tooth.

Wings. Fore wing with 1r and 3r absent; discal cell elongate, stigma 2.7 - 4.2 x as long as wide, Rs evenly curved along length; hind wing with 2r-m absent, 2-1A mostly absent (present in part in *Pol. explorator*), with 4 - 6 hamuli.

Metasoma. T1 1.0 - 2.7 x as long as broad; median field of T2 0.2 - 0.75 x as long as broad; ovipositor sheaths setose, 0.5 - 1.1 x as long as hind tibia, 0.1 - 0.26 x as broad as long, relatively straight along length; hypopygium with medial longitudinal desclerotisation, sometimes with desclerotised area membranous and folded fanlike in repose, pointed at apex.

Hosts

Pol. explorator from North America has been reared from Achyra (Loxostege) similalis Guenée (Pyralidae: Pyraustinae), Achyra (Loxostege) rantalis (Guenée) (Pyralidae), Phthorimaea operculella (Zeller) (Gelechioidea: Gelechiidae), a leaf-miner of tobacco and potatoes, and Tortrix sp. (Tortricidae - concealed feeders in rolled shoots or

104

rolled leaves), all of which have some pest status (Naumann 1991). *Pol. tibiator* (Say)has been reared in North America from a range of *Nephopterix* spp. (Pyralidae).

Distribution

Cosmopolitan.

Comments

Polycardiochiles is a monophyletic group as shown in the phylogenetic analysis presented in Chapter 5, but it has few obvious defining characters. Variability in the characters chosen for the analysis places *Pol. gwenae* and *Pol. tibiator* within the genus but they have the malar carina similar to *Austerocardiochiles*. Also *Pol. pedis* with reduced eye setae, an epicnemial carina defined, and an apical scutellar cup, has these characters uncommon to this genus but similar to *Toxoneuron*, *Hartemita*, *Psilommiscus* and *Bohayella*. *Pol. enderleini* has a pronounced ventrally-directed and expanded scutellum unlike that of any other cardiochilines examined. Even though *Polycardiochiles* forms a monophyletic group, it is possible that it eventually may be divided further, when more species are known, because of the apparent morphological diversity of the genus. The name '*Polycardiochiles'* is used to indicate the morphological variability of the included species.

World species included in Polycardiochiles.

- Pol. dissimulator (Turner) 1918: 50. Comb. nov. Transferred from Cardiochiles sensu lato. Distribution: Australia Thursday Island. Host: unknown.
- Pol. enderleini (Szépligeti) 1908: 50. Comb. nov. Transferred from Cardiochiles sensu lato. Distribution: Africa. Host: unknown.
- Pol. explorator (Say) 1836: 257. Comb. nov. Transferred from Cardiochiles sensu lato. Distribution: Nearctic. Host: Achyra (Loxostege) similalis (Guenée) (Pyralidae); Achyra (Loxostege) rantalis (Guenée) (Pyralidae); Phthorimaea operculella (Zeller) (Gelechiidae); Tortrix sp. (Tortricidae) (Huddleston and Walker 1988).
- Pol. fuscipennis (Szépligeti) 1900: 60. Comb. nov. Transferred from Cardiochiles sensu lato.

Cardiochiles assimilator Turner, 1918: 49. syn nov.

Cardiochiles fasciatus Szépligeti, 1900: 52. syn nov.

Cardiochiles similis Brues, 1918: 109. syn nov.

Cardiochelis trichiosomus Cameron, 1913: 84, (genus misspelling). syn nov.

Cardiochelis piliventris Cameron, 1913: 85, (genus misspelling). syn nov.

Distribution: Australia, New Guinea, Indonesia. Host: unknown.

Pol. gwenae sp. nov. Distribution: Australia. Host: unknown.

Pol. mexicanus (Cresson) 1873: 67. Comb. nov. Transferred from *Cardiochiles* sensu lato. Distribution: northern Neotropical - Mexico. Host: unknown.

- Pol. philippensis (Ashmead) 1905: 118. Transferred from Cardiochiles sensu lato.
 Comb. nov. Distribution: Oriental the Philippines, Indonesia, Malaysia, Taiwan,
 Nepal, India. Host: Cnaphalocrocis medinalis (Guenée) (Pyralidae) (Huddleston and Walker 1988).
- Pol. tibiator (Say) 1824: 332. Comb. nov. Transferred from Cardiochiles sensu lato. Distribution: North America. Host: Nephopterix celtidella (Hulst), N. crassifaciella Ragnot, N. dammersi floridensis Heinrich, N. subcaesiella Clemens, N. subfuscella (Ragnot).(Pyralidae) (Huddleston and Walker 1988).
- Pol. phostriae (De Saeger) 1948: 22. Comb. nov. Transferred from Cardiochiles sensu lato. Distribution: Africa Zaire, Cameroon, Sierra Leone Host: Phostria obscurata (Moore) (Pyralidae).
- *Pol. rufithorax* (Enderlein) 1906: 250. Comb. nov. Transferred from *Cardiochiles sensu lato*. Distribution: Africa Gambia, Nigeria, Guinea, Sierra Leone Host: unknown.

6.3.14. Genus Pseudcardiochilus Hedwig

(Figs 6.70 - 6.79)

Pseudcardiochilus Hedwig 1957: 116. [Type species, by monotypy,
 Pseudcardiochilus abnormipes Hedwig 1957: 116.] Synonymised with
 Cardiochiles sensu lato by Tobias and Alexeev 1977. Given valid status by
 Achterberg 1980.

Eye pilosity reduced to short sparse interommatidial setae; clypeal tubercles absent; clypeus 1.8 - 3.0 x as broad as high; face 1.9 - 2.4 x as broad as high; eye:temple ratio 1:0.5 - 1:1.0; malar carina absent; glossa short, rounded at apex; galea short or short and broad; maxillary palps six-segmented; mandibles bidentate; occiput in dorsal view 0.2 - 0.3 x length of head; antennae with 33 - 44 segments; antennal sockets

separated by 1.1 - 1.6 x width of antennal socket; scape short and rounded, 0.8 - 1.2 x as long as broad; notauli smooth; scutum smooth, without medial carina; scutellar sulcus wide or narrow; scutellum smooth, without apical cup; propodeum with complete areola, without medial furrow; epicnemial carina absent; hind tibia with apical projection, small with rounded apex or extremely large with blunt apex; hind basitarsus ovoid to slightly flattened; tarsal claws simple; for wing with 1r and 3r absent, discal cell elongate, stigma broad 2.0 - 3.0 x as long as wide, Rs of fore wing evenly arched to apex; hind with 2r-m absent, 2-1A present as a stump or reaching part way to wing margin; T1 rounded at apex, 1.0 - 2.5 x as long as broad; median field of T2 almost square, 0.6 - 1.0 x as long as broad; ovipositor sheaths densely setose, short, 0.1 - 0.2 x as long as hind tibia, 0.3 - 1.0 x as broad as long, down-turned to apex; hypopygium evenly sclerotised, with square to obtuse angled apex.

Hosts

Unknown.

Distribution

Known so far from Iran and Australia, but presumably when the Oriental species are better known the genus will be recorded from intermediate areas..

Comments

This genus was previously defined by having a wide and dorsally glabrous apex to the hind tibia (Hedwig 1957; Achterberg 1980), a character unusual within the subfamily. The analysis presented here indicates that several other characters are of importance in characterising *Pseudcardiochilus* but none are unique, *viz.* eyes appearing glabrous, propodeal areola complete, ovipositor sheaths short and down-curved, notauli smooth, and tarsal claws simple. *Pseudcardiochilus* is the sister-group of *Hymenicis* and can be easily distinguished from this genus by the evenly sclerotised hypopygium and the development of the hind tibial apical projection. World species included in Pseudcardiochilus.

(for full details of new species refer Chapter 7)

Pse. abnormipes Hedwig 1957: 116 Distribution: Iran. Host: unknown.

Pse. naumanni sp. nov.

Pse. acutus Tobias and Alexeev 1977: 94-110. Distribution: Russia. Host: unknown.

6.3.15. Genus Psilommiscus Enderlein, stat. rev.

Psilommiscus Enderlein 1912: 98. [Type species, by monotypy, Psilommiscus sumatranus Enderlein.] Transferred from Cardiochiles sensu lato. Synonymised with Cardiochiles sensu lato by Muesebeck 1949.

Diagnosis

Medium to moderately large in size, black or black and yellow in colour; eye pilosity reduced to sparse short interommatidial setae; clypeus with two well-defined tubercles; malar carina present though sometimes faint; glossa broad, weakly to moderately bilobed at apex; maxillary palps six-segmented; mandibles bidentate; notauli crenulate; scutum without medial carina; propodeum with areola complete, without medial furrow; epicnemial carina absent; hind tibia without apical projection; hind basitarsus cylindrical to ovoid in cross-section; tarsal claws pectinate; fore wing with 1r and 3r absent, discal cell elongate, Rs evenly curved to apex of wing; hind wing with 2r-m absent, 2-1A present, reaching half way to wing margin; T1 1.2 - 1.8 x as long as broad; median field of T2 0.3 x as long as broad; ovipositor sheaths setose, long, 0.7 - 1.5 x length of hind tibia, straight along length; hypopygium mostly evenly sclerotised throughout or with medially desclerotised area, pointed at apex.

Hosts

Some specimens are mounted with pupal cocoons one wrapped in a leaf, with the note 'larvae fed on Cystus' (see Chapter 4.3).

Distribution

Psilommiscus is so far restricted to the southern Oriental region from Brunei, Sabah, Sumatra, and Negri.

Comments

Based on the phylogenetic analysis presented in Chapter 5, this genus is brought out of synonymy with *Cardiochiles s. l.*. *Psilommiscus* is known only from the type species *Psi. sumatranus* and three undescribed species from Malaysia, *viz.* Brunei (BMNH), Negri (AEIC) and Sabah (RMNH) These species are vivid yellow and black in colour unlike *Psi sumatranus* which is mostly black. The Brunei species is only tentatively placed in this genus as it has the ovipositor sheaths 1.5 times longer than the hind tibia and abruptly down-turned at apex, and the medial hypopygium longitudinally desclerotised but not membranous and folded fan-like.

World species included in Psilommiscus.

Psi. sumatranus Enderlein 1912: 98. Distribution: Oriental - Sumatra. Host: unknown.

6.3.16. Genus Retusigaster, gen. nov.

(Figs 4.10, 6.80 - 6.89)

Type species, Cardiochiles rubidus (Mao), 1949: 251.

Description

Body. Medium to small in sized orange or yellow in colour with black markings.

Head. Eye pilosity reduced to minute sparse interommatidial setae; clypeal tubercles absent; clypeus 2.7 - 3.0 x as broad as high; face broad, 2.4 - 2.8 x as broad as high; eye:temple ratio 1:1.0 - 1:1.1; malar carina absent; glossa short, weakly bilobed at apex; galea broad and short; maxillary palps six-segmented; mandibles bidentate; occiput shallow in dorsal view, 0.2 - 0.3 x as deep as head; antennae broadly

separated by 1.4 -1.8 x width of antennal socket; antennae with 40 - 48 segments; scape rounded, 1.4 x as long as broad.

Mesosoma. Notauli smooth or crenulate; scutum with medial carina absent; scutellar sulcus 5 - 6 x as broad as long; scutellum smooth, apical scutellar cup present; propodeal areola complete, well-defined, ovoid; propodeum without medial longitudinal furrow; epicnemial carina absent.

Legs. Hind tibia with slight apical projection, tibia becoming flattened at apex; hind basitarsus ovoid to slightly flattened in cross-section; tarsal claws pectinate with broad apical tooth.

Wings. Fore wing with 1r and 3r absent, discal cell elongate, stigma broad 3.3 3.4 x as long as wide, Rs evenly curved to wing apex; hind wing with 2r-m absent, 21A present in basal half, with 6 or 7 hamuli.

Metasoma. T1 about 2 x as long as broad; median field of T2 narrow, roughly equidimensional, 0.8 - 0.9 x as long as broad; ovipositor sheaths setose in apical half, short, 0.1 - 0.2 x as long as hind tibia, 0.2 - 0.3 x as broad as long, down-turned along length; hypopygium evenly sclerotised throughout, broadly truncate at apex.

Hosts

Unknown.

Distribution

Nearctic and northern Neotropical.

Comments

The genus is closely related to *Hymenicis* and *Pseudcardiochilus* but can be easily distinguished from these by the presence of the scutellar apical cup. Further it differs from *Hymenicis* by the evenly sclerotised hypopygium and from *Pseudcardiochilus* by the bilobed form of the glossa and the crenulate notauli. The genus is named after the form of the hypopygium from the latin 'retusus' meaning blunt, rounded.

World species included in Retusigaster.

Ret. arugosus (Mao) 1949: 233. Distribution: Nearctic. Host: unknown.

Ret. brevitarsus (Mao) 1949: 235. Distribution: Nearctic - California. Host: unknown.

Ret. dignus (Mao) 1949: 237. Distribution: Nearctic - Texas. Host: unknown. Ret. noctis (Mao) 1945: 129. Distribution: Neotropical - Mexico. Host: unknown.

Ret. pullus (Mao) 1949: 234. Distribution: Nearctic. Host: unknown.

Ret. rubidus (Mao) 1949: 251. Distribution: Nearctic. Host: unknown.

6.3.17. Genus Toxoneuron Say, stat. rev.

(Figs 6.90 - 6.105)

Toxoneuron Say 1836: 258. [Type species, by subsequent designation, Bracon viator (Say) 1836, by Viereck, 1914.] Transferred from Cardiochiles sensu lato.
 Synonymised with Cardiochiles sensu lato by Ashmead 1900.

Tenthredoides Cresson 1865: 290. [Type species, by monotypy, Tenthredoides seminiger Cresson 1865: 291. Transferred from Cardiochiles sensu lato.
Synonymised with Cardiochiles sensu lato by Cresson 1873.

Diagnosis

Body moderate in size, black or orange and black in colour; eye pilosity reduced to short sparse interommatidial setae; clypeal margin without tubercles, mostly convex (*Tox. bicolor* with concave margin); clypeus broad, $2.8 - 3.6 \times as$ broad as high; face broad, $1.9 - 4.5 \times as$ broad as high; eye:temple ratio 1:0.8 - 1:1.2; occiput in dorsal view $0.2 - 0.4 \times as$ deep as length of head; malar carina absent; glossa short or long, mostly weakly bilobed but sometimes deeply bilobed; galea short or long and broad; maxillary palps six-segmented; mandibles bidentate; antennae separated by $0.8 - 1.7 \times as$ width of antennal socket, with 29 - 44 segments, scape $1.0 - 1.6 \times as$ long as broad;

notauli smooth or crenulate; medial scutum smooth, without longitudinal carina; scutellar sulcus broad or narrow; apical scutellum mostly with apico-medial cup-like pit (except in *Tox. dilatus*); propodeum mostly with well-defined complete areola (except in *Tox. magnus* where it is reduced posteriorly); epicnemial carina mostly absent (weakly-defined in *Tox. rubicundus*); hind tibia with apical projection well-developed with flat to cup-like apex; hind basitarsus ovoid in cross-section; tarsal claws pectinate; fore wing with 1r usually absent sometimes basally present, 3r usually absent, sometimes present spectrally, discal cell elongate, Rs evenly arched to apex or angled near base, stigma generally broad 2.0 - 4.2 x as long as wide; hind wing with 2r-m absent, 2-1A present in basal half; T1 with broadly rounded bulb, 1.0 - 2.0 x as long as broad; median field of T2 rectangular or trapezoidal, 0.5 - 1.0 x as long as broad; ovipositor sheaths straight along length or abruptly downturned at apex, usually completely setose or reduced to apex or completely smooth (*Tox. magnus*), very short or moderately long, 0.2 - 0.6 x as long as hind tibia, slender, 0.1 - 0.3 x as broad as long; hypopygium evenly sclerotised throughout, mostly broadly truncate at apex rarely evenly pointed.

Hosts

Toxoneuron species are so far recorded only from noctuid hosts (Huddleston and Walker 1988).

Distribution

Toxoneuron is confined to the southern Nearctic and northern Neotropical regions. It has however been introduced into the Philippines and Thailand as a biocontrol agent of *Helicoverpa assulta* and *H. armigera* on tobacco (Huddleston and Walker 1988).

Comments

Toxoneuron species are brought out of synonymy with *Cardiochiles sensu lato* based on the characters outlined in the diagnosis and the results of the cladistic analysis

(Chapter 5). *Tenthredoides* becomes a junior synonym of *Toxoneuron* also brought out of synonymy with *Cardiochiles s. l.* The genus is part of the distinct group of genera which have reduced eye setae and becomes the sister genus to *Bohayella* + *Hartemita* + *Brevicardiochiles* + *Hymenicis* + *Retusigaster* + *Pseudcardiochilus*. This new status is important in that the species *Tox. nigriceps* (Viereck) is much studied with respect to its physiology and behaviour as discussed in Chapter 2.

World species included in Toxoneuron.

- Tox. abdominale Cresson 1873: 68. Stat. rev. Transferred from Cardiochiles s. l. Distribution: Nearctic. Host. unknown.
- Tox. bicolor Szépligeti 1902: 78. Stat. rev. Transferred from Cardiochiles s. l. Distribution: Neotropical Mexico. Host: unknown.
- Tox. dilatus (Mao) 1949: 238. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic California. Host: unknown.
- Tox. magnus (Mao) 1949: 243. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic. Host: Schinia sp. (Noctuidae).
- Tox. nebrascensis (Mao) 1949: 245. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic - Nebrasca. Host: unknown.
- Tox. nigriceps (Viereck) 1912: 578. Comb. nov. Transferred from Cardiochiles s.
 l. Distribution: Nearctic and Philippines (introduced). Host: Helicoverpa assulta Guenée, Heliothis subflexa Guenée, Heliothis virescens Fabricius, Heliothis zea (Boddie), (Noctuidae).
- Tox. rubicundus (Mao) 1949: 250. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic N. Mexico and Arizona. Host: unknown.
- Tox. rufostigma (Mao) 1949: 252. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic California. Host: unknown.
- Tox. seminiger (Cresson) 1865: 291. Stat. rev. Transferred from Cardiochiles s. l. Distribution: Nearctic and northern Neotropical. Host: unknown.
- Tox. texensis (Mao) 1949: 255. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic Texas. Host: unknown.
- Tox. truncus (Mao) 1949: 261. Comb. nov. Transferred from Cardiochiles s. l. Distribution: Nearctic. Host: unknown.
- Tox. viator (Say) 1836: 258. Stat. rev. Transferred from Cardiochiles s. l. Distribution: Nearctic. Host: unknown.
6.3.18. Genus Wesmaelella Spinola

(Figs 6.106 - 6.110)

Wesmaelella Spinola, (1851) 1853: 32. [Type species, by monotypy, Wesmaelella rubricollis Spinola, (1851) 1853.]

Psilophthalmus Szépligeti, 1902: 79. [Type species, by monotypy, Psilophthalmus nigripennis Szépligeti, 1902.] Synonymised by Schulz 1911.

Diagnosis

Body very large in size, smooth and elongate, orange and black in colour with dark infuscate wings not patterned; eyes glabrous; clypeal tubercles absent; clypeus rectangular, 2.4 - 2.5 x as broad as high; face broad, 1.8 - 2.8 x as broad as high; temples deep behind eyes, eye:temple ratio 1:0.9 - 1:1.2; malar carina absent; glossa short, weakly bilobed at apex; galea broad and short; maxillary palps six-segmented; mandibles bidentate and projecting outward from face; occiput shallow in dorsal view, 0.1 - 0.15 x as long as length of head; antennal sockets separated by 1.0 - 1.2 x width of antennal socket; antennae with 48 segments; scape rounded in lateral view, 1.0 x as long as broad; notauli smooth; scutum smooth, elongate, without medial carina; scutellar sulcus shallow, 2.5 x as broad as long, with medial carina, appearing as two adjacent pits between scutum and scutellum; scutellum smooth long, broad at apex, posterior band with broad medial cleft; propodeum smooth, without medial furrow, but with two shallow basal pits medially; epicnemial carina absent; hind tibia without apical projection; hind basitarsus cylindrical in cross-section; tarsal claws simple; fore wing with 1r present and strong in apical half, 3r absent, Rs with break in basal fifth then angled and sinuate to apex, stigma elongate and narrow 4.0 - 5.0 x as long as wide, discal cell short, 1-M thick, apex of veins 3-M and 2-Cub bifurcate in Wes. rubricollis; hind wing with 2r-m present in part and spectral, 2-1A present to wing margin downturned at apex; T1 broad at apex, about as long as apically broad; median field of T2 not defined; ovipositor sheaths straight, setose along length, evenly broad, 0.5 x as long as hind tibia, 0.2 x as broad as long; hypopygium evenly sclerotised throughout, broadly truncate at apex

Hosts

Unknown.

Distribution

Wesmaelella is distributed throughout the central Neotropical region in Brazil, Peru and Paraguay.

Comments

Wesmaelella is the most unusual of all cardiochilines particularly because of the form of the wing venation and shape of the head. The wings (Figs 6.109, 6.110) have heavy dark venation unlike any other genus. The head (Fig. 6.107) has the face and frons meeting at right angles with the antennae on a shelf or prominence, and the mandibles projecting outward beyond the plane of the face and clypeus.

Psilophthalmus remains a junior synonym of *Wesmaelella* after the cladistic analyses presented in Chapter 5.

Two unidentified specimens (RMNH) have been collected from Peru and Paraguay extending the known range of the genus beyond Brazil.

World species included in Wesmaelella.

Wes. nigripennis (Szépligeti) 1902: 79. Distribution: Brazil. Host: unknown. Wes. rubricollis Spinola (1851) 1853: 32. Distribution: Brazil. Host: unknown.

6.4 Species incertae sedis

These species have been unable to be placed in the revised generic classification given that their holotypes were not easily available or that they are only known from male specimens. They are here referred to as *Cardiochiles sensu lato*. Host information was obtained from Huddleston and Walker (1988). Some species have included notes on

their potential generic placement based on original descriptions, these however, could not be placed due to incomplete or ambiguous descriptions given.

Car. acrenulatus Fischer 1958: 16. Distribution: Palaearctic - Egypt. Host: unknown.

- Car. aethiops (Cresson) 1873: 67. Distribution: Neotropical Mexico. Host: unknown.
- Car. alboannulatus Telenga 1955: 220. Distribution: Palaearctic Turkmenia. Host: unknown.
- Car. albocalcaratus Enderlein 1906: 247. Distribution: Oriental Sumatra. Host: unknown.
- Car. angustifrons Brues 1924: 94. Distribution. Ethiopian Natal, Madagascar. Host: unknown.
- Car. antennalis Telenga 1955: 217. Distribution: Palaearctic Turkmenia. Host: unknown.
- Car. apicalis (Cresson) 1873: 68. Distribution Nearctic. Host: unknown. Possibly *Polycardiochiles* based on the setose eyes, smooth scutum short galea and infolded hypopygium. These characters are taken from Mao (1949) however, the type needs to be seen to confirm its generic status.
- Car. apicalis (Cresson) 1873: 68. Distribution: Nearctic. Host: unknown.
- Car. ater Szépligeti 1914: 420. Distribution: Ethiopian Belgian Congo. Host: unknown.
- Car. aterrimus Fischer 1958: 33. Distribution: Neotropical Ecuador. Host: unknown.
- Car. atricornis (Ashmead) 1894: 132. Distribution: Neotropical St. Vincent, Granada. Host: unknown.
- Car. bequaerti Brues 1926: 61. Ethiopian Belgian Congo. Host: unknown.
- Car. bifoveatus Cameron 1912: 380. Distribution: Ethiopian Congo. Host: unknown.
- Car. calculator Telenga 1955: 224. Distribution: Palaearctic Turkmenia. Host: unknown.
- *Car. californicus* (Ashmead) 1894: 50. Distribution. Nearctic California. Host: unknown. Possibly *Toxoneuron* but with medial furrows on scutum, no hind tibial apical projection and polished bare ovipositor sheath moderately long with hook at apex.
- Car. ceylonicus Enderlein 1906: 251. Distribution: Oriental Sri Lanka. Host: unknown.
- Car. croceum (Cameron) 1887: 412. Distribution: Neotropical Panama. Host: unknown.

Car. desertus Telenga 1955: 216. Distribution: Palaearctic. Host: unknown.

- Car. eremita Kokoujev 1904: 215. Distribution: Palaearctic Caucasia. Host: unknown.
- Car. erythronotus Cameron 1906: 102. Distribution: Oriental Pakistan. Host: unknown.

Car. falcatus Tobias and Alexeev 1977: 103. Distribution: Palaearctic. Host: unknown.

Car. fallax Kokoujev 1895: 367. Distribution: Palaearctic. Host: unknown.

- Car. flavipennis Granger 1949: 346. Distribution: Ethiopian Madagascar. Host: unknown.
- Car. floridanus (Ashmead) 1894: 50. Distribution: southern Nearctic and northern Neotropical. Host: Epipaschia zelleri (Grote) (Pyralidae).
- Car. forticarinatus Cameron 1910: 445. Distribution: Ethiopian South Africa. Host: unknown.
- Car. fossatus Brues 1924: 97. Distribution: Ethiopian Natal. Host: unknown.
- Car. fulviventris (Cameron) 1906: 40. Distribution: Ethiopian South Africa. Host: unknown.
- Car. fulvus Cameron 1907; 466. Distribution: Oriental India and Sri Lanka. Host: Hedylepta indicata (Fabricius) (Pyralidae); Hymenia recurvalis (Fabricius) (Pyralidae); Syllepte lunalis (Guenée) (Pyralidae).
- Car. fumatus Telenga 1949: 387. Distribution: Palaearctic Tadzhikistan, Kazakhstan and Uzbekistan. Host: unknown.
- Car. fumipennis Szépligeti 1901: 151. Distribution: Palaearctic. Host: unknown.
- Car. fuscus Tobias and Alexeev 1977: 102. Distribution: Palaearctic. Host: unknown.
- Car. glaber Fischer 1958: 28. Distribution: Palaearctic Egypt. Host: unknown.
- Car. glaphyras Alexeev. Distribution: Palaearctic Siberia. Host: unknown.
- Car. gussakovskii Telenga 1949: 387. Distribution: Palaearctic Tadzhikistan, Kazakhstan and Uzbekistan. Host: unknown.
- Car. hyalinapennis Telenga 1955: 223. Distribution: Palaearctic Turkmenia. Host: unknown.
- Car. hymeniae Fischer and Parshad 1968: 807. Distribution: Oriental India. Host: Hymenia recurvalis Fabricius (Pyralidae).
- Car. insculptus Mao 1949: 241 Distribution: southern Nearctic. Host: Phthorimaea operculella (Zeller) (Gelechiidae).
- Car. japonicus Enderlein 1906: 249. Distribution: Oriental Java. Host: unknown.
- Car. javanus Enderlein 1906: 249. Distribution: Oriental Java. Host: unknown.
- Car. kasachstanicus Tobias and Alexeev 1977: 99. Distribution: Palaearctic. Host: unknown.
- Car. karakumicus Tobias and Alexeev 1977: 102. Distribution: Palaearctic. Host: unknown.

- Car. laevifossa Enderlein 1906: 248. Distribution: Oriental Java, Taiwan. Host: unknown.
- Car. latifrons Brues 1924: 93. Distribution: Ethiopian South Africa. Host: unknown.
- *Car. levis* Mao 1949: 242. Distribution: southern Nearctic and northern Neotropical. Possibly *Toxoneuron* but Mao (1949) describes the hind tibia without an apical projection. Still the eye setae are reduced, the hypopygium is very large, and the ovipositor sheaths are slightly down-turned broad at base narrowing to apex and pubescent.
- Car. longiceps Roman 1910: 116. Distribution: Ethiopia. Host: unknown.
- Car. longimala Mao 1945: 127. Distribution: Neotropical Mexico. Host: unknown.
- Car. longipennis Brues 1924: 98. Distribution: Ethiopian. Host: unknown.
- Car. lucidus Telenga 1955: 225. Distribution: Palaearctic Kazakhstan, Turkmenia. Host: unknown.
- Car. maculatus Fischer 1958: 14. Distribution: Palaearctic Egypt. Host: unknown.
- Car. melanotus Telenga 1955: 227. Distribution: Palaearctic Kazakhstan. Host: unknown.
- Car. microsomus Tobias and Alexeev 1977: 101. Distribution: Palaearctic. Host: unknown.
- Car. minor Szépligeti 1914: 189. Distribution: Ethiopian Kenya. Host: unknown.
- Car. munitigera Granger 1949: 342. Distribution: Palaearctic Madagascar. Host: unknown.
- Car. niger Szépligeti 1914: 221. Distribution: Ethiopian. Host: unknown.
- Car. nigricans Mao 1949: 246 (Male only). Distribution: Nearctic California. Host: unknown.
- Car. nigricornis Cameron 1910: 98. Distribution: Oriental Indonesia. Host: unknown.
- Car. nigricundus Cameron 1906: 102. Distribution: Oriental Pakistan. Host: unknown.
- Car. nigroclypeus Viereck 1905: 275 (male only). Distribution: southern Nearctic. Host: unknown.
- Car. nigromaculatus (Cameron) 1906: 170. Distribution: Ethiopian. Host: Helicoverpa armigera (Hübner) (Noctuidae).
- Car. nitidus Brues 1924: 96. Distribution: south-west Ethiopian. Host: unknown.
- Car. obscuriceps Fischer 1958: 19. Distribution: Palaearctic Egypt. Host: unknown.
- Car. orizabae (Cresson) 1873: 67. Distribution: Nearctic and northern Neotropical. Host: unknown.
- Car. ornatus (Cresson) 1873: 69. Distribution: Neotropical Mexico. Host: unknown.
- Car. phostriae De Saeger 1948: 22. Distribution: Ethiopian. Host: Phostria obscurata (Moore).

- Car. pictithorax Granger 1949: 344. Distribution: Ethiopian Madagascar. Host: unknown.
- Car. pluto (Ashmead) 1894: 49 (Male only). Distribution: Nearctic California. Host: unknown.
- Car. priesneri Fischer 1958: 30. Distribution: Palaearctic Egypt. Host: unknown.
- Car. pseudofallax Telenga 1955: 226. Distribution: Palaearctic Turkmenia. Host: unknown.
- Car. pulchripes Szépligeti 1914: 221. Distribution: Ethiopian. Host: unknown.
- Car. punctatus Szépligeti 1913: 603. Distribution: Ethiopian. Host: unknown. Car. striatus Brues 1924: 95. (Syn. Huddleston and Walker 1988)
- Car. purpureus Fischer 1958: 34. Distribution: Neotropical Ecuador. Host: unknown.
- Car. robustus Telenga 1955: 219. Distribution: Palaearctic Spain. Host: unknown.
- Car. rubicundus Mao 1949: 250. Distribution: southern Nearctic. Host: unknown. Close to Brevicardiochiles except without clypeal tubercles and does not have elongate T1 and laminate hind basitarsus like Hartemita. The galea is slightly elongate.
- Car. rufomaculatus Cameron 1910: 446. Distribution: Ethiopian South Africa. Host: unknown.
- Car. rufostigma Mao 1949: 252. Distribution: Nearctic California. Host: unknown.
- Car. rugosus Telenga 1955: 222. Distribution: Palaearctic Vladivostok. Host: unknown.
- Car. scapularis Brues 1926: 279. Distribution: Ethiopian South Africa. Host: unknown.
- Car. semenowi Kokoujev 1895: 372. Distribution: Palaearctic China. Host: unknown.
- Car. seyrigi Granger 1949: 344. Distribution: Ethiopia Madagascar. Host: unknown.
- Car. shestakovi Telenga 1949: 387. Distribution: Palaearctic Tadzhikistan, Turkmenia, Uzbekistan. Host: unknown.
- Car. striatifrons Brues 1926: 281. Distribution: Ethiopian Natal. Host: unknown.
- Car. sulcatus Granger 1949: 345. Distribution: Ethiopian Madagascar. Host: unknown.
- Car. szepligetii Enderlein 1906: 252.. Distribution: Oriental. Host: unknown.
- Car. tegularis Brues 1924: 100. Distribution: Ethiopian Kenya, Natal. Host: unknown.
- Car. temporalis Fischer 1958: 22. Distribution: Palaearctic Egypt. Host: unknown.
- Car. tennessensis Mao 1949: 254. Distribution: Nearctic Tennessee. Host: Heliothis virescens (Fabricius) (Noctuidae). Close to Toxoneuron however hind tibia

without apical projection. The ovipositor is straight, smooth and polished as in some other *Toxoneuron*.

- Car. testaceipes Cameron 1906: 331. Distribution: Ethiopian. Host: unknown.
- Car. testaceus Kriechbaumer 1894: 62. Distribution: Ethiopian and Palaearctic -Tunisia. Host: unknown.
- Car. therberiae Rohwer 1920: 226. Distribution southern Nearctic. Host: unknown. Possibly Polycardiochiles.
- Car. thoracicus (Cresson) 1873: 68. Distribution: southern Nearctic and northern Neotropical. Host: unknown.
- Car. tibialis Hedwig 1957: 116. Distribution: Palaearctic Iran. Host: unknown.
- Car. tjanshanicus Tobias and Alexeev 1977: 100. Distribution: Palaearctic. Host: unknown.
- *Car. transversus* Mao 1949: 269. Distribution: Nearctic California. Host: unknown. Possibly *Toxoneuron* but as hind tibia without an apical projection yet has long, straight, polished, bare ovipositor sheaths.
- Car. trimaculatus (Cameron) 1906: 171. Distribution: Ethiopian. Host: Helicoverpa armigera (Hübner) (Noctuidae).
- Car. triplus Hedwig 1957: 116. Distribution: Palaearctic Iran. Host: unknown.
- Car. tristis Granger 1949: 342. Distribution: Ethiopian Madagascar. Host: unknown.
- Car. turcmenicus Tobias and Alexeev 1977: 101. Distribution: Palaearctic. Host: unknown.
- Car. turkestanicus Telenga 1955: 219. Distribution: Palaearctic Kazakhstan, Turkmenia. Host: unknown.
- Car. variegatus Szépligeti 1913: 603. Distribution: Ethiopian Tanzania. Host: unknown.
- Car. vitripennis Tobias and Alexeev 1977: 102. Distribution: Palaearctic. Host: unknown.
- Car. volgensis Tobias 1954. Distribution: Palaearctic. Host: unknown.
- Car. weidholzi Fischer 1958: 25. Distribution: Palaearctic Egypt. Host: unknown.
- Car. xanthocarpus Szépligeti 1913: 604. Distribution: Ethiopian Tanzania. Host: unknown.
- Car. xanthostigma Granger 1949: 346. Distribution: Ethiopian Madagascar. Host: unknown.

CHAPTER 6

Figures 6.1 to 6.110

Figs 6.1 - 6.5. Asiacardiochiles minutus Telenga, female: 6.1, anterior head; 6.2, dorsal habitus; 6.3, antenna; 6.4, fore wing; 6.5, hind wing. Scale lines: 0.5 mm.



Figs 6.6 - 6.9. Austerocardiochiles pollinator sp. nov., holotype, female: 6.6, dorsal head to T3; 6.7, fore and hind wing; 6.8, posterior head (malar carina arrowed); 6.9, ventro-lateral mesosternum (epicnemial carina arrowed). Scale lines: 6.6 - 6.8, 1mm; 6.9, 0.5 mm.



Figs 6.10 - 6.12. *Bohayella tobiasi* Belokobylskij, holotype, female: 6.20, dorsal habitus; 6.11, antenna; 6.12, lateral habitus. **Fig. 6.13.** *Brevicardiochiles exiguurus* (Huddleston and Walker), female, dorsal habitus. Scale lines: 1 mm.



Figs 6.14 - 6.17. SEM's of *Cardiochiles s. str.* sp.: 6.14, anterior head; 6.15, postero-lateral head; 6.16, apex of outer hind tibia showing club tipped hairs; 6.17, apex of lateral metasoma showing ovipositor sheaths and hypopygium with slight medial longitudinal desclerotisation. Scale lines: 6.14, 6.15, 1 mm; 6.16, 0.2 mm; 6.17, 0.5 mm.

÷



Figs 6.18 - 6.20. Cardiochiles saltator (Fabricius), female: 6.18, dorsal habitus; 6.19, fore and hind wing; 6.20, anterior head. Figs 6.21 - 6.24. Circocardiochiles occidentalis sp. nov., holotype, female: 6.21, dorsal head to T2; 6.22, anterior head; 6.23, apex of lateral metasoma; 6.24, fore and hind wing. Scale lines: 6.18, 6.19, 6.21 - 6.24, 1 mm; 6.20, 0.5 mm.



Figs 6.25 - 6.29. *Hartemita latipes* Cameron, holotype, female: 6.25, fore wing; 6.26, anterior head; 6.27, dorsal head to T2; 6.28, lateral habitus; 6.29, outer lateral hind tibia and tarsae. Scale lines: 6.25, 2 mm; 6.26 - 6.29, 1 mm.



Figs 6.30 - 6.33. SEM's of *Hartemita rhadinotarsa* Dangerfield and Austin, holotype, female: 6.30, dorsal mesosoma; 6.31, dorsal metanotum and propodeum; 6.32, dorsal head; 6.33, outer hind tarsae. Scale lines: 6.30 - 6.32, 0.2 mm; 6.33, 0.5 mm.



Figs 6.34 - 6.38. *Heteropteron macula* Brullé, female: 6.34, dorsal head to T3; 6.35, anterior head; 6.36, lateral metasoma; 6.37, hind wing; 6.38, fore wing. Scale lines: 6.34 - 6.36, 1 mm; 6.37, 6.38, 2 mm.



Figs 6.39 - 6.43. *Hymenicis noongarensis* sp. nov., holotype, female: *6.39*, dorsal habitus; *6.40*, fore wing; *6.41*, hind wing; *6.42*, anterior head; *6.43*, apex of lateral metasoma. Scale lines: *6.39 - 6.42*, 1 mm; *6.43*, 0.5 mm.

.



Figs. 6.44 - 6.47. Latitergum areyongensis sp. nov., holotype, female: 6.44, dorsal head to T2; 6.45, anterior head; 6.46, fore wing; 6.47, hind wing. **Figs 6.48, 6.49.** Leptocardiochiles minutus (Cresson), female: 6.48, anterior head; 6.49, dorsal habitus. Scale lines: 6.44, 6.45, 0.5 mm; 6.46 - 6.49, 1 mm.



Figs 6.50 - 6.56. Neocardiochiles fasciipennis Szépligeti, female: 6.50, dorsal habitus; 6.51, anterior head; 6.52, hind tarsal claw; 6.53, apex of lateral meatsoma; 6.54, vento-lateral hypopygium; 6.55, fore wing; 6.56, hind wing. Scale lines: 6.50, 6.53 - 6.56, 1 mm; 6.51, 0.5 mm; 6.52, 0.25 mm.



Figs 6.57 - 6.61. Polycardiochiles fuscipennis (Szépligeti), female: 6.57, dorsal habitus; 6.58, fore wing; 6.59, hind wing; 6.60, lateral habitus; 6.61, anterior head. Scale lines: 1 mm.



Figs 6.62 - 6.65. SEM's of *Polycardiochiles fuscipennis* (Szépligeti), female: *6.62*, ventral clypeus, labrum and mandibles; *6.63*, hind tarsal claw with broad pectination; *6.64*, dorsal scutellum, metanotum and propodeum; *6.65*, dorsal scutum to metanotum. Scale lines: *6.62*, 0.1 mm; *6.63*, 0.02 mm; *6.64*, *6.65*, 0.4 mm.



Figs 6.66 - 6.69. SEM's of *Polycardiochiles fuscipennis* (Szépligeti), female: *6.66*, ovipositor sheaths, basal ovipositor, and apex of hypopygium; *6.67*, detail of feathered sculpturing on hypopygium; *6.68*, ventro-lateral hypopygium with medial longitudinal membrane; *6.69*, apex of ovipositor with disc-like sensillae. Scale lines: *6.66*, *6.68*, 0.25 mm; *6.67*, *6.69*, 0.02 mm.


Figs 6.70 - 6.74. *Pseudcardiochilus abnormipes* Hedwig, holotype, female: 6.70, dorsal habitus; 6.71, anterior head; 6.72, anterior hind tibia and tarsae; 6.73, outer lateral hind tibia and tarsae. Figs 6.75 - 6.77. *Pse. naumanni* sp. nov., holotype, female: 6.75, anterior head; 6.76, outer lateral hind tibia and tarsae; 6.77, dorsal head to T3. Figs 6.78, 6.79. *Pse. abnormipes*, holotype, female: 6.78, fore wing; 6.79, hind wing. Scale lines: 1 mm.







Figs 6.90 - 6.93. *Toxoneuron nigriceps* (Viereck), female: 6.90, dorsal habitus; 6.91, fore wing; 6.92, hind wing; 6.93, anterior head. Fig. 6.94. *Tox. magnus* (Mao), male, lateral metasoma with enlarged adeagus and parameres. Figs 6.95 - 6.97. *Tox. viator* (Say), female: 6.95, dorsal habitus; 6.96, fore wing; 6.97, hind wing. Scale lines: 1 mm.



Figs 6.98 - 6.100. SEM's of *Toxoneuron* sp., female: 6.98, anterior head; 6.99, posterior head; 6.100, cup-like projection at apex of hind tibia showing club-tipped setae. **Fig. 6.101.** *Tox. seminiger* (Cresson), female, detail of eye showing minute interommatidial pilosity. Scale lines: 6.98, 6.99, 1 mm; 6.100, 0.3 mm; 6.101, 0.06 mm.



Figs 6.102, 6.103. SEM's of *Toxoneuron nigriceps* (Viereck), female: 6.102, anterior head; 6.103, posterior head. Figs 6.104, 6.105. *Tox. seminiger* (Cresson), female: 6.104, dorsal metanotum and propodeum; 6.105, lateral ovipositor, sheaths and hypopygium. Scale lines: 0.6 mm.



Figs 6.106 - 6.110. Wesmaelella rubricollis Spinola, female: 6.106, dorsal habitus; 6.107, lateral habitus; 6.108, anterior head; 6.109, fore wing; 6.110, hind wing. Scale lines: 6.106 - 6.108, 1 mm; 6.109, 6.110, 2 mm.



CHAPTER 7

Revision of Australasian cardiochiline species

- 7.1. Introduction to Australasian cardiochiline fauna
- 7.2. Key to Australasian species of Cardiochilinae
- 7.3. Treatment of Australasian Cardiochilinae
 - 7.3.1. Austerocardiochiles callemondah
 - 7.3.2. Aus. deetoo
 - 7.3.3. Aus. exleyae
 - 7.3.4. Aus. morulus
 - 7.3.5. Aus. pollinator
 - 7.3.6. Bohayella adina

7.3.7. Boh. toxopeusi

- 7.3.8. Cardiochiles evelinae
- 7.3.9. Car. goosei
- 7.3.10. *Car. iqbali* 7.3.11. *Car rasi*
- 7.3.12. Car. rufator
- 7.3.13. Car. saeedi
- 7.3.14. Car. scotti
- 7.3.15. Car. uniformis
- 7.3.16. Car. verticalis
- 7.3.17. Circocardiochiles occidentalis
- 7.3.18. Hymenicis bubbur 7.3.19. Hym. nockatungensis
- 7.3.20. Hym. noongarensis
- 7.3.21. Latitergum areyongensis
- 7.3.22. Lat. eremophilasturtiae
- 7.3.23. Lat. turneri
- 7.3.24. Polycardiochiles dissimulator
- 7.3.25. Pol. fuscipennis 7.3.26. Pol. gwenae
- 7.3.27. Pol. philippensis
- 7.3.28. Pseudcardiochilus naumanni

7.4. Distribution patterns of Australasian fauna

7.5. Biology of the Australasian fauna

Figures 7.1 to 7.49.

CHAPTER 7

7.1 Introduction to Australasian cardiochiline Fauna

The Australasian Cardiochilinae belong to eight genera, two of which are endemic to the region. They are Austerocardiochiles (5 species), Bohayella (1 species), Cardiochiles (8 species), Circocardiochiles (1 species), Hymenicis (3 species - endemic), Latitergum (3 species - endemic), Polycardiochiles (3 species) and Pseudcardiochilus (1 species). This study records species of Bohayella and Pseudcardiochilus from Australasia for the first time with the description of one new species in each. The key to species is based on females due to the importance placed on the morphology of ovipositor and hypopygial structures in the subfamily. Males show little sexual dimorphism and can generally be related to females on morphological structures other than the genitalic characters. While male genitalia appears constant in many species, sternites 7 and 8 vary in form among some species as discussed in Section 4.4.7.

Distribution patterns of the Australasian fauna are discussed in detail in Section 7.4. There are radiations of species in the northern and north-eastern tropical rainforest regions as well as an abundant desert adapted fauna. No species are found in the south Bassian region. Six species, described here as new, represent two new endemic Australian genera *Latitergum* gen. nov. and *Hymenicis* gen. nov. *Hymenicis* has the apical desclerotisation of the hypopygium unlike any other genus (see Chapter 6).

Twenty-eight species are described here for the Australasian region, however many other single specimens have been examined that could not easily be placed and may represent new species. Estimated number of species for the region is about 40 based on single non-placed specimens.

The contents of this chapter were submitted for publication (Dangerfield and Austin in press) prior to the generic revision presented here (Chapter 6), and the species for that publication are placed in *Cardiochiles s. l.* and *Bohayella*.

7.2. Key to the Australasian species of Cardiochilinae Nees ab Esenbeck (Based on females)

Ovipositor sheaths short and down-turned; hypopygium short, with square 1. to obtuse angle at apex (Figs 7.31, 7.34) 2 Ovipositor sheaths long, sub-equal in length to hind tibia; hypopygium with acute point at apex (Fig. 6.60) 6 Eyes conspicuously pilose (Fig. 7.10); tarsal claws pectinate; T1 elongate 2(1).and narrow, ≥ 6.0 x as long as apically wide; dorsal medial node on T2 well-developed and ball-like (Fig. 7.12) Boh. toxopeusi, sp. nov. Eyes appearing glabrous or sparsely covered with very short hairs (Figs 7.30, 7.32); tarsal claws simple; T1 not elongate, < 3.0 x as long as wide; dorsal medial node on T2, if present, weakly transverse (Fig. 6.77) Propodeal areola complete (viz. longitudinally diamond- or oval-shaped) ... 4 3(2). Propodeal areola reduced to incomplete, carinae weakly defined anteriorly (Fig. 7.30) or represented only by posterior carinae which diverge anteriorly (Fig. 7.33) 5 4(3). Notauli smooth; wings sub-hyaline in basal half, lightly infuscate at apex; hypopygium short and evenly sclerotised throughout; median field of T2 0.7 x as long as broad; in dorsal view ratio of length of eye to length of temple 1:0.8 (Fig. 6.77) Pse. naumanni, sp. nov. Notauli sharply defined, deep and crenulate anteriorly (Fig. 7.30); wings yellow in basal half, darkly infuscate at apex; hypopygium evenly sclerotised basally, membranous and collapsible in apical one-quarter (Fig. 7.31); median field of T2 long, 1.2×10^{12} x as long as broad; in dorsal view ratio of length of eye to length of temple 1:0.5 (Fig. 7.30)

5(3).	Propodeum clothed with thick dense pilosity, areola represented by short
	posterior carinae which diverge anteriorly (Fig. 7.33)
	Propodeum sparsely pilose; anterior one-quarter of propodeal areola with
	carinae absent (Fig. 6.39) Hym. noongarensis, sp. nov.
6(1).	Epicnemial carina present at least ventrally (Fig. 6.9); medial longitudinal
	ridge present on scutum (Figs 7.1, 7.2, 7.5) (weak in Aus. morulus (Fig.
	7.6)); malar carina present as ventral part of occipital carina (Fig. 6.8) 7
	Epicnemial carina absent; medial scutum smooth; malar carina usually absent
	(present in Pol. gwenae) 11
7(6).	Dorsal scutellum enlarged, rounded and humped in lateral view (Figs 7.1,
	7.5)
	Dorsal scutellum flat or only slightly humped in lateral view (Figs 7.2, 7.6)
8(7).	T1 elongate, 3.6 x as long as broad; median field of T2 long and narrow, 5.0
	x as long as broad, 0.25 x as long as T3 (Fig. 7.11), lens-shaped,
	posterior edge forming a 90° shelf Aus. callemondah, sp. nov.
	T1 2.0 x as long as broad; median field of T2 3.6 x as long as broad, 0.7 x
	as long as T3 (Fig. 7.5) Aus. deetoo, sp. nov.
9(7).	Face with medial longitudinal carina and transverse rugulae laterally; dorsal
	scutellum bordered by lateral carinae (Fig. 7.6) Aus. morulus, sp. nov.
	Face smooth, with dorsal medial node (Fig. 7.3); dorsal scutellum not
	bordered by lateral carinae (Fig. 6.6) 10
10(9).	Second submarginal cell of fore wing 3.6 x as long as broad (Fig. 6.7); T2
	0.3 x as long as T3 (Fig. 6.6); body yellow-orange with black patches
	Aus. pollinator, sp. nov.
	Second submarginal cell of fore wing 2.5 x as long as broad (Fig. 7.4); T2
	0.4 x as long as T3 (Fig. 7.2); body black with white pilosity and white
	patches on legs Aus. exleyae, sp. nov.

11(6).	Notauli crenulate (Figs 6.57, 7.18); sternaulus crenulate (Figs 6.60, 7.19)
	Notauli smooth (Fig. 7.15); sternaulus smooth (Fig. 7.17)
12(11).	Hypopygium medially desclerotised and membranous, with apical sclerotised
	bridge (Fig. 6.68) 13
	Hypopygium evenly sclerotised throughout 15
13(12).	Mesosoma orange Pol. dissimulator (Turner)
	Mesosoma black to dark brown 14
14(13).	Propodeum < 2 x as broad as long (Figs 7.42 - 7.44); malar carina absent;
	ovipositor sheaths squarely truncated to rounded at apex (Fig. 6.60)
	Propodeum > 2.5 x as broad as long; malar carina present; ovipositor
	sheaths obliquely truncate and rounded at apex Pol. gwenae, sp. nov.
15(12).	Wings with even very dark infuscation (not patterned) 16
	Wings sub-hyaline to moderately infuscate or patterned with yellow and dark
	infuscation 17
16(15).	Antennae with 36-38 segments; body 4-5 mm in length; vertex yellow with
	black spots beside dorsal part of eye Car. goosei, sp. nov.
	Antennae with 41-46 segments; body 5-6 mm in length; vertex either all
	yellow or all black Car. scotti, sp. nov.
17(15).	Ovipositor sheaths squarely truncate to slightly rounded apically (Fig. 7.23)
	Car. uniformis Turner
	Ovipositor sheaths obliquely truncate or pointed apically
18(17).	Ovipositor sheaths pointed medially at apex, short, 0.4 x as long as hind
	tibia, broad and curved medially Car. rasi, sp. nov.
	Ovipositor sheaths with apex obliquely truncate and pointed ventro-apically,
	≥ 0.5 x as long as hind tibia, not curved medially
19(18).	Ovipositor sheaths 0.5 x as long as hind tibia, stout, < 5.2 x as long as wide

	Ovipositor sheaths long, 0.9 x as long as hind tibia, slender, > 7.0 x as long
	as wide Car. saeedi, sp nov.
20(11).	T1 short and broad, 0.75 x as long as broad (Fig. 7.37); propodeal areola
	broad and weakly defined anteriorly, with medial longitudinal carinae in
	anterior one-sixth; scutum 1.6 x as broad as long; posterior band of
	scutellum rounded and smooth medially; clypeus with broad central point
	(Fig. 7.41) 21
	T1 elongate, >2 x as long as broad; propodeal areola complete (diamond-
	shaped), diverging from anterior border of propodeum (Fig. 7.36);
	clypeus with 2 weakly-defined tubercles (Fig. 7.38)
21 (20).	Tarsal claws simple Lat. areyongensis, sp. nov.
	Tarsal claws pectinate Lat. turneri, sp. nov.
22(20),	Body large, > 6.0 mm in length; clypeal margin straight with small medial
	tubercles (Fig. 6.22) [ovipositor sheaths broadening to and rounded at
	apex (Fig. 6.23); clypeus and face broad, $> 2 x$ as broad as long (Fig.
	6.22)] Cir. occidentalis, sp. nov.
	Body small, < 5.0 mm in length; clypeal margin convex with tubercles not as
	small (Fig. 7.38) 23
23(22).	Ovipositor sheaths squarely truncate to slightly rounded at apex
	Car. iqbali, sp. nov.
	Ovipositor sheaths obliquely truncate or pointed at apex
24(23).	Head black; ovipositor sheaths broad, sharply and obliquely truncate at apex
	Lat. eremophilasturtiae, sp. nov.
	Head yellow; ovipositor sheaths narrow and pointed at apex (Fig. 7.16)
	Car. rufator Roman

7.3 Treatment of Australasian Cardiochilinae

7.3.1. Austerocardiochiles callemondah, sp. nov.

(Fig. 7.1)

Material Examined

Holotype. Q, Queensland, "vine forest 12 km N Palmer Riv Qld 16°01'S 144°48'E 16 May 1989 G. and A. Daniels" (UQIC).

Female

Length. 9.9 mm

Colour. Black to brown apart from the following which are orange to yellow: face, scape, pedicel, medial temples, dorsal pronotum, antero-lateral corners of medial scutum, medial stripe of lateral lobes of scutum, tegulae, medial scutellum, posterior half of lateral lobes of scutellum, metanotum, dorsal edge and posterior corner of lateral pronotum, posterior spot on propleuron, epicnemial ridge, apical spot on coxae, apical half of femora, tibiae and tarsi, posterior half of propodeum, T1, T2, T5-T7, S2 anterior half of S3 and wing venation; wings moderately infuscate with apico-dorsal spot on fore wing.

Head. Eyes and head with dense moderately short golden pilosity; labiomaxillary complex short just visible below mandibles, galea not dissected but as broad as long; malar carina extending half way up temples; epistomal suture prominent, reduced below tentorial pits, convex; clypeal margin convex, with medial clypeal tubercles indistinct; clypeus slightly raised and weakly rugulose laterally, 2.4 x as broad as high; face 1.4 x as broad as high; vertex raised slightly behind ocelli; depth of occiput in dorsal view 0.7 x length of head; face weakly rugulose with moderately dense fine pilosity and medial longitudinal ridge; frons transversely striate dorsally, with strong medial carina extending from between antennal sockets but becoming weaker to anterior ocellus; raised node present between antennal sockets; ratio of length of eye to length of temple in dorsal view 1.0:0.7; antennae with 43 segments, reaching to apex of T1; scape 1.8 x as long as broad; antennal sockets separated by 0.5 x width of antennal sockets. *Mesosoma*. Dorsal pronotum rugulose with six longitudinal carinae; scutum with punctation associated with moderately dense pilosity; parapsidal grooves moderately well-indented; scutellum densely pilose, punctate, as broad as long, rounded and humped in lateral view; scutellar sulcus 6.5 x as broad as long, with one medial and four lateral carinae; posterior band of scutellum rugulose medially; propodeal areola diamond-shaped, with two strong postero-laterally diverging carinae in anterior part and two weak posterior carinae diverging anteriorly, surrounded by rugulosity; dorsellum with medial longitudinal carina weakly defined; propodeal spiracles elongate, oval posteriorly, narrowing medially to a point anteriorly, 2.2 x as long as broad; epicnemial and sternaulus broad and crenulate; propleuron rugulose; epicnemial carina not extending to sternaulus.

Legs. Moderately robust, stout; fore tibial spur 0.9 x as long as basitarsus; hind tibia expanded at apex, 2.2 x as wide as base; hind tibia without spines among pilosity; inner hind tibial spur 1.7 x as long as outer spine, 0.6 x as long as basitarsus; hind basitarsus flattened, slightly lobed laterally with dorsal ridge at base; hind tarsal claw with 8 teeth of same width.

Wings. Fore wing with 1-SR+M 3.0 x as long as m-cu; 2-SR+M 1.5 x as long as m-cu; 1-M very slightly arched; m-cu 0.5 x as long as 1-M; 1-M 0.7 x as long as 1-SR+M; discal cell 1.5 x as long as wide; 2cu-a reduced to lightly infuscate trace; 1a present indicated by pigmented node; 1-2A+3A spectral, as pigmented as 2-2A+3A; 1-CUa thickened, 0.35 x as long as 1-CUb; 2r 0.4 x inside height of second submarginal cell, arising two-thirds along stigma; stigma 3.7 x as long as wide; 4-SRb arched in basal one-fifth then continuing straight and slightly down-turned at apex; angle between 4-SRa and 4-SRb 120°; second submarginal cell 3.2 x as long as wide; 2+3-SR convex; hind wing with 6 evenly spaced hamuli.

Metasoma. T1 3.6 x as long as broad, stem 0.55 x as long as bulb; suture between T2 and T3 represented by a well-defined groove; median field of T2 lens-shaped, humped, with anterior transverse ridge and 90° shelf at apex, 0.3 x as long as wide; ovipositor sheaths 0.5 x as long as hind tibia, o.3 x as broad as long, broadening

and rounded at apex, with dorsal notch; hypopygium with even moderate length pilosity throughout.

Male

Unknown.

Host

Unknown,

Comments

This species is most similar to *Aus. pollinator* and *Aus. deetoo*. It can be distinguished from these and other species in the genus by the length and narrowness of T1, the sharp posterior edge and raised median field of T2, the humped rounded shape of the scutellum (not as exaggerated as in *Aus. deetoo*), and the form of the propodeal areola which has prominent arched anterior carinae and reduced posterior carinae. It is known only from the holotype which was collected in vine thicket in north Queensland, and is named after the aboriginal word "callemondah", meaning many hills because of the humped scutellum and T2.

7.3.2. Austerocardiochiles deetoo, sp. nov.

(Fig. 7.5)

Material Examined

Holotype. O, Northern Territory, "11.09S 132.09E Black Point, Coburg Pen. NT, 31 Jan. 1977, E. D. Edwards" (ANIC).

Male

Length. 8.3 mm.

Colour. Yellow apart from the following which are brown: antennal flagellomeres, trochantelli, hind tarsi, and the following which are black: ocellar triangle, vertex, occipital region, mouthparts apart from apical palpal segments, medial lateral and

posterior pronotum, medial strip on anterior scutum, posterior scutum, medial scutellar sulcus, anterior and posterior margins of propodeum, postero-ventral mesopleuron, mesosternum, basal hind coxae, basal three-quarters of T1, T3-T5 and S3-S7. Fore and hind wing yellow basally, infuscate in apical one-third, venation brown to yellow medially.

Head. Eyes and head with dense moderately long golden pilosity; malar carina extending half way up temples; epistomal suture prominent, reduced medially, convex; clypeal margin convex; clypeus raised and rugulose, 2.2 x as broad as high; face 1.8 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.6 x length of head; face rugulose with moderately dense fine, long pilosity; face with medial longitudinal ridge; frons with strong medial carina extending from between antennae to anterior ocellus; ratio of length of eye to length of temple in dorsal view 1.0:0.9; antennae 41-segmented, stout not reaching past T1; scape 2.0 x as long as broad; antennal sockets separated by 0.6 x width of antennal socket.

Mesosoma. Dorsal pronotum with dorso-medial longitudinal furrow; notauli broadening posteriorly; scutum sparsely pilose; parapsidal grooves moderately well-indented; scutellum sparsely pilose, punctate, as broad as long, rounded and humped in lateral view; scutellar sulcus 8.0 x as broad as long, with ten variably spaced carinae; dorsellum with weakly defined medial longitudinal carina, and single lateral carina either side; propodeal areola slightly longer than broad, surrounded by slight rugosity; propodeal spiracles elongate, oval posteriorly, narrowing medially to a point anteriorly, 4.0 x as long as broad; sternaulus broad and crenulate; propleuron crenulate; epicnemial carina not extending to sternaulus.

Legs. Moderately robust, stout; fore tibial spur 0.77 x as long as basitarsus; hind tibia expanded at apex, 2.8 x as wide as base; hind tibia with poorly defined short golden spines among pilosity; inner hind tibial spur 1.7 x as long as outer spine, 0.5 x as long as basitarsus; hind basitarsus flattened, slightly lobed laterally with dorsal ridge at base; hind tarsal claw with eight teeth of even width.

Wings. Fore wing with 1-SR+M 3.7 x as long as m-cu; 2-SR+M 2.3 x as long as m-cu; 1-M arched slightly; m-cu 0.42 x as long as 1-M; 1-M 0.7 x as long as 1-SR+M; discal cell 1.5 x as long as wide; 2cu-a reduced to lightly infuscate trace; 1a present, indicated by pigmented node; 1-CUa 0.32 x as long as 1-CUb; 2r 0.6 x inside height of second submarginal cell, arising two-thirds along stigma; stigma 4 x as long as wide; 4-SRb evenly curved along length, slightly upturned at apex; angle between 4-SRa and 4-SRb 135°; second submarginal cell 2.9 x as long as wide; 2+3-SR sinuate; hind wing with 8 evenly spaced hamuli.

Metasoma. T1 2.4 x as long as broad, stem 0.35 x as long as bulb; suture between T2 and T3 represented by a well-defined groove; median field of T2 0.3 x as long as broad.

Female

Unknown.

Host

Unknown.

Comments

The very distinctive appearance of this one male specimen has prompted it's description as new and it is placed in *Austerocardiochiles* based on characters apart from the hypopygium. It can be distinguished from other species in the genus by the heavy sculpturing on the head and scutum and the enlarged rounded form of the scutellum. The species is known only from the holotype collected on the Coburg Peninsula, and it is named after the aboriginal word "deetoo" meaning "hill", because of the humped-shape of the scutellum.

7.3.3. Austerocardiochiles exleyae, sp. nov.

(Figs 7.2 - 7.4)

Material Examined

Holotype. Q, Queensland, "Carnarvon Range Q 30.I 1962 E Exley" (UQBA).

Paratypes. 1 \bigcirc , Qld, Westwood, 3 Mar. 1924, A. N. Burns (MVMA); 1 \bigcirc , Qld, Brisbane, 5 Jan. 1928, A. N. Burns (MVMA); 1 \bigcirc , Qld, 15 km S. W. Biggenden, Jan. 1974, H. Frauca (ANIC); 1 \bigcirc , S. E. Qld, W. of Brisbane, Moggill Farm, 25 m, 19-20 Dec. 1960, MT, J. L. Gressitt (BPBM); 3 \bigcirc , 1 \bigcirc Qld, Mt Tamborine, 22 Dec, no year, no collector (CNCI); 1 \bigcirc , Qld, Mt Cootha, Nov.-Dec., no year, no collector (CNCI).

Female

Length. 7.0 mm (range 6.7-7.3).

Colour. Black except for the following which are light yellow to white: fore femur, tibia and tarsi, basal one-third of mid tibia and basal half of hind tibia; fore wing hyaline in basal two-thirds grading to infuscate in apical one-third, hind wing hyaline in basal three-quarters infuscate in apical one-quarter; venation dark to mid brown.

Head. Eyes and head with dense short white pilosity; temples strigose; epistomal suture slightly reduced, convex; clypeal margin convex; clypeus 2.1-2.3 x as broad as high; face 1.8 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.4 x length of head; face rugulose with slight oblique ridges running to medial longitudinal ridge, with raised dorso-medial node, and two lateral nodes ventral to antennal sockets, with moderately dense fine long white pilosity; frons with strong medial carina extending from between antennae to middle of frons; ratio of length of eye to length of temple in dorsal view 1.0:1.0; antennae with 45-46 segments, stout, reaching to middle of T1; scape 1.5 x as long as broad; antennal sockets separated by 0.7 x width of antennal socket.

Mesosoma. Dorsal pronotum without dorso-medial longitudinal furrow; notauli of even width; parapsidal grooves lightly indented; scutellum sparsely pilose, punctate, as broad as long, rounded and humped in lateral view; scutellar sulcus 4.3 x as broad as long, with five - six carinae; dorsellum with medial longitudinal carina weakly indicated;

propodeal areola longitudinally lens-shaped; propodeum with long dense white pilosity; propodeal spiracles elongate, oval, rounded at both ends, 4 x as long as broad; sternaulus broad and crenulate; propleuron punctate; epicnemial not extending to sternaulus.

Legs. Moderately robust, stout; fore tibial spur as long as basitarsus; hind tibia expanded at apex, 2.2 x as wide as at base; hind tibia with poorly defined short brown spines among pilosity; inner hind tibial spur 1.7 x as long as outer spine, 0.7 x as long as basitarsus; hind basitarsus very slightly flattened with dorsal ridge at base; hind tarsal claw with an average of nine teeth.

Wings. Fore wing with 1-SR+M 5.6 x as long as m-cu; 2-SR+M 3.2 x as long as m-cu; 1-M straight; m-cu 0.3 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.6 x as long as wide; 2cu-a absent; 1a spectral lightly pigmented; 1-CUa 0.3 x as long as 1-CUb; 2r 0.6 x inside height of second submarginal cell, arising two-thirds along stigma; stigma 3.4 x as long as wide; 4-SRb curved along length, more noticeable medially; angle between 4-SRa and 4-SRb 130°; second submarginal cell 2.4 x as long as wide; 2+3-SR curved; hind wing with 7 evenly spaced hamuli.

Metasoma. T1 2.0 x as long as broad, stem 0.3 x as long as bulb; suture between T2 and T3 represented as well-defined groove; median field of T2 0.2 x as long as broad; ovipositor sheaths smooth hairless in basal one-eighth otherwise with long fine pilosity, 0.8 x as long as hind tibia, 0.25 x as broad as long, broadened to and rounded at apex, with dorsal notch; hypopygium moderate-sparsely hairy throughout.

Male

As for female.

Host

Unknown.

Comments

This species is morphologically most similar to *Aus. pollinator* and *Aus. deetoo*. However, it can be distinguished immediately by its black colour, the shortened form of fore wing second sub-marginal cell, and the presence of a medial node on the anterior face which has a small central pit. It is also similar in general appearance to *Psilommiscus sumatranus* Enderlein, but the medial ridge on the scutum and the presence of a ventral epicnemial carinae distinguish it from this species. *Aus. exleyae* is apparently restricted to south-east Queensland and it is named after the collector of the holotype, Dr Elizabeth Exley.

7.3.4. Austerocardiochiles morulus, sp. nov.

(Figs 7.6, 7.7)

Material Examined

Holotype. Q, Papua New Guinea, "Madang Province, Baiteta (12 km NW Alexishafen) 5°00'S 145°45'E, 6 December 1987, M. Wasbauer cllr." (CASC).

Paratype. 1 \bigcirc , same data as holotype (CASC).

Female

Length. 6.0 mm (range 5.9-6.0).

Colour. Black, except fore tibia and tarsi, and base of mid and hind tibiae which are white-cream; fore wing very lightly infuscate in basal half darker in apical half; hind wing hyaline in basal three-quarters, infuscate in apical one-quarter; venation brown.

Head. Eyes and head with dense short pilosity which is black on temples goldenwhite on rest of head; malar carina extending partly up occipital border; epistomal suture reduced, straight, not easily seen among rugulosity; clypeal margin convex; clypeus 1.7-2.0 x as broad as high; face 1.4-1.5 x as broad as high; vertex raised behind ocelli, as high as ocelli in anterior view; depth of occiput in dorsal view 0.5 x length of head; face rugose-punctate with two lateral transverse ridges running from anterior tentorial pits to middle of face, two lateral nodes present below antennal sockets; frons transversely strigose, with strong medial carina; ratio of length of eye to length of temple in dorsal view 1.0:1.0; antenna with 37 segments, stout reaching to about middle of propodeum; scape 1.8 x as long as broad; antennal sockets separated by 0.6 x width of antennal socket.

Mesosoma. Dorsal pronotum arched, punctate, without dorso-medial longitudinal furrow; notauli narrow, of even width; scutum mostly smooth, small punctations on antero-medial part; parapsidal grooves slightly indented; scutellum sparsely pilose, smooth, as broad as long, with slight medial furrow becoming deeper posteriorly, with narrow lateral crenulate furrow giving the impression of a narrow lateral ridge; scutellar sulcus 5.4 x as broad as long, with five to eight carinae; dorsellum with medial longitudinal carina well-developed; propodeal areola longitudinally lens-shaped; propodeum with long dense white pilosity; propodeal spiracles slightly elongate, kidney-shaped, 2,0 x as long as broad; sternaulus lightly crenulate; propleuron punctate; epicnemial carina extending to sternaulus.

Legs. Moderately robust; fore tibial spur as long as basitarsus; hind tibia expanded at apex, 2.4 x as wide as at base; hind tibia and tarsi with short brown spines among pilosity; inner hind tibial spur 1.5 x as long as outer spine, 0.6 x as long as basitarsus; hind basitarsus very slightly flattened with dorsal ridge at base; hind tarsal claw with an average of seven teeth, first tooth broad, other teeth becoming narrower.

Wings. Fore wing with 1-SR+M 4.2 x as long as m-cu; 2-SR+M 2.0 x as long as m-cu; 1-M straight; m-cu 0.4 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a virtually absent; 1a spectral lightly pigmented; 1-CUa 0.35 x as long as 1-CUb; 2r 0.7 x inside height of second submarginal cell, arising two-thirds along stigma; stigma 3.6 x as long as wide; 4-SRb straight in basal one-quarter then sharp 135° angle; angle between 4-SRa and 4-SRb 100°; second submarginal cell 2.7 x as long as wide; 2+3-SR mostly straight, curved near junction with 2-SR+M; hind wing with five to six evenly spaced hamuli; 2-1A as basal node, not pigmented.

Metasoma. T1 1.8 x as long as broad, stem 0.5 x as long as bulb; suture between T2 and T3 represented by well defined groove; median field of T2 poorly

defined; ovipositor sheaths 0.4 x as long as hind tibia, 0.3 x as broad as long, smooth and hairless in basal one-eighth otherwise with long fine pilosity, broadened medially, tapering and rounded to a point at apex; hypopygium moderately hairy throughout.

Male

As for female except as follows:

Body smaller, 4.1-4.3 mm; head and scutellum with denser pilosity; second submarginal cell slightly shorter.

Host

Unknown.

Comments

This species is most similar to *Aus. pollinator* but can be distinguished by its black coloration, the marked facial sculpturing, and the broader propodeal areola. It is also similar to *Psilommiscus sumatranus* but the medial ridge on the scutum and the presence of ventral epicnemial carinae separate it from this species. It is apparently restricted to Papua New Guinea, and is named after its black coloration.

7.3.5. Austerocardiochiles pollinator, sp. nov.

(Figs 4.7, 4.19, 6.6 - 6.9, 7.48)

Material Examined

Holotype. Q, Queensland, "Rockpool Gorge Bluff Range via Biggenden QLD 13 Jan 1977 H. Frauca" (ANIC).

Paratypes. 1Q, Qld, Mt. Walsh Nat. Pk., via Biggenden, 12 Jan. 1977, H. Frauca (ANIC); 2O^{*}, same data, 17 Jan. 1977 (ANIC); 2O^{*}, same data, 28 Jan. 1977 (ANIC); 1O^{*}, same data, 3 Jan. 1979, H. Frauca (ANIC); 1Q Qld, Caloundra, 19 Dec. 54, J. Kerr (MVMA); 1Q, Qld, Mackay, Feb. 1964, J. E. Dunwoody (UQBA); 1O^{*}, Qld, Blunder Cr., Brisbane, 15 Nov. 1979, H. E. & M. Evans (UQBA); 1O^{*}, Qld, Caloundra, 21 Mar. 1972, S. R. Monteith (ANIC); 1O^{*}, Qld, Dunwich, 30-31 Dec. 1963, B. V. Timms (UQBA); 1O^{*}, Qld, Glen Aplin, 17 Feb. 1964, J. C. Cardale (UQBA); 1Q, NSW, London Foundation, Kioloa, 14 Dec. 1980, J. Conran (ANIC); 1Q, 1°, Australia, no date or collector (BMNH).

Female

Length. 8.3 mm (range 7.5-8.5).

Colour. Variable (see below); holotype black except for the following: antennae and apical segment of maxillary palps which are brown; clypeus, dorsal pronotum, lateral pronotum apart from anterior one-fifth, anterior notauli, antero-lateral scutum, tegulae, dorsal and lateral scutellum, metanotum apart from posterior band, epistomal ridge, distal two-thirds of femora, tibiae, tarsi, T1, T2, lateral T5, T6, T7 and S1 which are yellow; wing venation yellow-orange, proximal three-quarters of fore wing yellow, distal one-quarter more darkly infuscate; hind wing evenly yellow.

Head. Eyes and head with dense moderately long golden pilosity; epistomal suture slightly reduced, gently convex; clypeal margin convex; clypeus 1.9-2.0 x as broad as high; face 1.4-1.6 (holotype 1.5) x as broad as high; vertex raised very slightly behind ocelli, but not higher than ocelli as seen in anterior view; depth of occiput in dorsal view 0.7 x length of head; face mostly smooth, with micro-punctures associated with moderately dense fine long pilosity, with medial dorsal node; frons with strong medial carina extending from between antennal sockets to mid point of frons; ratio of length of eye to length of temple in dorsal view 1.0:1.0; antennae with 41-44 segments (holotype 41), short, stout, not reaching past propodeum; scape 1.6-1.9 x as long as broad; antennal sockets separated by 0.8 x width of antennal socket.

Mesosoma. Dorsal pronotum with dorso-medial longitudinal furrow and four lateral furrows; notauli broadening posteriorly; scutum sparsely pilose; parapsidal grooves moderately well-indented; scutellum sparsely pilose, as broad as long, flat in lateral view, with slight raised ridge at lateral edges of dorsal scutellum; scutellar sulcus 4.0 x as broad as long with three to seven variably spaced carinae; dorsellum with medial longitudinal carina weakly to moderately well-defined; propodeal areola narrow, elongate; propodeal spiracles elongate, oval posteriorly, narrowing to a point anteriorly,

2.5 x as long as broad; sternaulus broad and crenulate; propleuron crenulate; epicnemial carina not extending to sternaulus.

Legs. Moderately robust, stout; fore tibial spur 0.8 x as long as basitarsus; hind tibia expanded at apex, 2.6 x as wide as base; hind tibia and tarsi with evenly spaced short golden spines among pilosity; inner hind tibial spur 1.5 x as long as outer spine, 0.7 x as long as basitarsus; hind basitarsus very slightly flattened, with dorsal ridge at base; hind tarsal claw with eight to ten teeth.

Wings. Fore wing with 1-SR+M 3.3 x as long as m-cu; 2-SR+M 1.9 x as long as m-cu; 1-M straight; m-cu 0.47 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a reduced to lightly infuscate trace; 1a and 1-2A+3A spectral; 1-CUa 0.375 x as long as 1-CUb; 2r 0.8 x inside height of second submarginal cell, arising two-thirds along stigma; stigma 3.3 x as long as wide; 4-SRb evenly curved along length; angle between 4-SRa and 4-SRb 135°; second submarginal cell 3 x as long as wide; 2+3-SR sinuate; hind wing with eight evenly spaced hamuli, 2A absent.

Metasoma. T1 2.8 x as long as broad, stem 0.6 x as long as bulb; suture between T2 and T3 represented by well-defined groove; median field of T2 broad and short, 0.1 x as long as broad; ovipositor sheaths 0.5 x as long as hind tibia, 0.4 x as broad as long, hairy along length, becoming broader towards and rounded at apex, with dorsal notch; hypopygium moderately hairy throughout.

Male

As for female but adeagal apodemes concealed within body, when visible yellow in colour.

Variation

Antennae orange to brown; head mostly orange with brown-black patterning around vertex, frons and occiput all black with clypeus always yellow; tegulae orangeyellow; lateral lobes of scutum all black to black-brown with orange in anterior one-fifth;

medial scutum all orange to all black; scutellum and metanotum orange; propodeum all orange to orange with anterior black transverse band; coxae trochanters and trochantellus black to brown, femur orange to brown, rest of legs orange; T1 mostly all orange sometimes with medial field all black to black anteriorly; T2 all yellow, orange or black; T3-T5 mostly black T5 sometimes orange with black transverse band anteriorly; remaining tergites yellow or orange; sternites mostly all black, sometimes with S1 yellow or orange; ovipositor sheaths brown or black.

Host

Unknown,

Comments

This species can be distinguished from other Australasian species by the dense golden pilosity on the body and the narrow form of the propodeal areola. Two specimens from BMNH labelled "Australia" have *Asclepias* spp. (milkweed) pollinia attached to their tarsal claws and were presumably collected from this plant. It is distributed along the south-east and central coast of Queensland and is here named after the pollen and pollinia attached to some specimens.

7.3.6. Bohayella adina (Wilkinson) comb. nov.

(Fig. 7.13)

Cardiochiles adina Wilkinson, 1930: 486. Beeson and Chatterjee, 1935: 120; Beeson,

1941: 365; Thompson, 1953: 100; Shenefelt 1973: 786.

Material Examined

Lectotype. Q, India, "New Forest Dehra Dun, U.P. R.N. Mathur. 23.ix.1929" (BMNH). Paralectotype. Q, same data as lectotype with date 18 Sept. 1929 (BMNH).

Other material examined. India: 20 Dehra Dun, U.P., S.N. Chatterjee, 24 Jul. 1932, on *Dirades theclata* larvae (BMNH); 10⁷, Karnataka, Mudigere, 26 Oct.-4 Nov. 1979, J. S. Noyes (BMNH). Malaysia: 10, Selangor, Ulu Gombok, 14 Dec.

1977, B. B. (CNCI); 10[°], SW Sabah, nr Long Pa Sia, Payakalaba, LT., C. van Achterberg & J. Huisman (RMNH).

Comments

This species was not recognised by Belokobylskij (1987) when he described *Bohayella* as a monospecific genus for *Boh. tobiasi* Belokobylskij. However, it clearly belongs here on the basis of the exaggerated form of the notauli, presence of prepectal carina, shape of the propodeal areola, and form of T1 and T2. *Boh. adina* can be distinguished from *Boh. tobiasi* by the shape of the median field of T1 which has a long stem and apical bulb in the former species, and very short stem and medial and apical bulbs of T1 in the latter. Further, *Boh. adina* can be separated from *Boh. toxopeusi* sp. nov. by the form of the median field of T1, which is apically broader in *Boh. toxopeusi*, it's smaller size, smoother mesopleuron, less well-developed scuto-scutellar crenulations, shorter white palps, and smoother face.

Host

Pupal cocoons of *Boh. adina* from India are mounted with some specimens (BMNH) and were reared from *Dirades theclata* (Uraniidae: Epiplemidae). They are about 4.5 mm long and 2.8 mm broad, with a relatively smooth, light brown surface. The exit hole is circular and just off centre at one end.

7.3.7. Bohayella toxopeusi, sp. nov.

(Figs 7.8 - 7.12)

Material Examined

Holotype. \bigcirc , Papua New Guinea, "Neth. Ind- American New Guinea Exped. Araucaria Camp 800m iii. 1939 L. J. Toxopeus" (CNCI) (The head detached from body and glued onto minuten pin.).

Female

Length. 5.7 mm

Colour. Body brown to black apart from the following which are white or yellow: segments 3 and 4, of labial palps, T1 apart from bulb of median field, T2 apart from median field, S1, S2 and S3; fore wing hyaline in basal half, moderately darkly infuscate in apical half; hind wing hyaline in basal three-quarters, lightly infuscate in apical one-quarter apart from dark infuscation in posterior half of costal and basal cells; venation dark brown.

Head. Eyes with moderately long sparse pilosity, small, 2.5 x as long as genal space; head smooth with sparse moderately long pilosity; mandibles bidentate; (maxillary and labial palps broken); epistomal suture well-defined; clypeal margin evenly convex; clypeus 2.1 x as broad as high; face 2.0 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.25 x length of head; face smooth with medial dorsal node; frons smooth with sharp medial carina which reaches 0.6 x distance to anterior ocellus; ratio of length of eye to length of temple in dorsal view 1.0:1.2; antennae broken with > 14 segments; scape 1.5 x as long as broad; antennal sockets separated by 1.3 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat, with medial anterior and posterior notch; notauli bordered by raised crenulate ridges, broadening slightly and meeting posteriorly; scutum with medial longitudinal crenulate carina not set in furrow, bordered by lateral crenulate carinae; parapsidal grooves absent; axillae concave with posterior edge bordered by carina; dorsal scutellum crenulate, bordered by carinae, 1.3 x as broad as long, posterior band with well-defined crenulate depression medially; (scutellar sulcus damaged by minuten pin); dorsellum with faint medial carina; propodeum rugose, propodeal areola oval-shaped, carinae prominent; propodeal spiracles ovoid, 2 x as long as wide; sternaulus deep, broad, crenulate; propleuron smooth.

Legs. Fore tibial spur as long as basitarsus; hind tibia expanded at apex, $3 \times as$ wide as at base, 0.2 x as wide as long; hind tibia and tarsi without spines among pilosity; inner hind tibial spur 1.5 x as long as outer spur, 0.7 x as long as basitarsus; hind basitarsus with slight flattening and dorsal ridge at base; fore tarsal claws pectinate (mid and hind claws missing).

Wings. Fore wing with 1-SR+M 2.1 x as long as m-cu; 2-SR+M 1.1 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.9 x as long as 1-SR+M; discal cell 1.4 x as long as wide; 2cu-a represented by pigmented area; 1a present in basal half, pigmented and spectral in apical half; 1-2A+3A present and spectral, joining spectral apex of 1a; 1-CUa 0.25 x as long as 1-CUb; 2r 0.7 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 2.8 x as long as wide; 4-SRb straight in basal one -fifth then angled and continuing straight to 0.64 x along length then angled and curved down to apex; angle between 4-SRa and 4-SRb 135°; second submarginal cell 3.2 x as long as wide; 2+3-SR arched at base; hind wing with six evenly spaced hamuli; 1-SRa well-developed; 2-1A as basal node, 2A indicated basally by pigmentation.

Metasoma. T1 long, 6.0 x as long as apical width, stem 1.6 x as long as bulb; suture between T2 and T3 not well defined; median field of T2 0.2 x as long as broad; ovipositor short, broad at base, down-curved; ovipositor sheaths short and paddle-like, hairy in apical three-quarters, broadly rounded at apex, 0.2 x as long as hind tibia, 0.4 x as broad as long; hypopygium with sparse, fine hair laterally, obtuse at apex.

Male

Unknown.

Host

Unknown.

Comments.

This is the first record of the genus from the Australasian region. *Boh. toxopeusi* is similar in colour to *Boh. adina* and *Boh. tobiasi* but can be distinguished from the former species by its heavily sculptured notauli, lateral pronotum, scutellum and propodeum. and by the medial ridge on the scutum. It differs from *Boh. tobiasi* by

having the median field of T1 with a long stem and apical bulb, a character it shares with *Boh. adina*. This species is named after its collector, L. J. Toxopeus.

7.3.8. Cardiochiles evelinae, sp. nov.

(Fig. 7.46)

Material Examined

Holotype. Q, Western Australia, "9.5 km SE of Banjiwarn HS (27.42'S 121.37'E) W. Aust. 22-28 FEB. 1980 T. F. Houston <u>ET AL</u> 316-13" (WAMP).

Paratypes. 1Q, W. Aust., Dumbleyung, 5 Oct. 1963, H. Udell (WAMP); 1Q, W. Aust., Forrest R. Mission, 24th Apr. 1953, R. Lukins (WADA). 1Q, N. T., Areyonga, 600m, Nov., no year or collector (AEIC); 1Q, N. T., Roe Creek, 12 km S.W. by W. Alice Springs, 9 Oct. 1978, J. C. Cardale (ANIC); 1Q, N. T., 32 km S. by E. Alice Springs, 23 Sep. 1978, J. C. Cardale (ANIC). 1Q, Qld, Brigalow Developmental Area, Moura, 13 Nov. 1970 (QDPI).

Female

As for *Car. uniformis* except as follows:

Length 4.9 mm (range 4.0-5.7); antennae with 34-38 segments; ovipositor sheaths 0.5 x hind tibia, broad, 0.19 x as broad as long, obliquely truncate at apex with ventral point.

Male

Unknown.

Host

Unknown.

Comments

This species is similar to *Car. rufator*, *Car. verticalis*, *Car. goosei* and *Car. scotti*, as it has an obliquely truncate apex to the ovipositor sheaths. However, in every

other respect it is virtually identical to *Car. uniformis*. It is widespread in distribution (Fig. 7.46) and is here named after Eveline Bartowsky.

7.3.9. Cardiochiles goosei, sp. nov.

(Fig. 7.14)

Material Examined

Holotype. Q, Papua New Guinea, "P. N. Guinea Laloki, 28 ix. 1992" "ex Crocidolomia binotalis on cabbage", no collector (BMNH).

Paratypes. 2Q, 10[°], same data as holotype (BMNH, WARI).

Female

Length. 4.5 mm (range 4.3-4.9).

Colour. Yellow apart from the following which are brown: spot on vertex at dorsal margin of either eye, flagellomeres, pedicel, posterior edge of scape, medial T5-T8, apex of femur, basal one-quarter and apical half of tibia, tarsi, ovipositor sheaths; fore and hind wings with even dark infuscation venation dark brown apart from basal one-quarter of stigma which is yellow.

Head. Eyes with moderately short fine golden pilosity; head smooth with moderately sparse long pilosity; galea 0.5 x as long as height of eye; epistomal suture convex medially; clypeal margin convex; clypeus 2.4 x as broad as high; face 1.7 x as broad as high; vertex slightly raised behind ocelli viewed anteriorly; depth of occiput in dorsal view 0.4 x length of head; face smooth, with very small medial dorsal node; frons smooth, with smooth node between antennal sockets; ratio of length of eye to length of temple in dorsal view 1.0:0.7; antenna with 36-37 segments, 0.9 x length of body; scape 1.8 x as long as broad; antennal sockets separated by 0.9 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, convex with slight dorso-medial pit posteriorly; notauli crenulate, meeting posteriorly; scutum smooth; parapsidal grooves slightly indented posteriorly; scutellum sparsely pilose, smooth, 1.4 x as broad as long, very slightly humped in lateral view, posterior edge emarginate medially; scutellar sulcus
5.0 x as broad as long, with six to seven irregularly spaced carinae; dorsellum with strong medial longitudinal carina; propodeum with faint rugulosity; propodeal areola diamond-shaped; propodeal spiracles ovoid to kidney-shaped, 0.4 x as broad as long; sternaulus shallow, arched ventrally in apical half, crenulate anteriorly, smooth posteriorly; propleuron smooth.

Legs. Fore tibial spur as long as basitarsus; hind tibia not broadened, with only slight flange at apex, $1.8 \times as$ wide at widest part as at base; hind tibia with longer black spines among pilosity; inner hind tibial spur $1.3 \times as$ long as outer spur, $0.7 \times as$ long as basitarsus; hind basitarsus $0.2 \times as$ wide as long; hind tarsal claw with six teeth becoming smaller basally, apical tooth same size as others.

Wings. Fore wing with 1-SR+M 3.1 x as long as m-cu; 2-SR+M 1.3 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.66 x as long as 1-SR+M; discal cell 1.7 x as long as wide; 2cu-a absent; 1a present basally; 1-2A+3A present, spectral basal to 1a, 2-2A+3A as pigmented postero-basal margin of wing; 1-CUa 0.25 x as long as 1-CUb; 2r 0.4 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 3.8 x as long as wide; 4-SRb gently arched in basal one-third then 150° angle and spectral node of 3r, 5-SR straight to slightly arched to apex; angle between 4-SRa and 4-SRb 135°; angle between 4-SRb and r-m 90°; second submarginal cell 2.9 x as long as wide; 2+3-SR arched basally, some with small node of 1r present dividing 2-SR and 3-SR; hind wing with five evenly spaced hamuli; 2-SC+R absent, r-m arising from 1-SR; 2-1A present in basal one-third; 2A spectral basally, otherwise absent.

Metasoma. T1 1.6 x as long as broad, stem 0.2 x as long as bulb; suture between T2 and T3 represented by a moderately well-defined groove; median field of T2 poorly defined, 0.5 x as long as broad; ovipositor sheaths broad and long, 0.5 x as long as hind tibia, 0.3 x as broad as long, hairy in apical three-quarters, obliquely truncate at apex with slight dorsal notch and apical point; hypopygium evenly sclerotised and pilose throughout.

Male

As for female except length 4.0 mm; antenna with 38 segments.

Host

The species has been reared from *Crocidolomia binotalis* (Pyralidae: Evergestinae) on cabbage in Papua New Guinea, a host which is thought to be oriental in origin (Common 1990). Two specimens are mounted with pupal cocoons which measure 6.5 mm in length, are buff coloured with longitudinal ridges (as seen in diapausing cocoons of the microgastrine, *Microplitis demolitor* Wilkinson), and have emergence holes with rough edges near the end of the cocoon.

Comments

This species is close to *Car. uniformis* but has the wings completely and darkly infuscate. It is also similar to *Car. scotti* but can be distinguished by its smaller size, having fewer antennal segments, and having small black spots on the vertex next to the eyes. It is named after Andrew (Goose) Wait.

7.3.10. Cardiochiles iqbali, sp. nov.

Material Examined

Holotype. \bigcirc , Northern Territory, "Areyonga, 600m N.T., Australia August 8" no year or collector (AEIC).

Paratypes. 2 \bigcirc , same data as holotype (AEIC); 1 \bigcirc , same data as holotype but with date 15 Sept. (AEIC).

Female

As for Car. rufator except as follows:

Length 4.4 mm (range 4.3-4.6); antenna with 32-33 segments; ovipositor sheaths squarely truncate to rounded at apex.

Male

Unknown,

Host

Unknown.

Comments

This species is closely allied to both *Car. uniformis* and *Car. rufator*. However, it has smooth notauli and sternauli unlike *Car. uniformis*, and the ovipositor sheaths squarely truncate at the apex unlike *Car. rufator*. It is known only from Areyonga in the MacDonnell Ranges and is here named after Muhammad (Miq) Iqbal.

7.3.11. Cardiochiles rasi, sp. nov.

(Fig. 7.47)

Material Examined

Holotype. \bigcirc , Queensland, "Australia, N. Qld. Bamaga, II. 18.84 J. Sedlacek Rain forest" (AEIC).

Paratypes. 6Q, 10[°], same data as holotype (AEIC); 8Q, 130[°], same data as holotype but with dates 1 Dec., no year - 20 Feb. 1984 (AEIC); 1Q, Escott Stn, W. of Burketown, 18th Apr. 1983, I. Donaldson (WARI); 10[°], W. Aust., Lone Dingo Mitchell Plateau, 14.35 S 125.45E, 9-19 May 1983, Naumann & Cardale (ANIC).

Female

As for Car. uniformis except for the following:

Length 4.2 mm (range 3.3-5.5); body all yellow apart from antennae, hind tarsi and apical four-fifths of ovipositor sheaths which are brown; antennae with 38-42 segments; ovipositor sheaths 0.3-0.4 x as long as hind tibia, 0.3 x as broad as long, narrow basally, broadening to apex, pointed medially at apex and slightly down-curved.

Male

As for female.

Host

Unknown.

Comments

This species can be distinguished from the other Australasian species by the form of the ovipositor sheaths, their colour and the number of antennal segments. It is widely distributed across northern Australia (Fig. 7.47) and is here named after Stephen (Ras) Wait.

7.3.12. Cardiochiles rufator Roman

(Figs 7.15 - 7.17, 7.25, 7.47)

Cardiochiles rufator Roman, 1915: 17. - Parrott, 1953: 202; Shenefelt, 1973: 798.

Material examined

Holotype. Q, Western Australia, "Kimberley District" "N. V. Austr. Mjöberg" "febr." (NHRS).

Other material examined. Western Australia: 10° , 8 km S. of Cape Bertholert, West Kimberley, 17.19S 122.10E, 21 Apr. 1977, D. H. Colless (ANIC). Northern Territory: 10° , Nourlangie Ck, 8 km N. of Mt Cahil, 12.48S 132.42E, 16-17 June 1973, J. C. Cardale (ANIC); 10° , Horn Islet, Pellew Group, 25-31 Jan. 1968, B. Cantrell (UQBA); 10° , 32 km S. by E. of Alice Springs, 23.59S 133.56E, 23 Sept. 1078, J. C. Cardale (ANIC). Queensland: 10° , Townsville, 60 km N. W. Hervey Range, Keelbottom Creek, 19 Sept. 1981, D. C. & R. Geijskes (RMNH); 10° , Cooloola Nat. Pk, 2-7 Mar. 1984, I. D. Galloway (TAMU). New South Wales: 10° , Billabong Ck nr Conargo, 35.17S 145,11E, 12-17 Apr. 1978, J. C. Cardale (ANIC).

Female

Length. 4.6 mm (range 3.6-5.0).

Colour. Yellow apart from the following which are brown: flagellomeres, scape, pedicel, hind tarsi and ovipositor sheaths apart from extreme base; fore and hind wings

evenly lightly infuscate; venation brown except basal one-third of stigma which is yellow.

Head. Eyes with short fine pilosity; head smooth with fine pilosity; galea $0.5 \times as$ long as height of eye; malar carina absent; epistomal suture convex medially; clypeal margin convex, tubercles weakly defined; clypeus 2.0 x as broad as high; face 1.5 x as broad as high; vertex not raised behind ocelli as seen in anterior view; depth of occiput in dorsal view 0.3 x length of head; face smooth, with medial dorsal node; frons smooth, with smooth node raised between antennal sockets; ratio of length of eye to length of temple in dorsal view 1.0:0.7; antennae with 33-34 segments, 0.9 x length of body; scape 1.6 x as long as broad; antennal sockets separated by 1.0 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat; notauli smooth, meeting posteriorly; scutum smooth; parapsidal grooves absent; scutellum smooth, sparsely pilose, 1.1 x as broad as long, very slightly humped in lateral view, posterior edge smooth, convex medially; scutellar sulcus 5.0 x as broad as long, with five carinae; dorsellum with medial longitudinal carina which is weakly to well-developed; propodeum with faint rugulosity, propodeal areola broad, diamond-shaped; propodeal spiracles ovoid, 2.0 x as long as broad; sternaulus shallow, arched ventrally in apical half, smooth; propleuron smooth.

Legs. Fore tibial spur 0.9 x as long as basitarsus; hind tibia not broadened but with slight flange at apex, widest part 1.8 x as wide as base; hind tibia with longer golden spines among pilosity; inner hind tibial spur 1.6 x as long as outer spur, 0.8 x as long as basitarsus; hind basitarsus mostly cylindrical, with slight flattening, dorsal ridge at base, 0.2 x as wide as long; hind tarsal claw with > six teeth, apical tooth broad, about 1.5 x as wide as others.

Wings. Fore wing with 1-SR+M 3.2 x as long as m-cu; 2-SR+M 1.3 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.7 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a and 1a absent; 1-2A+3A present spectral; 2-2A+3A pigmented along postero-medial margin of wing; 1-CUa 0.2 x as long as 1-CUb;

2r 0.4 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 3.6 x as long as wide; 4-SRb straight in basal one-third then 140° angle and spectral node of 3r present, 5-SR straight to apex; angle between 4-SRa and 4-SRb 110°; angle between 4-SRb and r-m 110°; second submarginal cell 2.9 x as long as wide; 2+3-SR very slightly arched basally; hind wing with six evenly spaced hamuli; 2-SC+R reduced to spot; r-m arising from 1-SC+R; 2-1A as small basal node or absent; 2A spectral.

Metasoma. T1 1.3 x as long as broad, stem 0.2 x as long as bulb; suture between T2 and T3 represented by weakly-defined groove; median field of T2 poorly defined, 0.4 x as long as broad; ovipositor sheaths short, 0.4 x as long as hind tibia, 0.3 x as broad as long, down-turned slightly, hairy in apical two-thirds, obliquely truncate at apex with dorsal notch and apical point.

Male

As for female except clypeal tubercles reduced.

Host

Unknown.

Comments

This species is similar to *Car. uniformis* in size, antennal segment number and wing infuscation. It is differentiated from this and other Australasian species by its smooth notauli and sternauli, and the ovipositor sheaths which have a pointed obliquely truncate apex. *Car. rufator* has been collected over a very wide area covering central and northern Australia (Fig. 7.47).

7.3.13. Cardiochiles saeedi, sp. nov.

(Fig. 7.47)

Material Examined

Holotype. \bigcirc , Queensland, "Normanton Australia Mar. 9-20" no year or collector (AEIC).

Paratypes. 1Q, same data as holotype (AEIC); 1Q, same data as holotype with date 24 Feb.-1 Mar. (AEIC); 2Q, 1O, same data as holotype with dates 21 Mar. -4 Apr. (AEIC); 1Q, Rex Range Lookout via Julatten, 22 Dec.- 13 Jan. 1982, Storey & Brown (WARI); 1Q, Northern Territory, Arnhem Land, Maningrida, 5 m, 18 Mar. 1961, J. L. & M. Gressitt (BPBM).

Female

As for Car. uniformis except as follows:

Length 4.0 mm (range 3.6-4.4); body yellow apart from antennae hind tarsi and apical three-quarters of ovipositor sheaths which are black; antennae with 32-35 segments; sternaulus with well-defined crenulae; median field of T2 very weakly defined; ovipositor sheaths long, 0.9 x hind tibia, slender, 0.1 x as broad as long.

Male

As for female but with vertex and T4-T7 black-brown medially.

Host

Unknown.

Comments

This species can be distinguished from the other Australasian species by the moderately long slender ovipositor sheaths which are yellow in the basal one-quarter. It is been recorded from several localities in north-eastern Australia (Fig. 7.47) and is here named after Azhar Saeed.

7.3.14. Cardiochiles scotti, sp. nov.

(Fig. 7.46)

Material Examined

Holotype. Q, Papua New Guinea, "West New Guinea Nabire, 5-50m, 25 viii-2 ix. 62" "Malaise Trap, BISHOP" no collector (BPBM).

Paratypes. 1 \bigcirc , P. N. G., Kiunga, Fly River, 21-24 Oct. 1957 (BPBM); 1°, P. N. G., Onombususu, 26-28 Aug. 1971, J. Stibick (AEIC); 4°, P. N. G., Busu R., 20 m, 60 km E. of Lae, 15 Jan 1979, J. Sedlacek (AEIC); 19°, same data as previous with date 13 Jan.-10 Mar. 1979 (AEIC); 1 \bigcirc , P. N. G., Jimmi Valley, 900-1400 m, 25 Dec. 1978, J. Sedlacek (AEIC); 1 \bigcirc , P. N. G., Muru River, 10 m, 22 Dec. 1964, J. Sedlacek (BPBM); 3°, P. N. G., Normanby I., Wakaiuna, Sewa Bay, 11-20 Dec 1956, W. W. Brandt (BPBM); 1°, P. N. G., Popondetta, 60 m, 2 Sep. 1963, J. Sedlacek (BPBM). °, New Britain, Gaulim, Gazelle Pen., 130 m, 23-28 Oct. 1962, J. Sedlacek (BPBM).

Female

As for *Car. verticalis* except as follows: Length 6.7 mm (range 6.5-6.8); wings with dark even infuscation; venation all brown; vertex all yellow or all black.

Male

As for female except antennae with 41-46 segments.

Host

Unknown.

Comments

This species is most similar in morphology to *Car. verticalis* and *Car. goosei*. It can be distinguished from the former species by having evenly infuscate wings and from the latter species by the colour, larger number of antennal segments, and larger size. It is apparently restricted to Papua New Guinea (Fig. 7.46) and is here named after Scott Field.

7.3.15. Cardiochiles uniformis Turner

(Figs 7.18 - 7.23, 7.27, 7.46)

Cardiochiles uniformis Turner, 1918: 51. - Parrott, 1953: 202; Shenefelt, 1973: 803.

Material Examined

Holotype. ♀, Australia, "Mackay, Queensland. 1909-45." "1054", "Mackay 2-4. 00" (BMNH).

Other specimens examined. Queensland: 7Q, 4O, Mackay, 1909-45, (ANIC, BMNH); 2Q, Moura, Brigalow Development Area, 8 Nov. 1968, ex *Heliothis*, F. D. Page & L. Rigby (QDPI); 2Q, 60 km S. E. Augathella, 10 Oct. 1988, R. J. Lloyd, ex *Heliothis* larvae (QDPI); 1Q, Gatton, DPI Research Station, 21-28 Sept. 1981, no collector (QDPI). New South Wales: 1Q, 32 km S.W. Wilcannia, 11 Sept. 1981, R. Pigott (NSWA); 1Q, Mt Lindesay State Forest, 480 m via Woodenbong, 24 Feb. 1974, I. Naumann (UQBA); 1Q, Narrabri, 12 Apr. 1973, no collector, parasite of larvae of *Heliothis* sp. (NSWA); 1Q, Mundowie, 5 Mar. 1941., C. R. W. (NSWA). Western Australia: 1Q, 9 mi. W. Pithara 20 Sept. 1968, H. Evans & R. W. Matthews (USNM); 1Q, Meredin, 150 mi. E. of Perth, 17 Oct. 1952, H. F. Broadbent (BMNH); 1Q, Bolgart, Nov. 1947, no collector (ANIC).

Female

Length. 5.4 mm (range 5.0-6.0).

Colour. Yellow apart from the following which are variably brown to black: antennae, sometimes with brown-black spot on stemmaticum and lateral brown-black spots on vertex near eyes (not in holotype of *Car. uniformis*), central areas of medial and lateral lobes of scutellum (very faint in holotype), medial bands on T4-T7, mesosternum, hind tarsi and ovipositor sheaths; wings evenly lightly infuscate; venation yellowbrown, stigma with proximal one-fifth yellow.

Head. Eyes with moderately dense white pilosity; head smooth with sparse moderately long pilosity; epistomal suture convex medially; clypeal margin convex to straight, tubercles not well-defined; clypeus 2.4 x as broad as high; face 1.7 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.3 x length of head; face smooth with faint indication of medial dorsal node; frons smooth with

smooth node raised between antennal sockets; ratio of length of eye to length of temple in dorsal view 1.0:0.9; antennae with 33-36 segments, 0.9 x length of body; scape, 1.6 x as long as broad; antennal sockets separated by 1.1 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat with dorso-medial longitudinal furrow; notauli weakly crenulate, sometimes smooth anteriorly, of even width, meeting broadly posteriorly; scutum smooth; parapsidal grooves absent; scutellum sparsely pilose, smooth, 1.1 x as broad as long, very slightly humped in lateral view, posterior edge smooth medially but with small extended ledge over antero-medial part of dorsellum; scutellar sulcus 5.0 x as broad as long, with seven carinae; dorsellum with medial longitudinal carina well-defined; propodeum with faint rugulosity; propodeal areola diamond-shaped, with anterior medial carina; propodeal spiracles ovoid, 1.4 x as long as broad; sternaulus shallow, arched ventrally at apex, weakly crenulate; propleuron smooth.

Legs. Fore tibial spur 0.8 x as long as basitarsus; hind tibia not broadened with only slight flange at apex, widest part 1.8 x as wide as base; hind tibia with long golden spines among pilosity; inner hind tibial spur 1.5 x as long as outer spur, 0.8 x as long as basitarsus; hind tarsal claw with four teeth, apical tooth broad, about 2 x as wide as others.

Wings. Fore wing with 1-SR+M 3.5 x as long as m-cu; 2-SR+M 1.3 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.6 x as long as wide; 2cu-a represented by pigmented area; 1a present, spectral; 1-2A+3A present proximal to 1a; 2-2A+3A present as pigmented medio-posterior margin of wing; 1-CUa 0.3 x as long as 1-CUb; 2r length 0.6 x inside height of second submarginal cell, arising 0.5-0.6 x length along stigma; stigma 3.4 x as long as wide; 4-SRb straight in basal one-third then 145° angle with small node of 3r, 5-SR straight to apex; angle between 4-SRa and 4-SRb 135°; angle between 4-SRb and r-m 90°; second submarginal cell 3.2 x as long as wide; 2+3-SR arched moderately at middle to strongly at base; hind wing with four evenly spaced hamuli; 2-SC+R present, r-m arising from apex of 2-SC+R; 2-1A as small basal node; 2A spectral.

Metasoma. T1 1.9 x as long as broad, stem absent; suture between T2 and T3 represented by moderately well-defined groove; median field of T2 0.5 x as long as broad; ovipositor sheaths broad and long, 0.6 x as long as hind tibia, 0.2 x as broad as long, hairy in apical three-quarters, broadest and rounded at apex, with slight dorsal notch; hypopygium evenly pilose throughout.

Male

As for female except slightly darker; antenna with 37 segments,

Host

Helicoverpa sp. (Lepidoptera: Noctuidae).

Comments

Car. uniformis can be distinguished from the other Australasian species by having the notauli and sternauli crenulate and the ovipositor sheaths squarely truncate to slightly rounded at the apex. This species is broadly distributed across Australia, but has been mostly collected from the southern part of the continent (Fig. 7.46) with 2 disjunct populations, one in the south-west of Western Australia and the other in southern Queensland and northern New South Wales.

7.3.16. Cardiochiles verticalis Turner

(Figs 7.24, 7.28, 7.46)

Cardiochiles verticalis Turner, 1918: 51. - Parrott, 1953: 202; Shenefelt, 1973: 803.

Material Examined

Holotype. Q, Queensland, "Mackay, Queensland. 1909-45." "Mackay 2-4. 00" (BMNH) (metasoma missing).

Other material examined. Queensland: 4Q, 10[°], Mackay, 1909-45 (BMNH); 1Q, Mackay, 1966-578, R. E. & G. Turner (BMNH); 6Q, Bamaga, 3 Feb. 1984, J. Sedlacek, rainforest (AEIC); 1Q, Kuramba, 4 March, no year or collector (AEIC); 1Q, Mt Walker, Nov.- Dec., no year or collector (AEIC); 10[°], Lockerbie area, Cape York,

13-27 Apr. 1973, S. R. Monteith (ANIC); 10, 10, 10, Ban-Ban Range., via Coalstoun Lakes, Jan. 1974, H. Frauca (BMNH); 20, 4 km up Black Mt. Rd via Kuranda, 12-26 Oct. 1982, no collector, MT (QDPI); 1Q, 10, Mt Webb Nat. Pk, 27-30 Apr. 1981, I. D. Naumann (ANIC); 10, Wongabel State Forest. 6 km S. Atherton, 21 Jun.-26 Jul. 1984, Storey & Brown (QDPI); 1Q, 14 km W. by N. of Hope Vale Mission, 15.04S 145.07E, 7-10 May 1981, I. D. Naumann (ANIC); 10, 3.5 km S. by W. Mt Baird, 15.10S 145.07E, 3-5 May 1981, I. D. Naumann (ANIC); 1Q, 10, 10, Cairns, 30 May 1963, E. C. Corbet (BMNH). Northern Territory: 1Q, 7 km E. S. E. of Smith Point Coburg Pen., 11.09S 132.11E, 23 Jan. 1977, E. D. Edwards (ANIC); 1Q, Darwin nr coast, 24 Mar. 1991, C. v. Achterberg (RMNH); 2Q, 10, Darwin, 8 Jan. 1964, J. Sedlacek (BPBM); 1Q, Kakadu Nat. Pk, Obiri Rock area, 29 Mar 1980, M. B. Malipatil (MNTD); 1Q, Kakadu Nat. Pk, Border Store, Manngara walk, 29 Mar. 1991, C. v. Achterberg (RMNH); 10, Kakadu Nat. Pk, nr entrance Nourlangie Rock, 30 Mar. 1991, C. v. Achterberg (RMNH); 1Q, 20, Black Point, Coburg Pen. 15 -23 Feb. 1977, T. A. Weir (ANIC); 2Q, Black Point, Coburg Pen., 23 Jan. 1977 E. D. Edwards (ANIC); 10, N. of Cahills Crossing, East Alligator River, 7-8 Jun. 1973, J. C. Cardale (ANIC); 10[°], 19 km N. E. by E. of Mt. Cahill, 16 Nov. 1972, J. C. Cardale (ANIC). Western Australia: 50, 10, Lone Dingo, Mitchell Plateau, 9-19 May 1983, I. D. Naumann & J. C. Cardale.(ANIC, WARI). Indonesia: 20, Irian Jaya, Merauke, 0 m, 8.30S 140.22 E, 3 Apr. 1988, R. Hensen (RMNH).

Female

Length. 6.5 mm (range 5.8 - 7.2).

Colour. Yellow apart from the following which are variably brown to black: antennae, stemmaticum, vertex, frons and one-third dorso-posterior temples, apical onequarter of hind tibia, hind tarsi and ovipositor sheaths; fore wing yellow in basal twothirds, dark infuscation in apical one-third, sometimes with medial spot around proximal discal cell, stigma yellow in basal half; hind wing yellow in basal half, infuscate in apical half.

Head. Eyes with moderately dense golden pilosity; head smooth with moderately sparse long pilosity; epistomal suture convex medially; clypeal margin convex to straight, tubercles well-defined; clypeus 2.0 x as broad as high; face 1.6 x as broad as high; vertex slightly raised behind ocelli as seen in anterior view; depth of occiput in dorsal view 0.2 x length of head; face smooth, with medial dorsal node; frons

smooth, with smooth node raised between antennal sockets; ratio of length of eye to length of temple in dorsal view 1.0:0.9; antennae with 40-45 segments, 0.9×1.0 k length of body; scape 1.6 x as long as broad; antennal sockets separated by 1.1 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat, with dorso-medial longitudinal furrow; notauli crenulate, broadening, meeting posteriorly; scutum smooth; parapsidal grooves absent; scutellum sparsely pilose, smooth, 1.1 x as broad as long, very slightly humped in lateral view, posterior edge smooth medially but with small extended ledge over postero-medial part of dorsellum; scutellar sulcus 5.0 x as broad as long, with seven carinae; dorsellum with medial longitudinal carina well-defined; propodeum with faint rugulosity; propodeal areola diamond-shaped to lens-shaped; propodeal spiracles kidney-shaped, 0.7 x as broad as long; sternaulus shallow, arched ventrally in apical half, weakly crenulate; propleuron smooth.

Legs. Fore tibial spur 0.7 x as long as basitarsus; hind tibia not broadened with only slight flange at apex, widest part 1.8 x as wide as base; hind tibia with long golden and black spines among pilosity; inner hind tibial spur 1.5 x as long as outer spur, 0.8 x as long as basitarsus; hind tarsal claw with six teeth, apical tooth broad, about 2 x as wide as others.

Wings. Fore wing with 1-SR+M 3.5 x as long as m-cu; 2-SR+M 1.4 x as long as m-cu; 1-M straight; m-cu 0.4 x as long as 1-M; 1-M 0.66 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a and 1a absent; 1-2A+3A present, spectral basal of 1a; 2-2A+3A pigmented, along postero-medial margin of wing; 1-CUa 0.3 x as long as 1-CUb; 2r length 0.6 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 4 x as long as wide; 4-SRb straight in basal one-third then 145° angle with spectral node of 3r present, 5-SR straight to slightly arched towards apex; angle between 4-SRa and 4-SRb 135°; angle between 4-SRb and r-m 100°; second submarginal cell 2.5 x as long as wide; 2+3-SR arched medially; hind wing with four to six evenly spaced hamuli; 2-SC+R absent, r-m arising from 1-SR; 2-1A as small basal node or absent; 2A spectral.

Metasoma. T1 1.5 x as long as broad, stem 0.3 x as long as bulb; suture between T2 and T3 represented by moderately well defined groove; median field of T2 poorly defined, 0.4 x as long as broad; ovipositor sheaths broad and long, 0.5 x as long as hind tibia, 0.2 x as broad as long, arched downwards slightly, hairy in apical three-quarters, obliquely truncate at apex with slight dorsal notch and apical point; hypopygium evenly pilose throughout.

Variation

This species varies greatly in size and colour but is uniform in other morphological characters. The vertex may be black or yellow, and the wings range from darkly infuscate in the apical half and yellow basally to having infuscate patches medially and basally.

Male

As for female.

Host

Unknown.

Comments

The original description for *Car. verticalis* (Turner 1918) does not agree with the holotype in that the notauli are definitely crenulate but are described as smooth. This species can be distinguished from the other Australasian species by the darkly infuscate and yellow patterned wings, the crenulate notauli and sternaulus, and the pointed apex of the ovipositor sheaths. It is distributed across northern Australia and the adjacent part of New Guinea (Fig. 7.46).

7.3.17. Circocardiochiles occidentalis, sp. nov.

(Figs 6.21 - 6.24)

Material Examined

Holotype. Q, Western Australia, "3.5 km W. of Mt Gould, (25°48'S 117°23'E), W. Aust. 4 Sept. 1980, C. A. Howard & T. F. Houston 355-1" "ON FLOWERS OF EREMOPHILA FRASERI SPP. PARVA CHINNOCK" (WAMP).

Paratypes. 20, same data as holotype (WAMP, WARI).

Female

Length. 6.4 mm.

Colour. Black apart from the following which are orange: ocelli, pronotum scutum, tegulae, dorsal scutellum, antero-dorsal mesopleuron, fore femora, tibiae and tarsi, mid tibiae and tarsi, hind tibial spurs and metasoma excluding ovipositor sheaths; fore wing hyaline, with infuscation in apical one-quarter; venation brown.

Head. Eyes with moderately sparse very fine pilosity; head smooth with moderately sparse long pilosity; epistomal suture reduced medially between tentorial pits, absent laterally fused with gena, gently convex with slight medial concavity; clypeal margin convex laterally, with straight medio-lateral part; clypeus broad, 2.7 x as broad as high; face 2.1 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.3 x length of head; face smooth, with medial dorsal node indicated; frons smooth, with sharp smooth medial carina reaching 0.5 x distance to anterior ocellus; ratio of length of eye to length of temple in dorsal view 1.0:0.8; antennae with 33 segments, short, slender, reaching to apex of T1; scape 1.7 x as long as broad; antennal sockets separated by 0.9 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat, without dorso-medial longitudinal furrow; notauli shallow, of even width, meeting posteriorly; scutum smooth; parapsidal grooves absent; scutellum sparsely pilose, smooth, as broad as long, slightly humped in lateral view, posterior edge with fine short longitudinal striations medially; scutellar sulcus narrow, 6.3 x as broad as long, with one strong medial and six shorter lateral carinae; dorsellum with medial longitudinal carina weakly defined; propodeum with

crenulae branching from areola; propodeal areola lens-shaped, 1.8 x as broad as long; propodeal spiracles ovoid, 1.6 x as long as broad; sternaulus shallow, broad, smooth; propleuron short, smooth, without flange.

Legs. Fore tibial spur 0.9 x as long as basitarsus; hind tibia expanded slightly at apex, 2.3 x as wide as at base, apex with very slight dorsal flange armed with row of thick brown spines; hind tibia and tarsi with brown spines among pilosity; inner hind tibial spur 1.4 x as long as outer spur, 0.7 x as long as basitarsus; hind tarsal claw with three teeth.

Wings. Fore wing pilosity sparse at base, becoming thicker towards apex; 1-SR+M 3.1 x as long as m-cu; 2-SR+M 1.7 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.7 x as long as wide; 2cu-a represented by pigmented area; 1a present, spectral in apical two-thirds; 1-2A+3A spectral, reaching to 1a; 1-CUa 0.3 x as long as 1-CUb; 2r 0.4 x inside height of second submarginal cell, arising 0.7 x length along stigma; stigma 3.7 x as long as wide; 4-SRb straight in basal one-third with 145° angle, straight to apex; angle between 4-SRa and 4-SRb 140°; second submarginal cell 2.4 x as long as wide; 2+3-SR slightly arched near 2-M; hind wing with four to five evenly spaced hamuli; 2A absent.

Metasoma. T1 short, 1.4 x as long as broad, stem 0.2 x as long as bulb; suture between T2 and T3 represented by well-defined groove; median field of T2 0.5 x as long as broad; ovipositor sheaths broad and long, 0.7 x as long as hind tibia, 0.3 x as broad as long, sparsely hairy along length, broadening to and rounded at apex with dorsal notch; hypopygium with sparse fine hair laterally, hairless at apex, rounded to acutely pointed at apex.

Male

As for female except for the following:

Length 5.4 mm; basal T1 black; hind wing with four hamuli.

Host

Unknown.

Comments.

This monotypic genus is very distinctive in that it has long broad ovipositor sheaths, evenly sclerotised hypopygium, setose eyes, clypeal tubercles on a straight clypeal margin, fully-developed propodeal areola, and pectinate tarsal claws. Pollen grains on T1 of the male specimen are assumed to be from *Eremophila fraseri* on which all specimens have so far been collected. It is named after the westerly locality of the holotype, Mt Gould, Western Australia.

7.3.18. Hymenicis bubbur, sp. nov.

(Figs 7.29 - 7.31)

Material Examined

Holotype. ♀, Queensland, "Australia: Queensland: Townsville, 20-I-3-II-1988. T. Goertemiller, Malaise trap" (USNM).

Paratypes. 1Q, 2°, Qld, Townsville, Feb. 1903, F. P. Dodd (BMNH); 1°, as previous with date 27. Feb. 1903.

Other material examined. 1Q, Qld, Normanton, 2-8 March, no year or collector (CNCI).

Female

Length. 8.5 mm (range 7.8-9.4).

Colour. Orange to yellow except for the following which are black: antennae except inside spot on apical scape, medial frons leading up to area around ocelli, scutum, scutellum, propodeum, mesopleuron, mesosternum, metasternum, basal mid and hind coxae, apex of metasoma and ovipositor sheaths; fore wing yellow with infuscation in apical one-third; hind wing yellow with infuscation in apical half; venation yellow; brown in infuscate part. The specimen from Normanton has the scutellum and metanotum orange.

Head. Head smooth with sparse moderate length golden pilosity; epistomal suture slightly reduced, gently convex; clypeal margin evenly convex; clypeus broad, 2.6-3.1 x as broad as high; face broad, 2.2-2.3 x as broad as high; vertex rounded, not raised behind ocelli; depth of occiput in dorsal view 0.3 x length of head; face smooth with dorso-medial node very slightly indicated; frons smooth with broad smooth medial carina; ratio of length of eye to length of temple in dorsal view 1.0:0.8; antennae with 50-53 segments, subequal to length of body; scape broad, rounded, geniculate, 1.3 x as long as broad; antennal sockets broadly separated by 1.2 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth without dorso-medial longitudinal furrow; notauli crenulate in anterior one-third otherwise smooth, narrow, of even width, meeting posteriorly; scutum smooth; parapsidal grooves shallow and weakly-defined; scutellum sparsely pilose, smooth, 0.9 x as broad as long, narrowing in posterior one-third, slightly humped in lateral view (the Normanton specimen has a very smooth broad apical trough in scutellum); scutellar sulcus 3.0 x as broad as long, with one strong medial and two shorter lateral carinae; dorsellum with medial longitudinal carinae well-defined; propodeum with crenulae branching from areola; propodeal areola diamond-shaped, rounded anteriorly, as broad as long, carinae weaker anteriorly, with faint medial longitudinal carina; propodeal spiracles elongate, oval posteriorly, narrowing to point anteriorly, 2.7 x as long as broad; sternaulus shallow, broad, smooth; propleuron smooth.

Legs. Moderately slender; fore tibial spur 0.6 x as long as basitarsus; hind tibia expanded slightly at apex, 2.5 x as wide as at base, with very slight dorsal flange; hind tibia and tarsi without spines among pilosity; inner hind tibial spur 1.6 x as long as outer spur, 0.8 x as long as basitarsus.

Wings. Fore wing with 1-SR+M 3.8 x as long as m-cu; 2-SR+M 1.6 x as long as m-cu; 1-M moderately convex; m-cu 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a absent; 1a present, pigmented; 1-2A+3A absent; 1-CUa 0.3 x as long as 1-CUb; 2r 0.7 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 2.9 x as long as wide; 4-SRb

straight, 0.1 x as long as 5-SR; angle between 4-SRb and 5-SR 135° with small node of 3r at junction; angle between 4-SRa and 4-SRb 100°; second submarginal cell 3.6 x as long as wide; 2+3-SR evenly convex; 2A absent.

Metasoma. T1 2.4 x as long as broad, stem absent, without furrow in basal part of T1, broadest and rounded three-quarters along length; suture between T2 and T3 represented by well-defined groove; median field of T2 long and narrow, 1.2 x as long as broad; ovipositor short and down-curved; ovipositor sheaths short, moderately hairy along length, broadest medially, rounded at apex, 0.1 x as long as hind tibia, 0.5 x as broad as long; sclerotised part of hypopygium with sparse fine hairs throughout.

Male

As for female. It is often difficult to differentiate males from females as the ovipositor sheaths and male parametes appear similar. However, S7 and S8 are broadly emarginate medially in the male and there are no membranous folds at the apex of S8.

Host

Unknown.

Comments

Hym. bubbur can be distinguished from other species by its large size, the broad stem and rounded bulb of T1, the narrow long median field on T2, the faint medial longitudinal carina on the propodeum, the relative completeness of the anterior carinae of the propodeum, and the anteriorly crenulate notauli. One specimen from Normanton was excluded from the type series because of its colour differences. Although it most certainly belongs to this species it has a yellow scutellum differing from the type series which have a black scutellum. It is known from northern coastal Queensland and is named after the aboriginal word "bubbur" meaning large black and yellow snake because of its relatively large size and striking black and yellow coloration.

7.3.19. Hymenicis nockatungensis, sp. nov.

(Figs 7.32 - 7.34)

Material Examined

Holotype. Q, Queensland, "5 N Nocatunga 13 Nov 49 E F Riek" (Nockatunga, S. W. Qld, 27°43S 142°43 E, near Jackson Oil Field) (ANIC).

Female

Length. 7.1 mm.

Colour. Orange apart from the following which are black; frons between antennal sockets to stemmaticum, propleuron, scutum apart from postero-lateral lines and medial area at junction of notauli, posterior band of scutellum, epicnemial ridge, mesosternum, T4-T7, ovipositor sheaths, coxae, trochanters, basal half of femora and hind tibiae; fore and hind wings yellow in basal half with infuscation in apical half; venation brown.

Head. Head smooth with sparse short fine golden pilosity; epistomal suture reduced, gently convex; clypeal margin convex; clypeus broad, $3.2 \times as$ broad as high; face broad, $2.2 \times as$ broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.2 x length of head; face smooth, without medial dorsal node; frons smooth, with broad smooth medial hump; ratio of length of eye to length of temple in dorsal view 1.0:0.7; antennae with 46 segments, about equal to length of body; scape broad, rounded, geniculate, 1.3 x as long as broad; antennal sockets broadly separated by 1.7 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, with slight dorso-medial longitudinal furrow; notauli smooth, narrow, of even width, meeting posteriorly; scutum smooth; parapsidal furrows slightly indented; scutellum sparsely pilose, smooth, 0.8 x as broad as long, slightly humped in lateral view; scutellar sulcus 3.5 x as broad as long, with one medial and four shorter lateral carinae; dorsellum with medial longitudinal carina weakly defined; propodeum smooth, with fine punctation associated with long dense thick white pilosity; propodeal areola absent reduced to posterior diverging carinae; propodeal

spiracles elongate, ovoid, 3.3 x as long as broad; sternaulus shallow, broad, smooth; propleuron smooth.

Legs. Moderately slender; fore tibial spur 0.75 x as long as basitarsus; hind tibia expanded slightly at apex, $2.4 \times as$ wide as at base, with very slight dorsal flange at apex; hind tibia and tarsi without spines among pilosity; inner hind tibial spur 2.7 x as long as outer spur, 0.8 x as long as basitarsus.

Wings. Fore wing with 1-SR+M 3.2 x as long as m-cu; 2-SR+M 1.1 x as long as m-cu; 1-M moderately convex; m-cu 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a virtually absent; 1a present, pigmented, meeting 1-2A+3A; 1-2A+3A present and spectral, partly pigmented; 1-CUa 0.3 x as long as 1-CUb; 2r 0.7 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 2.9 x as long as wide; 4-SRb evenly curved along length; angle between 4-SRa and 4-SRb 135°; second submarginal cell 3.2 x as long as wide; 2+3-SR evenly convex; 2A present.

Metasoma. Covered with thick white pilosity; T1 1.9 x as long as broad, stem absent; suture between T2 and T3 represented by well-defined groove; T2 without defined median field; ovipositor sheaths short, 0.1 x as long as hind tibia, 0.5 x as broad as long, hairy along length, broad and rounded at apex; sclerotised part of hypopygium sparsely hairy throughout.

Male

Unknown.

Host

Unknown.

Comments

Hym. nockatungensis can be distinguished from other *Hymenicis* species by the propodeal areola being dramatically reduced to two small posterior carina and the absence of a median field on T2. It is named after the type locality, Nockatunga.

7.3.20. Hymenicis noongarensis, sp. nov.

(Figs 4.5, 4.20, 6.39 - 6.43)

Material Examined

Holotype. Q, Western Australia, "31.21S 118.57E 2 km SW by W Noongar WA 9 Oct. 1981 I. D. Naumann J. C. Cardale" (ANIC).

Paratypes. 1 \bigcirc same data as holotype (ANIC); 2 \bigcirc , W. Aust. 49 km N. E. Wubin, 29.47E, 117.00S, 27 Sept. 1981, Naumann & Cardale (ANIC); 6 \bigcirc , 4 \bigcirc , W. Aust., Carnarvon, 20 Aug. 1954, A. Snell (MVMA, WARI).

Female

Length. 5.9 mm (range 5.0-6.6).

Colour. Head orange, antennae, frons, stemmaticum and mouthparts apart from mandibles black; mesosoma black; legs black apart from fore leg, apical three-quarters of femur, tibia and tarsi which are orange; metasoma with T1 light yellow except for medial part of median field; T2 light yellow apart from medial part of median field and small lateral spots; T3 light yellow with medial transverse lens-shaped area black; rest of metasoma black apart from apex of hypopygium which is white; wings lightly infuscate in basal half, darker apically; venation black.

Head. Head smooth, with moderately dense long pilosity; epistomal suture distinct, convex; clypeal margin convex, with slight medial lobe; clypeus smooth, 2.8 x as broad as high; face broad, 2.6 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.3 x length of head; face smooth, with medial node extending between antennal sockets; frons smooth with sparse pilosity; ratio of length of eye to length of temple in dorsal view 1.0:1.0; antennae with 42 segments, subequal to

length of body; scape broad and rounded, 1.1 x as long as broad; antennal sockets separated by 1.7 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth and flat; notauli smooth, of even width, meeting posteriorly; scutum smooth, with sparse long fine pilosity; parapsidal grooves very weakly indented; scutellum sparsely pilose, smooth, as broad as long, weakly humped in lateral view; scutellar sulcus 3.7 x as broad as long, with one medial and two to four lateral carinae; posterior band of scutellum rugulose medially; dorsellum with medial longitudinal carina well-defined; propodeum mostly smooth, with scattered punctures apico-medially, with sparse long fine pilosity; propodeal areola not defined, reduced to two posterior carinae diverging anteriorly; propodeal spiracles ovoid, 2.1 x as long as broad; epicnemial groove and sternaulus broad, shallow and smooth; propleuron smooth.

Legs. Fore tibial spur 0.7 x as long as basitarsus; hind tibia expanded at apex, 2.5 x as wide as base; hind tibia without spines among pilosity; inner hind tibial spur 1.4 x as long as outer spine, 0.7 x as long as basitarsus, cylindrical, with weak dorsal ridge at base; tarsal claws with a few stout hairs.

Wings. Fore wing with 1-SR+M 3.5 x as long as m-cu; 2-SR+M 1.7 x as long as m-cu; 1-M very slightly arched; m-cu 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.7 x as long as wide; 2cu-a reduced to lightly infuscate trace; 1a present, meeting 1-2A+3A; 1-2A+3A spectral, pigmented; 1-CUa thickened, 0.2 x as long as 1-CUb; 2r 0.5 x inside height of second submarginal cell, arising 0.6 x along length of stigma; stigma 2.4 x as long as wide; 4-SRb evenly arched along length; angle between 4-SRa and 4-SRb 120°; second submarginal cell 3.6 x as long as wide; 2-SR straight, 1r present 2-SR 0.25 x as long as 3-SR.

Metasoma. T1 2.0 x as long as broad, stem absent; suture between T2 and T3 represented by well defined groove; median field of T2 oval, weakly defined, as broad as long; ovipositor sheaths, 0.1 x as long as hind tibia, 0.5 x as broad as long, broad and rounded at apex; sclerotised part of hypopygium sparsely pilose throughout.

Male

As for females but node of 1r absent.

Host

Unknown.

Comments

Hym. noongarensis can be distinguished from other *Hymenicis* species by its small size, coloration, the presence of two relatively long posterior carinae on the propodeum, the form of median field of T2, and the presence of the small node of 1r in the fore wing. It is found in the south-western part of Western Australia and is named after the type locality, Noongar. A single specimens from Boulia, central Queensland (in ANIC) is very similar to *Hym. noongarensis* but it has been excluded from the species because of its strikingly different orange colour.

7.3.21. Latitergum areyongensis, sp. nov.

(Figs 6.44 - 6.47)

Material Examined

Holotype. \bigcirc , Northern Territory, "Areyonga, 600 m N.T., Australia, October 12", no collector (AEIC).

Paratypes. 2 \bigcirc , same data as holotype (AEIC); 1 \bigcirc , 1 \bigcirc same data as holotype with dates 8 Aug. and 10 Nov., respectively (AEIC).

Female

Length. 3.7 mm (range 3.1-4.0).

Colour. Yellow-orange apart from the following which are black-brown: antennae, stemmaticum, lateral bands on medial scutum, lateral lobes of scutum, apical transverse stripe on propodeum, posterior propleuron, posterior two-thirds of mesopleuron, metapleuron, mid coxae and basal two-thirds of femur, hind legs, and metasoma; fore and hind wing lightly infuscate in basal half, darker in apical half; venation brown.

Head. Eyes appearing glabrous but with very short sparse inter-ommatidial hairs; head smooth with sparse moderately long pilosity; epistomal suture reduced and gently convex medially; clypeal margin convex with slight beak-like point medially; clypeus 1.9-2.3 x as broad as high; face 2.0 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.3 x length of head; face smooth with faint indication of medial dorsal node; frons smooth with smooth medial carina reaching 0.5 x distance to anterior ocellus; ratio of length of eye to length of temple in dorsal view 1.0:0.6; antennae with 27-30 segments, 0.9 x length of body; scape 1.5 x as long as broad; antennal sockets separated by 1.1 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat with dorso-medial longitudinal furrow; notauli of even width, meeting weakly posteriorly; scutum smooth; parapsidal grooves absent; scutellum sparsely pilose, smooth, 1.2 x as broad as long, flat in lateral view, posterior edge smooth medially; scutellar sulcus 5.0 x as broad as long, with eight to ten carinae; dorsellum with medial longitudinal carinae absent to very weakly defined; propodeum with faint background rugulosity, propodeal areola reduced to anteriorly diverging carinae apically, absent in basal one-quarter; propodeal spiracles circular; sternaulus shallow, broad, smooth; propleuron smooth.

Legs. Moderately small, stout; fore tibial spur 0.9 x as long as basitarsus; hind tibia expanded three-quarters along length, narrower at apex, apex 1.5 x as wide as at base, 0.8 x as wide as widest part; hind tibia and tarsi with brown spines amongst pilosity; inner hind tibial spur as long as outer spur, 0.6 x as long as basitarsus.

Wings. Fore wing with 1-SR+M 3.6 x as long as m-cu; 2-SR+M 1.3 x as long as m-cu; 1-M straight; m-cu 0.4 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.6 x as long as wide; 2cu-a represented by pigmented area; 1a present as small node with pigmented area posterior of node; 1-2A+3A absent; 1-CUa 0.3 x as long as 1-CUb; 2r 0.6 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 2.6 x as long as wide; 4-SRb evenly curved in basal one-quarter

becoming less curved and straight towards apex; angle between 4-SRa and 4-SRb 115°; second submarginal cell 2.3 x as long as wide; 2+3-SR straight to slightly arched near 2-M; hind wing with 4 evenly spaced hamuli; 2-1A reaching two-thirds of length to wing margin; 2A absent.

Metasoma. T1 0.7-0.9 x as long as broad, stem absent; suture between T2 and T3 represented by well defined groove; median field of T2 0.4 x as long as broad; ovipositor sheaths broad and long 0.9 x as long as hind tibia, 0.2 x as broad as long, sparsely hairy along length, broadest medially pointed at apex with dorsal notch; hypopygium with sparse, fine hair laterally.

Male

As for female except as follows:

Antennae with 32-33 segments; T1 as long as broad; vertex, frons and dorsal occiput black, scutum and scutellum orange, T1-3 white to yellow, median field of T1 with two brown medio-lateral spots.

Host

Unknown.

Comments

This species is morphologically similar to *Lat. turneri* but can be distinguished from it by having very reduced eye setae, a deeper occiput, broader median field of T2, the clypeal margin pointed medially, and simple tarsal claws. The species is named after the type locality, Areyonga (Northern Territory) which has revealed a large number of new braconid species (Austin and Dangerfield 1992, 1993). Areyonga is located in the western MacDonnell Ranges and is known for its rocky topography and extremes in temperature.

7.2.22. Latitergum eremophilasturtiae, sp. nov.

(Figs 7.38, 7.39)

Material Examined

Holotype. Q, Northern Territory, "N.T., 195 km E. of Uluru/Ayers rock on Lassiters Highway, 5 Nov. 1992, P. C. Dangerfield, sweeping on *Eremophila sturtii*" (ANIC).

Paratypes. 3Q, 5° same data as holotype (ANIC, WARI); 1°, W. Aust. 29 km S. E. by E. Coolgardie, 31.07S 121.24E, 11 Oct. 1981, Naumann & Cardale (ANIC).

Female

Length. 4.0 mm (range 3.5-4.5).

Colour. Head black apart from apex of mandibles and palps; mesosoma orange apart from tegulae, metanotum, propodeum and mesosternum which are black; fore and mid legs orange apart from coxa, trochanter, trochantellus and basal femur of mid leg which are brown; hind leg black-brown apart from basal tibia and basitarsus which are yellow; metasoma black apart from T1 and basal half of median field and T2 which are yellow.

Head. Eyes conspicuously pilose; head smooth and pilose; epistomal suture convex; clypeal margin convex; clypeus smooth, 2.7 x as broad as high; face 2.2 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.4 x length of head; face smooth with dorsal medial node; frons smooth with sparse pilosity, medial carina extending from between antennal sockets, extending half way to anterior ocellus; ratio of length of eye to length of temple in dorsal view 1.0:0.5; antennae with 29 segments, reaching to about T2; scape 1.3 x as long as broad; distance between antennal sockets 1.2 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth; notauli very weakly defined, meeting posteriorly; scutum smooth with sparse long fine pilosity; parapsidal grooves very weakly indented; scutellum sparsely pilose, smooth, 1.1 x as broad as long, weakly humped in lateral view; scutellar sulcus 5.0 x as broad as long, with one medial and six smaller lateral carinae; posterior band of scutellum smooth to very faintly crenulate

medially; dorsellum without medial longitudinal carina; propodeum mostly smooth, with sparse long fine pilosity; propodeal areola present, diamond-shaped with radiating short crenulae; propodeal spiracles ovoid, 1.7 x as long as broad; sternaulus broad, shallow and smooth; propleuron smooth.

Legs. Fore tibial spur as long as basitarsus; hind tibia expanded at apex, $2.4 \times as$ wide as base, without spines scattered among pilosity but with row of stout spines near apex forming a transverse ridge; inner hind tibial spur 1.4 x as long as outer spur, 0.8 x as long as basitarsus; tarsal claws pectinate, hind claws with 1-4 teeth.

Wings. Fore wing with 1-SR+M 4.1 x as long as m-cu; 2-SR+M 1.9 x as long as m-cu; 1-M very slightly arched; m-cu 0.4 x as long as 1-M; 1-M 0.5 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a reduced to lightly infuscate trace; 1a present and defined basally as infuscate node then continuing spectrally and meeting 1-2A+3A; 1-2A+3A spectral; 1-CUa thickened, 0.3 x as long as 1-CUb; 2r 0.4 x inside height of second submarginal cell, arising 0.7 x along length of stigma; stigma 2.6 x as long as wide; 4-SRb straight apart from arch 0.3 x length from base and upturned at apex; angle between 4-SRa and 4-SRb 110°; second submarginal cell short, 1.7 x as long as wide; 2+3-SR weakly arched; hind wing with four evenly spaced hamuli; 2-1A as basal node.

Metasoma. T1 1.1 x as long as broad, stem 0.2 x length of bulb; suture between T2 and T3 weakly defined; median field of T2 broad, weakly defined, 0.3 x as long as broad; ovipositor sheaths 0.7 x as long as hind tibia, 0.25 x as broad as long, broadening to and truncate at apex, with dorsal notch; hypopygium with sparse long pilosity.

Male

As for females except scutellum black.

Host

Unknown.

Comments

This species is not clearly related to any others in the Australasian Region but has been placed in this genus because of its superficial similarity with other *Latitergum* species. *Lat. eremophilasturtiae* is distinguished by the following characters: eyes hairy, hypopygium evenly sclerotised, propodeal areola complete, galea short, and notauli smooth. It is known from central and western Australia and has been collected on *Eremophila sturtii* in flower (after which it has been named), east of Uluru along Lassiters Highway, in association with other braconid and ichneumonids wasps of similar coloration and size.

7.3.23. Latitergum turneri, sp. nov.

(Figs 7.35 - 7.37, 7.40, 7.41, 7.48)

Material Examined

Holotype. Q, Western Australia, "Kalamunda, S.W. Australia. 14 Mch. 14 Apl. 1914. R. E. Turner. 1914-349.", (31.58S, 116.03E) (BMNH).

Paratypes. 1Q, 1C, Northern Territory, Areyonga, 600 m, 8 Dec., no year, no collector (AEIC); 1Q, Queensland, Cairns, 10 m, 23 Jan. 1964, J. Sedlacek (BPBM).

Female

Length. 3.9 mm (range 3.5-4.0).

Colour. Yellow apart from the frons and vertex which are black and the antennae, apical half of mid tibia, mid tarsi, hind tibia and tarsi, T6-T8 and ovipositor sheaths which are brown. Sometimes with the metasoma darker or the stemmaticum black and T6-T8 yellow.

Head. Eyes with moderately sparse short fine pilosity; head smooth and pilose; epistomal suture very weak, convex; clypeal margin evenly convex, without clypeal tubercles; clypeus smooth, 1.7 x as broad as high; face 1.8 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.2 x length of head; face smooth, with dorsal medial node; frons smooth, with sparse pilosity, with broad medial carina extending from between antennal sockets to midpoint of frons; ratio of length of

eye to length of temple in dorsal view 1.0:0.6; antennae with 26-29 segments, reaching to about apex of T2; scape 1.6 x as long as broad; distance between antennal sockets 1.3 x width of socket.

Mesosoma. Dorsal pronotum smooth; notauli meeting posteriorly; scutum smooth with sparse long fine pilosity, 1.6 x as broad as long; parapsidal grooves very weakly indented; scutellum sparsely pilose, smooth, 1.2 x as broad as long, weakly humped in lateral view; scutellar sulcus 5.0 x as broad as long with one medial and four smaller lateral carinae; posterior band of scutellum smooth medially; dorsellum with medial longitudinal carina well-developed; propodeum with sparse pilosity; propodeal areola broadly diamond-shaped, 0.9-1.0 x as broad as long, anterior weakly to moderately-defined, with radiating short crenulae; propodeal spiracles ovoid, 1.2 x as long as broad; sternaulus virtually absent, shallow and smooth; propleuron smooth.

Legs. Fore tibial spur 0.8 x as long as basitarsus; hind tibia expanded at apex, 2.3 x as wide as base, with stout golden spines scattered among pilosity; inner hind tibial spur 1.4 x as long as outer spine, 0.7 x as long as basitarsus; tarsal claws pectinate, hind claw with five teeth.

Wings. Fore wing with 1-SR+M weak, $3.3 \times as \log as m-cu; 2-SR+M 1.1 \times as long as m-cu; 1-M straight; m-cu weak, 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.9 x as long as wide; 2cu-a reduced to lightly infuscate line; 1a pigmented in basal half then spectral to junction with 1-2A+3A; 1-2A+3A spectral; 1-CUa 0.3 x as long as 1-CUb; 2r 0.8 x inside height of second submarginal cell, arising 0.5 x along length of stigma; stigma 2.2 x as long as wide; 4-SRb straight in basal one-fifth then arched and straight to apex; angle between 4-SRa and 4-SRb 100°; second submarginal cell 2.7 x as long as wide; 2+3-SR weakly arched near base; hind wing with four evenly spaced hamuli; 2-1A present, reaching one-third to half way to wing margin; 2A spectral.$

Metasoma. T1 1.1 x as long as broad, stem absent; suture between T2 and T3 weakly defined; median field of T2 broad, weakly defined, 2.2 x as broad as long; ovipositor sheaths long, 0.8 x as long as hind tibia, 0.2 x as broad as long, slightly

broader medially, rounding to broad point at apex without dorsal notch; hypopygium with moderately sparse long pilosity.

Male

As for females except body 3.7 mm in length.

Host

Unknown.

Comments

Lat. turneri appears morphologically similar to Lat. areyongensis from which it can be distinguished by having longer eye setae, a narrower median field of T2, a more rounded clypeal margin, and pectinate tarsal claws. Lat. turneri also has the propodeal areola more complete in that the anterior part has a short medial longitudinal carina. It is broadly distributed across the continent from north-east Queensland to south-western Western Australia (Fig. 7.48).

7.3.24. Polycardiochiles dissimulator (Turner), Comb. nov.

Cardiochiles dissimulator Turner, 1918: 50. - Parrott, 1953: 202; Shenefelt, 1973: 789.

Material Examined

Holotype. \bigcirc , (head missing), Queensland, "Thursd Is. 5. 02" [Thursday Island, May 1902] (BMNH).

Female

As for *Pol. fuscipennis* except as follows:

Body orange except for the following which are brown-black: propleuron, fore coxa and basal three-quarters of fore femur, mid coxa to tibia, hind legs apart from basal

patches on coxa, T2-T8, sternites and ovipositor sheaths; medial desclerotised part of the hypopygium yellow; wings hyaline basally, infuscate in apical one-third.

Male

Unknown.

Host

Unknown.

Comments

This species is very similar to *Pol. fuscipennis*. It can be distinguished from other species in the group by the distinctive orange colour of the mesosoma and black metasoma. In all other respects it is identical to *Pol. fuscipennis* and may represent an aberrant colour form of this species. However, until further material is available, it has been retained as a distinct species. *Pol. dissimulator* has not been collected since its original description in 1918, and it is known only from Thursday Is.

Polycardiochiles fuscipennis (Szépligeti), Comb. nov.

(Figs 4.21, 6.62 - 6.69, 7.42 -7.44, 7.49)

Cardiochiles fuscipennis Szépligeti, 1900: 52. - Szépligeti 1904: 143; Shenefelt 1973: 791.

Cardiochiles fasciatus Szépligeti, 1900: 52. - Szépligeti, 1902: 78; Szépligeti, 1904: 143; Enderlein, 1906: 250; Shenefelt, 1973: 790, syn nov.

Cardiochiles assimilator Turner, 1918: 49. - Parrott, 1953: 202; Shenefelt, 1973: 787, syn nov.

Cardiochiles similis Brues, 1918: 109, syn nov.

Cardiochelis trichiosomus Cameron, 1913: 84, (genus misspelling), syn nov.

Cardiochelis piliventris Cameron, 1913: 85, (genus misspelling), syn nov.

Material Examined

Lectotype. O', Papua New Guinea, "N. Guinea Biro 96" Friedrich Wilh.hafen" (HNHM).

Paralectotype. 1Q, same data as holotype (HNHM).

Other material examined. Several hundred Q and O specimens with the following data abbreviated. Papua New Guinea: Madang District, Wanuma (BPBM); Sentani, SW Cyclops Mts (BPBM); Fly R., Cisobip (BPBM); Morobe District, Ulap (BPBM); Finschhafen (CASC); Maprik, (ANIC, BPBM); Nabire (BPBM); Humboldt Bay (BMNH); Cyclops Mts, Sabron (BMNH); Torricelli Mts, Siaute (BPBM); Hollandia (BPBM); River Tor, Mafen (BPBM); SE Biak Is. (BPBM); NW Nabire, S. Geelvink Bay (BPBM); Petoi, Nr. Kerama (BPBM); Genjam (BPBM); Koroba (BPBM); Kiunga, Fly River (BPBM); Maffin Bay (CASC); Madang Province, Baiteta (BPBM); Subitana, Musgrove Distr. (BPBM); Fak Fak (BPBM); Madang Prov., Nagada Harbour (CASC); Banz (BPBM); Wau (BPBM); Kar Kar I., Namau (BPBM); Dreikikir, Sepik Distr. (BPBM); Umboi I., Semoto Awelkom (BPBM); W. Highlands Distr., Mt Hagen (CNCI). Solomon Islands: Malaita, Auki (BPBM); Guadalcanal, Betikama R. (BPBM); Malaita, Dala, (BPBM); Guadalcanal, Tambalia (BPBM); Florida Is., Nggela I. Haleta (BPBM); Guadalcanal, Honiara, (BPBM); Guadalcanal, Roroni, (BPBM); Bellona (BPBM); Russell Is., Yandina-Banika I. (BPBM); Guadalcanal, Lunga (BMNH); Guadalcanal, Tenaru R. (CASC); Guadalcanal (AEIC); Guadalcanal, Poha R. (BPBM); Guadalcanal, Tadhimboko (BPBM); Bouganville, Kokure (BPBM); Kolombangara I, Gizo (BPBM); Gizo, Gizo (BPBM); Kolombangara I. Poitete (BPBM); Vella Lavella, Ulo Crater (BPBM); San Cristobal I., Kirakira (BPBM); Guadalcanal, Kukum (BMNH). New Britain: Gazelle Pen. Gaulim (BPBM); Ti, Nakanai Mts (BPBM); Lindenhafen (BPBM); Bialla (BPBM); Dami Res. Stn (AEIC); Cape Hoskins (AEIC); Baronga I. (BPBM); Vunabakan (BPBM). New Ireland: Kandan (BPBM). Indonesia: Ceram, Piroe? (BPBM). Bismark Archepelago: Manus I., Momote (BPBM, BMNH). Queensland: Mt Webb Nat. Pk (ANIC); Baldwin Swamp, Bundaberg (ANIC); Iron Range, Cape York Pen. (ANIC); Brisbane, Long Pocket (BMNH); Rex Range Lookout, Via Julatten (QDPI, WARI); Gordonvale (UQBA); Cairns (UQBA); Buderim (WARI); Babinda (BPBM); Redlynch (BPBM); Camp Mt. (WARI); Mt Cootha (AEIC); Wangan, Innisfail (ANIC); Kuranda (BMNH); Mackay (BMNH); 4 km up Black Mt Rd, via Kuranda (QDPI); Maroochy Hort. Res Stn, Nambour (QDPI); Beside Noahs Ck, 15 km N Daintree R. (QDPI); Mission Beach (QDPI); Sth Johnstone (QDPI); Tully (QDPI). Northern Territory: Magela Ck (ANIC).

Female

Length. 6.5 mm (range 5.7 - 7.1).

Colour. Black to dark brown except for the following which are yellow to white: maxillary palps, apical one-quarter of fore femur, fore tibia and tarsi, mid tarsi, hind tibial spurs and the medial desclerotised part of the hypopygium.

Head. Eyes with fine white pilosity; head smooth with moderately long pilosity; malar carina absent; epistomal suture convex medially; clypeal margin convex, two tubercles present and well-defined; clypeus 1.7 x as broad as high; face 1.8 x as broad as high; vertex with gentle post ocellar depression, raised behind ocelli when seen in anterior view; depth of occiput 0.3 x length of head; face smooth with very small medial dorsal node; frons smooth, with smooth node between antennal sockets; ratio of length of eye to length of temple in dorsal view 1.0:0.6; antenna with 35-37 segments, 0.9 x length of body; scape 1.9 x as long as broad; antennal sockets separated by 1.2 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, convex, with slight dorso-medial pit posteriorly; notauli crenulate, meeting posteriorly; scutum smooth; parapsidal grooves slightly indented posteriorly; scutellum with moderately dense long white pilosity, smooth, 1.1 x as broad as long, very slightly humped in lateral view, posterior band with medial crenulae; scutellar sulcus 3.6 x as broad as long, with five evenly spaced carinae; dorsellum with medial carina very weak to absent and postero-lateral pits; propodeum with faint to moderately well-defined rugulosity; propodeal areola diamond-shaped; propodeal spiracles ovoid to kidney-shaped, 0.4 x as broad as long; sternaulus shallow, arched ventrally in apical half, crenulate; propleuron smooth; epicnemial carina absent.

Legs. Fore tibial spur as long as basitarsus; hind tibia not broadened with only slight flange at apex, 2.5 x as wide at widest part as at base; hind tibia with long black spines among shorter pilosity; inner hind tibial spur 1.3 x as long as outer spur, 0.5 x as long as basitarsus; hind tarsal claw with about six teeth becoming smaller basally, apical tooth about 2 x as wide as others.

Wings. Fore wing with 1-SR+M 3.3 x as long as m-cu; 2-SR+M 1.6 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.60 x as long as 1-SR+M; discal cell 2 x as long as wide; 2cu-a absent; 1a absent; 1-2A+3A present basally, 2-2A+3A as pigmented postero-basal margin of wing; 1-CUa 0.45 x as long as 1-CUb; 2r 0.7 x inside height of second submarginal cell, arising 0.7 x length along stigma; stigma 4.2 x as long as wide; 4-SRb straight in basal one-third then 140° angle and spectral node of 3r, 5-SR straight or slightly arched to apex; angle between 4-SRa and 4-SRb 110°; angle between 4-SRb and r-m 140°; second submarginal cell 2.7 x as long as wide; 2+3-SR straight, without node of 1r present; hind wing with 4-5 evenly spaced hamuli; 2-SC+R absent, r-m arising from 1-SR, 1-SRa variable; 2-1A absent; 2A spectral and slightly pigmented basally, otherwise absent.

Metasoma. T1 2.0 x as long as broad, stem 0.3 x as long as bulb; suture between T2 and T3 represented by a moderately well-defined groove; median field of T2 poorly defined, 0.7 x as long as basal width; ovipositor sheaths broad and long, 0.7 x as long as hind tibia, 0.2 x as broad as long, arched downwards slightly, hairy in apical three-quarters, squarely truncate at apex; hypopygium evenly pilose throughout.

Variation

The wing infuscation in this species varies in intensity from almost hyaline to moderately darkly infuscate but the same pattern is maintained. The propodeal areola varies from having a long basal medial carina one-quarter the length of the propodeum (Fig. 7.42) to this carina being completely absent (Fig. 7.44). The lateral carinae of the areola may be horizontal or slightly oblique, and arise medially (Fig. 7.44) or slightly posterior to the middle of the areola (Fig. 7.43). The length of 1-SRa in the hind wing also varies in length.

Male

As for female.

Unknown.

Comments

Even with the large number of specimens available for study, none has associated host data, and most have been taken in malaise traps or at light. *Cardiochiles assimilator*, *Car. fasciatus*, *Car. piliventris*, *Car. similis* and *Car. trichiosomus* are here synonymised with *Pol. fuscipennis* as they fall within the broader morphological limits defined here for this species. Several characters, as discussed above, show a substantial degree of variation over a wide geographic range, and none are correlated with each other or show consistent differences that can be used to recognise separate morpho-species. *Pol. fuscipennis* is distributed across tropical Australia north to Wallace's line. It is most similar to *Pol. philippensis* which is found north of Wallace's Line (Fig. 7.49) and can be distinguished from the latter species by having crenulate notauli.

7.3.26. Polycardiochiles gwenae, sp. nov.

Material Examined

Holotype. Q, Western Australia, "W. Aust., 25 km E of New Yamarna HS (28.10S, 123.41 E) 21 Sept. 1982, B Hanich & T. F. Houston 478-1" " On flowers of *Micromyrtus flaviflora*" (WAMP).

Paratypes. 10, Qld, Townsville, 20 Jan.- 3 Feb. 1988, T. Goertemiller, MT. (USNM); 10, W. Aust., 12.5 km SSE of Banjiwarn HS, (27.42S, 121.37E) 22 -28 Feb. 1980, T. F. Houston 316-26, on flowers of *Scaevola* affin. *spinescens* (WAMP).

Female

Length. 5.0 mm.

Colour. Body black except for the following which are yellow: fore and mid apical femur, tibia and tarsi, basal half of hind tibia; wings sub-hyaline in basal half, infuscate in apical half.
Head. Eyes with moderately dense white pilosity; head smooth with sparse moderately long pilosity; malar carina present; epistomal suture reduced, gently convex medially; clypeal margin convex, two tubercles present; clypeus 2.3 x as broad as high; face 2.0 x as broad as high; vertex not raised behind ocelli; depth of occiput in dorsal view 0.5 x length of head; face smooth with medial dorsal node and weak longitudinal carina; frons smooth, with smooth medial carina reaching 0.5 x distance to anterior ocellus; ratio of length of eye to length of temple in dorsal view 1.0:0.7; antennae not complete, > 27 segments; scape 1.4 x as long as broad; antennal sockets separated by 0.6 x width of antennal socket.

Mesosoma. Dorsal pronotum smooth, flat; notauli crenulate, of even width, meeting posteriorly; scutum smooth; parapsidal grooves absent; dorsal scutellum with increasing pilosity towards apex, smooth, 1.0 x as broad as long, slightly humped in lateral view, posterior band with crenulate depression medially; scutellar sulcus 5.0 x as broad as long with seven evenly spaced carinae; dorsellum without medial carina; propodeum with faint rugulosity, broad, distance between outer margins of spiracles 2.5 x as medially long; propodeal spiracles ovoid; sternaulus deep, broad, crenulate, down-curved in apical half; propleuron smooth; epicnemial carina absent.

Legs. Fore tibial spur as long as basitarsus; hind tibia expanded at apex, 1.7 x as wide as at base, 0.2 x as wide as long; hind tibia and tarsi with light brown spines among pilosity; inner hind tibial spur 1.4 x as long as outer spur, 0.6 x as long as basitarsus; hind basitarsus with slight flattening, dorsal ridge at base; hind tarsal claw with six teeth of even width.

Wings. Fore wing with 1-SR+M 4 x as long as m-cu; 2-SR+M 1.8 x as long as m-cu; 1-M straight; m-cu 0.5 x as long as 1-M; 1-M 0.5 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a represented by pigmented node; 1a represented by small node, pigmented and spectral posterior to node; 1-2A+3A present and spectral, joining spectral apex of 1a; 1-CUa 0.4 x as long as 1-CUb; 2r 0.6 x inside height of second submarginal cell, arising 0.6 x length along stigma; stigma 3.0 x as long as wide; 4-SRb evenly curved in basal half, then straight to upturned to apex; angle between 4-

SRa and 4-SRb 130°; second submarginal cell 2.5 x as long as wide; 2+3-SR arched at base; hind wing with 4 evenly spaced hamuli; 2-1A represented by basal node; 2A indicated basally by pigmentation.

Metasoma. T1 short, 1.2 x as long as broad, stem 0.2 x as long as bulb; suture between T2 and T3 represented by defined groove; median field of T2 0.3 x as long as broad; ovipositor sheaths broad and long, 0.7 x as long as hind tibia, 0.2 x as broad as long, hairy in apical three-quarters, broadly rounded at apex, with dorsal notch; hypopygium with sparse fine hair laterally.

Male

As for female except for the following:

Antenna with 32-33 segments; propodeal areola rounded basally; sometimes scape and pedicel yellow; sometimes wings more darkly infuscate basally.

Host

Unknown.

Comments

Pol. gwenae can be interpreted as an intermediate between *Polycardiochiles* and *Austerocardiochiles*. It has the even width tarsal claw pectination, malar carina, propodeum and head sculpturing of *Austerocardiochiles*, but does not have a medial carina on the scutum or an epicnemial carina, which define *Polycardiochiles*. It is widely distributed from north Queensland to south-western Western Australia and is here named after Gwenda Mayo.

7.3.27. Polycardiochiles philippensis (Ashmead), Comb. nov. (Figs 7.45, 7.49)

Car. philippensis (Ashmead), 1905: 118. - Shenefelt, 1973: 796. Car. philippinensis (misspelling); Baltazar, 1966: 29.

Material Examined

Holotype. Q, Philippines, "Manila. PI" "Robt Brown Collector" "Q Type No. 453 USNM" "Cardiochiles philippinensis Q Ashmead" (USNM).

Other material examined. Indonesia: 180, 130, Sulawesi, Bantimurung Nat. Pk., 19 Apr. 1991, 30 m, C. v. Achterberg (RMNH); 100, 10, Sulawesi, nr Bantimurung, Leang-Leang, 17 Apr. 1991, 60 m, C. v. Achterberg (RMNH); 1Q, Sulawesi, nr Bantimurung, Karaente Nat. Res., 18 Apr. 1991, 250-300 m, C. v. Achterberg (RMNH); 7Q, 10, Sulawesi, nr Bantimurung, Pattunuang Asue, 17-20 Apr. 1991, 60 m, C. v. Achterberg (RMNH); 8Q, 10, Sulawesi, Dumoga-Bone Nat. Pk, 1-19 Nov. 1985, C. v. Achterberg (RMNH); 30Q, 190, Sulawesi, Toraut, 200m, 9-16 May 1985, J. S. Noyes (BMNH, WARI); 12Q, 140, Sulawesi, Dumoga-Bone Nat. Pk, 30 May -6 Jun. 1985, J. S. Noyes (BMNH, WARI); 1Q, Java, Buitenzorg, 1906-1907, T. Barbour (MCZC); 2Q, 30, W. Java, Bibidjilum, Aug. no year, Sternitzky (MCZC); 10, W. Java, Timerang, Sep. no year, Sternitzky (MCZC); 10, 20[°], Sumatra, Tandjon Morawa, 16 Dec. 1954, J. V. D. Vecht (RMNH). Philippines: 23Q, 25O, differing localities (Los Banos, Tacloban, Maripipi, Pto Princesca, Cotabato, Antipolo, Manila, San Teodoro, Masbate, San Mauel, Alcate, Lipa, Babuyan) Sep. 1952-Feb. 1953, Townes family (AEIC); 1Q, Leyte Bay, Sept. 1980 (BMNH); 1Q, Palawan, Panitian, 9 May 1967, M. D. Delfinado (BPBM). Malaysia: 20, Terengganu State, 7 km N. W. Ayer Putek, 100 m 27 Feb.-2 Mar. 1990, P. T. & F. I. T. (CNCI); 4Q, Borneo, Sabah State, Poring, 26-29 May 1970, T. W. & M. C. Davies (CASC); 10, Singapore, 12 Feb. 1968, C. G. Rochie (BMNH). Thailand: 2Q, Chiang Mai, 12 Nov. 1976, Pronk (RMNH); 1Q, 18 km E. Trang, Khao Chong Nat. Pk, 400 m, 24 May 1988, R. Hensen (HNHM); 1Q, Nakhon Ratchasima, Pak Chong, Mu Si, Yai Chong, Vil, 15-23 Aug. 1969, G. R. Balmer (CASC). Nepal: 1Q, Katmandu (Balaju), 16 Sep. 1983, N. Mohr (RMNH). Formosa: 60, Sauter, Taihorinaho, Sep. 1908 (HNHM). Laos: 1Q, Borikhane Prov., Paskane, 14 Jan. 1966, native collector (BPBM); 1Q, Vientane Prov., Ban Van Eue, Oct. 1965, native collector (BPBM).

Female

As for Pol. fuscipennis except as follows:

Notauli and sternaulus smooth; infuscation and pattern on wings uniform (not variable as in *Pol. fuscipennis*); fore wing very lightly infuscate medially, with

moderately dark infuscation in basal one-eighth and apical one-quarter; hind wing lightly infuscate medially, with moderately dark infuscation in basal one-quarter and apical one-sixth; propodeal areola with medial longitudinal carina in anterior one-fifth, generally uniform in shape (not variable as in *Pol. fuscipennis* - Figs 7.42 - 7.44).

Male

As for female.

Host

Unknown.

Comments

This species is almost identical to *Pol. fuscipennis* apart from the smooth notauli and sternaulus. Generally, *Pol. philippensis* is much less variable in morphology than *Pol. fuscipennis*, particularly with respect to the degree and pattern of wing infuscation, and shape of the propodeal areola. This species is found north of Wallace's Line and has been recorded from the Philippines, Indonesia, Malaysia, Indo-China and Taiwan (Fig. 7.49). It has been included in this study, even though it does not occur in the Australasian Region, so that previous confusion between it and *Pol. fuscipennis* can be resolved. Previously this species has often been misspelt, the correct spelling being *Pol. philippensis*. This has come about because the type label reads "*Car. philippinensis*" but the original published description is entitled "*Car. philippensis*".

7.3.28. Pseudcardiochilus naumanni, sp. nov.

(Figs 6.75 - 6.77)

Material Examined

Holotype. Q, Western Australia, "31.17S 119.30E 15 km W by N Yellowdine WA 10 Oct. 1981 I. D. Naumann, J. C. Cardale" (ANIC).

Paratype. 10⁷, same data as holotype (ANIC).

Female

Length. 5.3 mm.

Colour. Orange apart from the following which are black: vertex, frons posterior temples to occiput, scutum, dorsal scutellum, anterior propodeum except carinae, mesopleuron below epicnemial ridge, mesosternum, metasternum, mid coxae, hind legs except distal coxae trochanter and proximal femora, ovipositor; fore and hind wings hyaline to lightly infuscate in basal half, darker in apical half; venation brown.

Head. Head with moderately sparse medium length fine golden pilosity; epistomal suture reduced, gently convex; clypeal margin convex, with slight broad lobe medially and two lobes laterally; clypeus broad, 2.8 x as broad as high; face broad, 2.1 x as broad as high; vertex reduced behind ocelli, lower than ocelli in anterior view; depth of occiput in dorsal view 0.2 x length of head; face smooth, with medial dorsal node; frons smooth with shallow medial pit; ratio of length of eye to length of temple in dorsal view 1.0:0.5; antennae with 44 segments, subequal to length of body; scape rounded, geniculate, 1.2 x as long as broad; antennal sockets broadly separated by 1.5 x width of antennal socket.

Mesosoma. Dorsal pronotum with slight dorso-medial longitudinal furrow; notauli narrow, of even width, meeting posteriorly; scutum smooth; parapsidal grooves lightly indented; scutellum sparsely pilose, smooth, as broad as long, slightly humped in lateral view; scutellar sulcus 3.8 x as broad as long with four irregularly spaced carinae; dorsellum with medial longitudinal carina well-developed; propodeal areola broad, diamond-shaped; propodeal spiracles slightly elongate, kidney shaped, 2.7 x as long as broad; sternaulus shallow, smooth; propleuron smooth.

Legs. Moderately stout; fore tibial spur 0.8 x as long as basitarsus; hind tibia expanded slightly with slight rounded flange at apex, 2.4 x as wide as at base; hind tibia and tarsi with short brown spines among pilosity; inner hind tibial spur 1.3 x as long as outer spur, 0.7 x as long as basitarsus; hind basitarsus mostly cylindrical, with slight flattening at base.

Wings. Fore wing with 1-SR+M 3.4 x as long as m-cu; 2-SR+M 1.5 x as long as m-cu; 1-M slightly convex; m-cu 0.5 x as long as 1-M; 1-M 0.6 x as long as 1-SR+M; discal cell 1.8 x as long as wide; 2cu-a virtually absent, slightly pigmented; 1a present pigmented in apical half; 1-CUa 0.2 x as long as 1-CUb; 2r 0.6 x inside height of second submarginal cell, arising two-thirds along stigma; stigma 3.1 x as long as wide; 4-SRb evenly curved along length, sinuate at apex; angle between 4-SRa and 4-SRb 130°; second submarginal cell 3.4 x as long as wide; 2+3-SR evenly convex; hind wing with 5 unevenly spaced hamuli and 3 stout hairs proximal to hamuli; 2-1A present, pigmented, reaching almost half way to edge of wing; 2A absent.

Metasoma. T1 1.7 x as long as broad, stem absent; suture between T2 and T3 represented by poorly defined groove; median field of T2 rectangular, 0.6 x as long as broad; ovipositor sheaths 0.1 x as long as hind tibia, as broad as long, hairy along length, broad and rounded at apex; hypopygium sparsely hairy throughout, right angled at apex.

Male

As for female.

Host

Unknown.

Comments.

Pseudcardiochilus naumanni is similar to the *Pse. abnormipes* Hedwig, however the morphology of the hind tibia is different (see Figs 6.72, 6.73 and 6.76). In *Pse. naumanni* the hind tibia is projecting slightly with a pointed ridge at the apex, unlike *Pse. abnormipes* which has the hind tibia with a large glabrous projection and truncate concave apex. The latter character is also found in some *Toxoneuron* species from North America, but not in association with the other characters which define *Pseudcardiochilus*. This species is known only from the south-west of Western Australia and is here named after Ian Naumann, hymenopterist at the Australian National Insect Collection.

7.4. Distribution patterns of Australasian fauna

Although the information available on the distribution of most Australasian species can be considered tentative at best, it is clear that a number of species have distinct distributions and are probably associated with particular habitats or climate zones. Several species are restricted to tropical and/or subtropical rainforest remnants. These include the widespread *Pol. fuscipennis* which is found along the east coast of Queensland, Papua New Guinea to the Solomon Islands and north-west to Sulawesi (Fig. 7.49). The closely related species, *Pol philippensis*, has a parapatric distribution and extends from Sulawesi through Indonesia to the Philippines and Indo-China. Other species apparently associated with rainforest or remnants of wet vegetation on the Australian mainland are *Aus. callemondah*, *Aus. deetoo*, *Aus. pollinator* (Fig. 7.48), *Car. rasi, Car. saeedi* (Fig. 7.47), *Car. verticalis* (Fig. 7.46), *Hym. bubbur* and possibly *Aus. exleyae*. Three species are possibly endemic to Papua New Guinea, *viz. Aus. morulus*, *Car. goosei* and *Car. scotti* (Fig. 7,46), while *Pol. dissimulator* is so far known only from Thursday Is.

A number of species are apparently restricted to desert regions, particularly the region from the MacDonnell Ranges to Uluru (Ayers Rock) (*Car. iqbali, Lat. areyongensis* and *Lat. eremophilasturtiae*) and central Western Australia (*Circ. occidentalis*). Other species known with only restricted distributions are *Boh. naumanni* and *Hym. noongarensis* from south-western Western Australia and *Hym. nockatungensis* from south-western Queensland.

Species with very broad distributions that are seemingly not associated with particular habitats include *Car. evelinae, Car. rufator, Car. uniformis, Lat. turneri and Pol. gwenae* (Figs 7.46 - 7.48). Future collecting will undoubtedly extend some of the distributions documented here, however, the substantial amount of material available in collections to date surprisingly has revealed cardiochilines to be absent from the extended

south-eastern Bassian Region (South Australia, New South Wales except for the northern coastal region and one *Car. uniformis* specimen from central New South Wales, Victoria and Tasmania), as well as New Zealand, and the Pacific Islands east of the Solomon's.

7.5. Biology of the Australasian fauna

Very little is known about the biology of the Australasian species. Only two of 27 species have been reared from identified hosts, *viz. Car. goosei* from *Crocidolomia binotalis* (Pyralidae: Evergestinae) on cabbage in Papua New Guinea and *Car. uniformis* from *Helicoverpa* sp. (Noctuidae).

Specimens in museum collections have mostly been collected by malaise trapping or by sweeping vegetation which is in flower. Like many parasitic wasps, cardiochilines appear to feed on nectar or pollen or both as an energy and protein source, respectively, and the head and mouthparts of specimens in collections are often covered with pollen grains. Several species show interesting associations with particular plant species and they may be involved in their pollination. For instance, *Aus. pollinator* sp. nov. is presumed to feed at flowers of *Asclepias* spp. 'milkweed' (Asclepiadaceae) as pollinia of this plant have been found on the tarsal claws of some specimens. *Lat. eremophilasturtiae* sp. nov. has been collected in central Australia on *Eremophila sturtii* 'turpentine bush' (Myoporaceae) in full flower, along with several other braconids and ichneumonids of similar colour and size.

CHAPTER 7

Figures 7.1 to 7.49

Fig. 7.1. Austerocardiochiles callemondah sp. nov., holotype, female, dorsal head to T3. Figs 7.2 - 7.4. Aus. exleyae sp. nov., holotype, female: 7.2, dorsal head to T3; 7.3, anterior head; 7.4, second submarginal cell of fore wing. Fig. 7.5. Aus. deetoo sp. nov., holotype, male, dorsal head to T3. Figs 7.6, 7.7. Aus. morulus sp. nov., holotype, female: 7.6, dorsal head to T3; 7.7, anterior head. Scale lines: 7.1, 0.5 mm; 7.2 - 7.4, 7.6, 7.7, 1 mm; 7.5, 0.25 mm.



Figs 7.8 - 7.12. *Bohayella toxopeusi* sp. nov., holotype, female: 7.8, fore wing; 7.9, hind wing; 7.10, anterior head; 7.11, lateral propodeum; 7.12, dorsal propodeum to T3 with 'ball-like' joint of T2 arrowed. **Fig. 7.13.** *Boh. adina* (Wilkinson), holotype, female, dorsal T1 and T2. Scale lines: 7.8, 7.9, 7.13, 1 mm; 7.10 - 7.12, 0.5 mm.

Ļ



Fig. 7.14. Cardiochiles goosei sp. nov, holotype, female, ovipositor sheaths. Figs 7.15 - 7.17. Car. rufator Roman, holotype, female: 7.15, dorsal habitus; 7.16, ovipositor sheaths; 7.17, lateral mesopleuron and mesosternum. Figs 7.18 - 7.23. Car. uniformis Turner, holotype, female: 7.18, dorsal habitus; 7.19, lateral mesopleuron and mesosternum; 7.20, anterior head; 7.21, fore wing; 7.22, hind wing; 7.23, ovipositor sheath. Fig. 7.24. Car. verticalis Turner, holotype, female, proximal hind wing. Scale lines: 7.14, 0.25 mm; 7.15, 7.18 - 7.24, 1 mm; 7.16, 7.17, 0.5 mm.



Fig. 7.25. *Cardiochiles rufator* Roman, female, lower dorso-lateral head. Fig. 7.26. *Car. verticalis* Turner, female, hind tarsal claw. Fig. 7.27. *Car. uniformis* Turner, female, dorsal metanotum to T2. Fig. 7.28. *Car. verticalis* Turner, female, dorsal scutum to propodeum. Scale lines: 7.25, 0.2 mm; 7.26, 7.28, 0.4 mm; 7.27, 0.25 mm.

ł.



Figs 7.29 - 7.31. *Hymenicis bubbur* sp. nov., holotype, female: 7.29, anterior head; 7.30, dorsal head to T2; 7.31, lateral apex of metasoma. Figs 7.32 - 7.34. *Hym. nockatungensis* sp nov., holotype, female: 7.32, anterior head; 7.33, dosal head to T2; 7.34, lateral apex of metasoma. Scale lines: 7.29, 7.30, 7.32 - 7.34, 1 mm; 7.31, 0.5 mm.



Figs 7.35 - 7.37. E-SEM's of *Latitergum turneri* sp. nov., holotype, female: 7.35, anterior eye; 7.36, dorsal propodeum; 7.37, dorsal T1 and T2. Scale lines: 7.35, 0.04 mm; 7.36, 7.37, 0.1 mm.



Figs 7.38, 7.39. Latitergum eremophilasturtiae sp nov., holotype, female: 7.38, anterior head; 7.39, dorsal head to T3. Figs 7.40, 7.41. Lat. turneri sp. nov., holotype, female: 7.40, dorsal head to T3; 7.41, anterior head. Scale lines: 7.38 - 7.41, 0.5 mm.



Figs 7.42 - 7.44. *Polycardiochiles fuscipennis* (Szépligeti), female, variation in the form of propodeal sculpturing and shape. **Fig. 7.45.** *Pol. philippensis* (Ashmead), female, dorsal habitus. Scale lines: 7.42 - 7.44, 0.5 mm; 7.45, 1 mm.

je.









Figs 7.46, 7.47. Distribution maps of Cardiochiles s. str. spp.



Fig. 7.48. Distribution map of Austerocardiochiles pollinator sp. nov., Aus. exleyae sp. nov. and Latitergum turneri sp. nov. Fig. 7.49. Distribution map of Polycardiochiles fuscipennis (Szépligeti) and Pol. philippensis (Ashmead).

į.



CHAPTER 8

General Discussion

CHAPTER 8

General Discussion

The major outcomes of this project have been the development of the first cladistic-based classification for the braconid subfamily Cardiochilinae, and a revision of the Australasian species. This has resulted in a reduction in number of species in the genus *Cardiochiles s. l.* from 170 to 22 and the transfer of 52 species to other genera. Unfortunately, 104 species remain *incertae sedis* because their descriptions are too superficial to place them in the new generic classification outlined here, and time constraints on this project preclude the examination of all type specimens. *Cardiochiles s. str.* is now recognised as one of 18 genera for the subfamily worldwide and, rather than accommodating 95% of described species, it now comprises only 22%. Four of the genera previously treated as junior synonyms of *Cardiochiles s. l.* have been reinstated to generic rank. The description of eight new genera clearly points to a morphological diversity within the subfamily not previously recognised by other authors (Quicke and van Achterberg 1990; Whitfield and Mason 1994) who have incorrectly coded many characters (see Chapters 2 and 5) in attempts to resolve the relationships among braconid subfamilies.

Taxonomic revisions of genera and species are imperative to understanding higher level relationships, as such studies provide basic information on the structure and diversity of a group. This is particularly so for the Hymenoptera, which is poorly known taxonomically, and where revisionary studies often increase the number of known species by five to ten fold. Using the Australian fauna as an example, Naumann (1982) described six new genera and 35 new species of ambositrine diapriids, representing a two-fold increase of species, while Boucek (1988) listed over 2360 species of Chalcidoidea in 550 genera, and added 15 new subfamilies, 13 tribes, 138 genera and 190 species. A similar trend is evident for the Braconidae. For example, a revision of *Microplitis* Foerster and *Snellenius* Westwood for Australasia (Austin and Dangerfield 1993) described 23 new species representing a four and a half fold increase. Austin (1990) described eight new species of the endemic Australian genus *Miropotes* Nixon, representing a four fold increase, while for the genus *Mesocentrus* Szépligeti, the number of Australasian species is likely to increase by five to ten times (Austin *pers. comm.*). Austin and Dangerfield (1992) treated 26 genera and 118 species of Microgastrinae from Australasia, but given that the highly speciose genera *Cotesia* Cameron, *Apanteles* Förster *s. str.* and *Glyptapanteles* Ashmead remain virtually undescribed, these figures may represent as little as 10-20% of the real fauna (Mason 1981).

Prior to this study only eight species of Cardiochilinae were recognised for the Australasian region. This study reduced that number to five, through synonymy of species with *Polycardiochiles fuscipennis* (Szépligeti), and in addition described twenty-one new species. This four-fold increase in species for the region probably represents only about two-thirds of the real size of the fauna given that at least six additional species were recognised during the study. These could not be formally described, firstly because of a lack of material, and secondly, because unrecorded new species undoubtedly exist in remote regions of the continent.

Fundamentally, it is not until biological species are recognised that work can be undertaken on their behaviour, physiology and ecology. Biological species are the only truly objective taxonomic unit within a classification and all higher level groupings represent hypotheses of how species have evolved, or more precisely, they constitute species deemed to be more closely related to each other. One of the most powerful attributes of higher level categories resulting from phylogenetic studies is that they have substantial predictive value for inferring information about the biology of species (i.e. their physiology, behaviour and ecology) and, in the case of the parasitic Hymenoptera, their host relationships.

As well as there being a need to document the species richness of the parasitic Hymenoptera for biodiversity studies (LaSalle and Gauld 1993), the major justification for systematic research on the group remains their pre-eminence as biocontrol agents and the need to provide taxonomic support for this activity. Interestingly, LaSalle and

Gauld (1993) link the two areas, biodiversity and biocontrol, and discuss the importance of assessing arthropod biodiversity for biocontrol programs, stating that organisms introduced and established against any given pest have an actual value in the control they provide. A premise to this statement indicates that there is a wealth of unknown species that need to be documented before they can be utilised in agricultural systems. For example, recent studies on a number of potential pest species of eucalypt trees in Australia and overseas reveal them to have 17-20 species of associated wasp parasitoids per host, of which only 50% could be recognised to species level (Austin and Allen 1989; Thumlert and Austin 1994)

Knowing the phylogenetic relationships among species can be a useful tool in the search for potential biocontrol agents. Closely related species often have similar host associations and ranges and so, having determined which species are related may lead to the recognition of biocontrol agents of the same or similar pests. For example, Qin *et al.* (1994) used cladistic analyses of wax scale insects (Coccidae) to predict the native range of *Ceroplastes sinensis* del Guercio, now a pest in all temperate regions, in an attempt to facilitate the location of successful biocontrol agents.

The generic reclassification and elucidation of generic relationships developed here has relied heavily on computer-based analyses using the maximum parsimony algorithm PAUP 3.1.1 (Swofford 1993). The use of computers has revolutionised taxonomy and phylogenetic studies in the past ten years. Where once only small data sets could be analysed with confidence, now groups containing extremely large numbers of taxa and characters can be investigated using such algorithms. For example, Klompen and Oliver (1993) revise the phylogeny of argasid ticks with a matrix of 41 taxa and 83 characters, and Knight and Webb (1993) revise the relationships of deltocephaline leafhoppers, analysing a matrix of 61 taxa by 81 characters using Hennig86 (Farris 1988).

The computer allows complex mathematical analyses to be undertaken (Mangel and Clarke 1988), and allows the interplay among related factors such as biology and morphology to be determined and used for evolutionary inference. The ability of

modern desktop computers to accommodate large data sets has been instrumental in the application of molecular data to phylogenetic studies, that inherently use very large data sets (Weller *et al.* 1992). Further, the role of computers in analysing molecular data has paralleled technical developments that have facilitated easier determination of DNA sequences, particularly the polymerase chain reaction and autosequencing technology (Cameron *et al.* 1992; Dowton and Austin 1994).

Due to the large morphological data set generated in this study, (greater than ten taxa by ten characters), the 'heuristic search option' was used (Swofford et al. 1993). However, this search option does not evaluate all possible solutions to the data, as does the 'exhaustive search option'. Therefore, the results obtained can never be guaranteed as the most parsimonious for the data set. The use of the recently proposed PTP and T-PTP statistical test can provide confidence estimates of the results obtained. These tests for significance have a simple underlying concept, in that they test the null hypothesis that the trees obtained could have been generated by chance alone. However, the methodology of the T-PTP tests appears somewhat confused. For these tests the differences in lengths between the trees generated by an analysis with particular nodes constrained, and the same analysis forced not to have that constraint, are always treated as positive. The quandary comes from the expectation that the nonconstrained trees should be longer than the constraint trees in order to confirm that the information was not found by chance alone. Unexpectedly, the randomised searches required for these tests always gave the reverse of this, in this study. However, according to Trueman (pers. comm.) the differences should always be treated as positive and, so in this study, the significance of the results was confirmed. Trueman (1993) states that PTP and T-PTP tests cannot show whether a tree is phylogenetically accurate or not, merely whether the tree could have arisen by chance. Many authors have discussed the validity of the different tests available (Carpenter 1992; Trueman 1993; Farris et al. 1994; and Faith et al. 1994) and, even though the PTP and T-PTP tests may not appear logical in some respects, they are the best available for confirming the significance of the cladistic information and structure of a tree (see Section 3.6.6).

However, for the practicing systematist these tests have two important drawbacks. Firstly, one of the major areas of current development in phylogenetic systematics is in improving tests of significance at both the theoretical and practical level, and so one is faced with assessing criticisms and modifications to tests on a frequent basis. Indeed, when this study began, the PTP and T-PTP tests did not exist! Secondly, in practise, undertaking these tests on moderately large-sized data sets is extremely difficult and time consuming, unless substantial access to computer time is available. The last of these problems could be overcome if the relevant software was available in different computing formats. The 'windows' format available for Macintosh computers means that the program is initially easier to comprehend, or more 'user friendly'. The problem with this algorithm format is that it is plagued by the "tyranny of complexity" (von Neumann and Morgenstern 1947), viz. with 'n' taxa to classify, the polynomial algorithm time taken, Aⁿ, is exponentially increased with the addition of each new taxon. The PAUP program is basically a numerical algorithm which could be rewritten in, or adapted to, a 'windows' independent format that could be transferred to different operating systems, for instance the UNIX mainframe system, that would reduce analysis time greatly. For example, if written in Language 'C' the program could be run in FORTRAN 90 or PASCAL formats which have the capacity to run parallel computations rather than in sequential form, as is currently the case for Macintosh format.

Hopefully, the robustness of the phylogenetic analyses undertaken here and the resultant generic classification for the Cardiochilinae, will be tested by subsequent workers. This classification must be considered as preliminary, but one that nonetheless is far superior to previous arrangements for the group. The world fauna still remain poorly studied, particularly for three zoogeographic regions, the Afrotropical, Oriental and Neotropical regions. The key to genera presented here will hopefully render the fauna of these regions more amenable to study, but in so doing such studies will provide the means for testing the monophyly of these genera. This will undoubtedly lead to an improvement of the current taxonomic understanding of the

Cardiochilinae, their application in biodiversity studies, and the use of select species as biocontrol agents of lepidopteran pests.
APPENDICES

A1 to A5

Appendix A1. The standard 10x10 matrix analysed by PAUP 3.1.1 to test relative speeds of different computers used in this study. The matrix was constructed using the random fill option of MacClade 3.02.

6.00

	1:2	2.	3.	4.	5.	6.	7.	8.	9.	10.
1.	0	1	1	0	0	1	0	0	1	0
2.	0	1	0	1	1	0	0	0	0	1
3.	0	1	0	1	0	0	1	1	1	1
4.	0	1	1	0	1	1	0	0	0	0
5.	0	0	1	0	1	0	1	1	1	1
6.	1	1	0	0	1	1	0	0	1	0
7,	0	0	1	0	1	1	1	1	0	1
8.	0	1	1	0	1	0	0	1	0	1
9,	1	0	1	1	0	1	1	1	0	1
10.	1	1	0	1	1	0	1	1	1	0

Appendix A2.1. Graphical representation of means of morphometric data obtained from clypeal breadth x height (character 30) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Taxa in ascending order

Appendix A2.2. Graphical representation of means of morphometric data obtained from facial breadth x height (character 31) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Taxa in ascending order

Appendix A2.3. Graphical representation of means of morphometric data obtained from eye to temple length ratio (character 32) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Taxa in ascending order

Appendix A2.4. Graphical representation of means of morphometric data obtained from dorsal occipital depth to head depth ratio (character 33) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.5. Graphical representation of means of morphometric data obtained from scape length to breadth ratio (character 34) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.6. Graphical representation of means of morphometric data obtained from ratio of distance between antennal sockets to width of socket (character 35) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.7. Graphical representation of means of morphometric data obtained from antennal segment number (character 36) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.8. Graphical representation of means of morphometric data obtained from scutellar sulcus width to length ratio (character 37) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.9. Graphical representation of means of morphometric data obtained from stigmal width to length ratio (character 38) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.10. Graphical representation of means of morphometric data obtained from hamuli number (character 39) arranged in ascending order. The taxa are in the order represented in Appendix A3. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.11. Graphical representation of means of morphometric data obtained from T1 length to width ratio (character 40) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.12. Graphical representation of means of morphometric data obtained from T2 median field length to width ratio (character 41) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.13. Graphical representation of means of morphometric data obtained from ovipositor sheath length to hind tibial length ratio (character 42) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A2.14. Graphical representation of means of morphometric data obtained from ovipositor sheath breadth to length ratio (character 43) arranged in ascending order. The taxa are in the order represented in Appendix A3, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation (SD) from the mean. See Section 3.6.2 for the method of coding morphometric characters.



Appendix A3. Means for morphometric characters (Section 5.3.2) in ascending order. Bold subheadings represent the character state coding, and outgroups used in analyses are in italics. Refer Appendices A2.1 - A2.14 for graphical representation of data, Section 3.6.2 for method of coding morphometric data, and Section 5.3.2 for discussion of characters used in analyses.

30. Clypeal dimensions		31. Facial dimensions	32. Eye:Temple ra	tlo	33. Occipital depth		
					0.92		0.31
lean	2.28		1.87		0.03		0.12
5.D.	0.43	0.4.4.0	0.5	Coded 0	0.101	Code 0	
Coded 0	111	Coded U	0.88	eremonhilasturtiae	0.5	rubricollis	0.11
tricornis	1.14	Prasmadon	1	naumanoi	0.5	macula	0.12
Coded 1	1 57	Coded 1		Prasmadon	0.56	Prasmadon	0.12
ngromaculata	1.57	bymeniae	1.38	diaphaniae	0.56	fasciipennis	0.13
lineimulator	1.0	Microniitis	1.4	arevongensis	0.6	nigripennis	0.14
	1.7	callemondah	1.4	dissimulator	0.6	Microplitis	0.15
uscipeniis	1.7	morulus	1.45	fuscipeniis	0.6	Code 1	
biliopensis	1.7	sumatranus	1.46	turneri	0.6	naumanni	0.2
ohiari	1.75	Ensilogaster	1.47	philippensis	0.6	nockatungensis	0.2
dianhaniae	1.8	evelinae	1.5	Coded 1		seminiger	0.2
Coded2		pollinator	1.5	Epsilogaster	0.67	turneri	0.2
morulue	1.85	rufator	1.5	A. minutus	0.67	verticalis	0.2
nordius	1.95	saeedi	1.5	explorator	0.69	explorator	0.21
obnormines	1.96	nedis	1.5	nigromaculata	0.69	magnus	0.21
Microplitie	2	nigromaculata	1.5	callemondah	0.7	rubidum	0.22
ovaliaaa	2	ruficollis	1.5	evelinae	0.7	vlator	0.22
evennae	2	sp. indet.	1.57	goosei	0.7	acutus	0.24
saeadi	2	atricornis	1.6	gwenae	0.7	rubicundus	0.24
lasciinennis	2	diaphaniae	1.6	nockatungensis	0.7	toxopeusi	0.25
A minutus	2	minutus	1.6	rufator	0.7	subflavus	0.26
toxopeusi	2.1	goosei	1.7	saeedi	0.7	sumatranus	0.26
arovondonsie	21	lobali	1.7	scotti	0.7	saltator	0.27
minutue	21	rasi	1.7	macula	0.72	Epsilogaster	0.28
ruficollis	2.1	scotti	1.7	mexicanus	0.73	mexicanus	0.29
latioes	2.15	uniformis	1.7	pedis	0.74	minutus	0.29
enderleini	2.15	verticalis	1.7	latipes	0.76	A. minutus	0.3
macula	2.17	enderleinl	1.7	bubbur	0.8	areyongensis	0.3
deetoo	2.2	saltator	1.75	occidentalis	0.8	bicolor	0.3
evievae	2.2	deetoo	1.8	saltator	0.8	bubbur	0.3
subflavus	2.2	dissimulator	1.8	tibiator	0.81	dissimulator	0.3
sumatranus	2.24	exievae	1.8	ruficollis	0.82	evelinae	0.3
Presmadon	2.25	fuscipeniis	1.8	Coded 2		fuscipeniis	0.3
acutus	2.25	turnerl	1.8	vlator	0.83	iqbali	0.3
Coded 3		philippensis	1.8	acutus	0.83	latipes	0.3
gwenae	2.3	nigripennis	1.8	abnormipes	0.83	noongarensis	0.3
pedis	2.3	mexicanus	1.8	atricornis	0.86	occidentalis	0.3
mexicanus	2.3	A. minulus	1.8	dilatus	0.87	philippensis	0.3
tibiator	2.3	Coded 2		minutus	0.88	rasi	0.3
saltator	2.3	subflavus	1.88	subflavus	0.89	rufator	0.3
callemondah	2.4	tiblator	1.9	nlgriceps	0.89	saeedi	0.3
goosei	2.4	toxopeusi	2	deetoo	0.9	uniformis	0.3
inhali	2.4	arevongensis	2	iqbali	0.9	Code 2	
rasi	2.4	gwenae	2	rasi	0.9	enderleini	0.31
scotti	2.4	macula	2	uniformis	0.9	hymeniae	0.32
uniformis	2.4	explorator	2	verticalis	0.9	nigromaculata	0.32
verticalis	2.4	magnus	2	rubricollis	0.9	diaphaniae	0.33
nioripennis	2.4	2 tobiasi	2.03	3 enderleini	0.93	2 tobiasi	0.3;
sp. indet.	2.4	B fasciipennis	2.00	6 sumatranus	0.9	5 nigriceps	0.36
Epsilogaster	2.5	naumanni	2.1	fasclipennis	0.9	5 pedis	0.3
muirii	2.5	occidentalis	2.1	blcolor	0.9	5 tibiator	0.3
rubricollis	2.5	muirli	2.1	magnus	0.9	7 atricornis	0.4
viator	2.5	9 nigriceps	2.11	3 Microplitis	1	eremophilasturtiae	0.4
nigriceps	2.6	acutus	2.1	7 exleyae	1	exleyae	0.4
eremophilasturtiae	2.7	eremophilasturtiae	2.2	morulus	1	goosel	0.4
occidentalis	2.7	nockatungensis	2.2	noongarensis	1	muirii	0.4
Coded 4		abnormipes	2.2	4 pollinator	1	scotti	0.4
bicolor	2.7	5 bubbur	2.2	5 hymeniae	1	Code 3	
naumanni	2.8	3 seminiger	2.3	3 Coded 3		sp. indet.	0.4
noongarensis	2.8	Coded 3		rubidum	1.0	5 gwenae	0.5
rubidum	2.1	3 rubricollis	2.4	tobiasi	1.0	8 morulus	0.5
bubbur	2.8	5 rubidum	2.4	sp. Indet.	1.0	9 Code 4	-
seminiger	2.8	8 viator	2.5	5 seminiger	1.1	2 deetoo	0.6
dilatus	3	noongarensis	2.6	6 Coded 4		Code 5	
Coded 5		dilatus	2.8	5 toxopeusi	1.3	2 callemondah	0.7
explorator	3.1	4 Coded 7		nigripennis	1.3	2 pollinator	0.7
nockatungensis	3	2 bicolor	4.	5 Coded 5			
Coded 6				mulril	1.4	.3	
magnus	3	5					

1.6 0.26 0.7 1.1 1.2 1.2 1.2 1.3 1.3 1.3 1.3 1.3 1.3 1.3 1.4 1.4 1.4	Coded 0 Prasmadon Coded 1 callemondah deetoo gwenae morulus muirii macula saltator Epsilogaster exleyae mexicanus exploreator	1.06 0.31 0.38 0.5 0.6 0.6 0.6 0.6 0.6 0.63 0.67 0.7	Coded 0 Microplitis Prasmadon Coded 2 A. minutus Epsilogaster turneri areyongensis eremophilasturtiae dilatus	37.2 7.05 18 18 26 28 28 28 28 28 28 28 29
$\begin{array}{c} 1.0 \\ 0.26 \\ \hline \\ 0.7 \\ \hline \\ 1.1 \\ 1.2 \\ 1.2 \\ 1.2 \\ 1.3 \\ 1.3 \\ 1.3 \\ 1.3 \\ 1.3 \\ 1.4 \\ 1.4 \\ 1.4 \\ 1.4 \\ 1.4 \end{array}$	Coded 0 Prasmadon Coded 1 Callemondah deetoo gwenae morulus muirii macula saltator Epsilogaster exleyae mexicanus exploreator	0.31 0.38 0.5 0.6 0.6 0.6 0.6 0.63 0.67 0.7	Coded 0 MicropIllis Prasmadon Coded 2 A. minutus Epsilogaster turneri areyongensis eremophilasturtiae dilatus	7.05 18 18 26 28 28 28 28 28 29
0.7 1.1 1.2 1.2 1.3 1.3 1.3 1.3 1.3 1.4 1.4 1.4 1.4	Coded 0 Prasmadon Coded 1 Callemondah deetoo gwenae morulus muirii macula saltator Epsilogaster exleyae mexicanus exploreator	0.38 0.5 0.6 0.6 0.6 0.6 0.63 0.67 0.7	Coded 0 Microplitis Prasmadon Coded 2 A. minutus Epsilogaster turneri areyongensis eremophilasturtiae dilatus	18 18 26 28 28 28 28 28 29
0.7 1.1 1.2 1.2 1.3 1.3 1.3 1.3 1.3 1.4 1.4 1.4 1.4	Prasmadon Coded 1 Callemondah deetoo gwenae morulus muirii macula saltator Epsilogaster exleyae mexicanus explorator	0.38 0.5 0.6 0.6 0.6 0.6 0.63 0.67 0.7	Microplitis Prasmadon Coded 2 A. minutus Epsilogaster turneri areyongensis eremophilasturtiae dilatus	18 18 26 28 28 28 28 28 29
1.1 1.2 1.2 1.2 1.3 1.3 1.3 1.3 1.3 1.3 1.4 1.4 1.4 1.4	Coded 1 callemondah deetoo gwenae morulus muirii macula saltator <i>Epsilogaster</i> exleyae mexicanus explorator	0.5 0.6 0.6 0.6 0.6 0.63 0.63 0.67 0.7	Prasmadon Coded 2 A. minutus Epsilogaster turneri areyongensis eremophilasturtiae dilatus	18 26 28 28 28 28 29
1.1 1.2 1.2 1.3 1.3 1.3 1.4 1.4 1.4 1.4	callemondah deetoo gwenae morulus muirii macula saltator <i>Epsilogaster</i> exleyae mexicanus exployator	0.5 0.6 0.6 0.6 0.6 0.6 0.63 0.63 0.67 0.7	Coded 2 A. minutus Epsilogaster turneri areyongensis eremophilasturtiae dilatus	26 28 28 28 28 29
1.2 1.2 1.3 1.3 1.3 1.4 1.4 1.4 1.4	deetoo gwenae morulus muirii macula saltator <i>Epsilogaster</i> exleyae mexicanus exployator	0.6 0.6 0.6 0.6 0.63 0.63 0.67 0.7	A. minutus <i>Epsilogaster</i> turneri areyongensis eremophilasturtiae dilatus	28 28 28 28 28 29
1.2 1.3 1.3 1.3 1.4 1.4 1.4 1.4	gwenae morulus muirii macula saltator <i>Epsilogaster</i> exleyae mexicanus exployator	0.6 0.6 0.6 0.63 0.63 0.67 0.7	Epsilogaster turneri areyongensis eremophilasturtiae dilatus	28 28 28 29
1.2 1.3 1.3 1.3 1.3 1.4 1.4 1.4 1.4	morulus muirii macula saltator <i>Epsilogaster</i> exleyae mexicanus exployator	0.6 0.6 0.63 0.67 0.7	turneri areyongensis eremophilasturtiae dilatus	28 28 29
1.3 1.3 1.3 1.3 1.4 1.4 1.4 1.4	muiril macula saltator <i>Epsilogaster</i> exleyae mexicanus exployator	0.6 0.63 0.67 0.7	areyongensis eremophilasturtiae dilatus	28
1.3 1.3 1.3 1.4 1.4 1.4 1.4	macula saltator <i>Epsilogaster</i> exleyae mexicanus explorator	0.6 0.63 0.67 0.7	eremophilasturtiae dilatus	29
1.3 1.3 1.4 1.4 1.4 1.4	saltator Epsilogaster exleyae mexicanus explorator	0.63 0.67 0.7	dilatus	20
1.3 1.4 1.4 1.4 1.4	Epsilogaster exleyae mexicanus	0.67		23
1.4 1.4 1.4 1.4	exleyae mexicanus	0.7	Coded 3	1 22
1.4 1.4 1.4 1.4	mexicanus		occidentalis	23
1.4 1.4 1.4	ovalorator	0.7	viator	33
1.4	avhiorator	0.71	iqbali	34
1.4	Coded 2		diaphaniae	34
	fasciipennis	0.77	tobiasi	34
1.42	Microplitis	0.8	rulator	35
1.44	pollinator	0.8	welformie	35
1.46	nigriceps	0.89	verticalis	35
1.46	goosei	0.9	tibiator	36
1.5	occidentalis	0.9	tiolator	36
1.5	scotti	0.9	avelinae	36
1.5	diaphaniae	0.94	dissimulator	36
1.5	evelinae		fuscioeniis	36
1.5	rufator	-	mondus	37
1.57	saeedi		chilippensis	37
1 2 8	sp. indet.		primppensis	37
1.6	sumatranus		gooser	
1.6	minutus		Coded 4	38
1.6	tibiator		humoniae	38
1.6	hymeniae		nymetrapus	39
1.6	A. minutus		Sumarianus	39
1.6	ruficollis		rasciperinis	39
1.6	Coded 3	1.00	seminiger	39
1.6	rubricollis	1.00	moviespus	40
1.6	enderleini	1.00	rosi	40
1.6	areyongensis	4.4	deetoo	41
1.6	iqbali	4.4	latines	41
1.7	rasi	1.1	noongaransis	42
1.7		1 1 1	hicolor	42
1.7	verticalis	1.1	callemondab	43
1.7	nigripennis	1.14	calemondari	43
1.75	bubbur	1.2	polimator	44
1.75	dissimulator	1.2	Coed 5	
1.8	eremophilasturnae	1.2	macula	45
1.8	luscipentis	1.2	pockatungensis	46
1.8	pedis	1.2	rubidum	46
1.8	philippensis	1.2	exlevee	46
1.8	viator	1.2	rubricollis	48
1.8	nigromaculata	1.2	Coded 6	
1.8	seminiger	1.20	multi	52
1.8	5 toxopeusi	1.3	bubbur	52
1.0		1.3		
1.8	e maapus	1.3		
1.8	o magnus	1.0		
1.9	Coded 4		-	
1.8		1.4		
1.9		1.4		
	subliavus	1.4	5	
	histor	1.4	5	
1.5		1.4		
2		1.0		
2	ahaorminan	1.0		
2	Coded 5	1.5		
2		4 -	7	
	nockatuligensis	1.1	7	
	tabiaci	4	7	
	1.46 1.46 1.5 1.5 1.5 1.5 1.5 1.6 1.7 1.77 1.77 1.77 1.77 1.77 1.8 1.8 1.8 1.8 1.5 1.5 1.5 1.5 1.5 1.5 <tr td=""></tr>	1.46 nigriceps 1.46 goosei 1.5 occidentalis 1.5 scotti 1.5 scotti 1.5 rufator 1.5 rufator 1.57 saeedi sp. indet. 1.6 minutus 1.6 minutus 1.6 hymeniae 1.6 hymeniae 1.6 nioutus 1.6 nioutus 1.6 ruficollis 1.6 rubricollis 1.6 rubricollis 1.6 rubricollis 1.6 rubricollis 1.6 rubricollis 1.6 rubricollis 1.6 revongensis 1.6 idpali 1.7 rasi 1.7 rasi 1.7 rasi 1.7 rasi 1.7 dissimulator 1.8 remophilasturtiae 1.8 pedis 1.8 pedis 1.8 nigr	1.46 nigriceps 0.89 1.46 goosei 0.9 1.5 occidentalis 0.9 1.5 scotti 1 1.5 scotti 1 1.6 sumatranus 1 1.6 minutus 1 1.6 hymeniae 1 1.6 rubicollis 1 1.6 rubicollis 1 1.6 rubicollis 1.06 1.6 areyongensis 1.1 1.7 rasi 1.1 1.7 rasi 1.1 1.7 i	1.46 nigriceps 0.89 unitormis 1.5 occidentalis 0.9 tbiator 1.5 scotti 0.9 acutus 1.5 scotti 0.9 acutus 1.5 scotti 0.9 acutus 1.5 scotti 0.94 evelinae 1.5 rufator 1 fuscipenils 1.5 scotti possi morulus 1.5 scotti possi possi 1.6 minutus 1 Coded 4 1.6 minutus 1 sumatranus 1.6 thintonis 1 hymeniae 1.6 thintonis 1 fuscipennis 1.6 todd 3 seminiger maxinanus 1.6 todd 3 seminiger maxinanus 1.6 todd 3 seminiger maxinanus 1.6 todd 3 tascipennis ni 1.7 rasi 1.1 tascipenis

37. Scutellar sulcus		38. Stigmal dimensions	39. Hamull number		40. T1 dimensions		
			2.44		5.3		1.9
	4.9	Mean	3.44		1.5		0.9
Deded 0	1.5	SU Coded 0	0.72	Coded 0		Coded 0	
coded u	24	turneri	2.2	Epsilogaster	3	areyongensis	0.8
ations	2.5	Ensilogaster	2.28	Prasmadon	3	Coded 1	
rubricollis	2.5	noongarensis	2.4	Microplitis	3	rubricollis	1.05
lasciinennis	2.9	Microplitis	2.45	minutus	3	pedis	1.06
picolor	2.9	acutus	2.5	abnormipes	3	eremophilasturtiae	1.1
pubbur	3	arevongensis	2.6	Coded 1		turneri	1.1
niariceps	3.06	eremophilasturtiae	2.6	areyongensis	4	nigripennis	1.1
Coded 1		minutus	2.6	eremophilasturtiae	4	viator	1.1
Prasmadon	3.4	magnus	2.7	gwenae	4	gwenae	1.2
subflavus	3.4	A. minutus	2.7	iqball	4	sumatranus	1.2
macula	3.4	Coded 1		rasi	4	fasciipennis	1.2
nockatungensis	3.5	toxopeusi	2.8	turneri	4	evelinae	1.3
dissimulator	3.6	dilatus	2.8	uniformis	4	iqbali	1.3
luscipeniis	3.6	bubbur	2.9	verticalis	4	rasi	1.3
philippensis	3.6	nockatungensis	2.9	atricornis	4	rufator	1.3
seminiger	3.6	seminlger	2.9	dilatus	4	saeedi	1.3
noongarensis	3.7	tobiasl	2.9	bicolor	4	dilatus	1.3
naumanni	3.8	abnormipes	2.9	nlgromaculata	4	hymeniae	1.3
sp. indet.	3.9	gwenae	3	hymeniae	4	occidentalis	1.4
nigromaculata	3.9	explorator	3	A. minutus	4	A. minutus	1.4
pollinator	4	viator	3.06	tobiasl	4	saltator	1.45
hymenlae	4	naumanni	3.1	acutus	4	verticalis	1.5
exleyae	4.3	tiblator	3.2	dissimulator	5	sp. Indet.	1.5
enderleini	4.6	pollinator	3.3	fuscipeniis	5	seminiger	1.5
dilatus	4.7	atricornis	3.3	goosei	5	enderleini	1.5
Epsilogaster	4.75	subflavus	3.3	naumanni	5	nigriceps	1.52
pedis	4.8	nigriceps	3.3	occidentalis	5	Microplitis	1.6
sumatranus	4.8	rubidum	3.36	scotti	5	goosei	1.6
Coded 2		Prasmadon	3.4	pedis	5	scotti	1.6
arevongensis	5	exleyae	3.4	philippensis	5	diaphaniae	1.6
eremophllasturtiae	5	igball	3.4	subflavus	5	naumanni	1.7
evelinae	5	rasi	3.4	sumatranus	5	atricornis	1.7
goosei	5	uniformis	3.4	diaphaniae	5	macula	1.7
gwenae	5	verticalis	3.4	explorator	5	morulus	1.8
iqbali	5	Coded 2		magnus	5	magnus	1.8
rasi	5	diaphaniae	3.46	mexicanus	5	minutus	1.8
rufator	5	saltator	3.48	tiblator	5	acutus	1.8
saeedi	5	mexicanus	3.5	viator	5	Coded 2	_
scotti	5	hymeniae	3.57	Coded 2		nockatungensis	1.9
turneri	5	evelinae	3.6	toxopeusl	6	uniformis	1.9
uniformIs	5	morulus	3.6	callemondah	6	explorator	1.9
verticalis	5	rufator	3.6	evelinae	6	rubicundus	1.9
atricornis	5.1	saeedi	3.6	morulus	6	tibiator	1.9
viator	5.2	callemondah	3.7	nockatungensis	6	rubidum	1.9
morulus	5.4	occidentalls	3.7	noongarensis	6	bicolor	1.9
A. minutus	5.4	goosel	3.8	rufator	6	dissimulator	2
muiril	5.5	scotti	3.8	saeedi	6	exleyae	2
rubidum	5.67	pedis	3.8	nigriceps	6	fuscipenils	2
Microplitis	5.7	ruficollis	3.8	seminiger	6	noongarensis	2
magnus	5.8	sumatranus	3.9	enderleinl	6	philippensis	2
saltator	5.9	latipes	3.94	Coded 3		mexicanus	2
minutus	6.25	deetoo	4	bubbur	7	abnormipes	2.0
ruficollis	6.25	enderleini	4.04	exleyae	7	nigromaculata	2.1
occidentalis	6.3	nigromaculata	4.08	sp. indet.	7	bubbur	2.4
callemondah	6.5	nigripennis	4.15	macula	7	deetoo	2,4
Coded 4		bicolor	4.18	rubidum	7	Prasmadon	2.0
diaphaniae	7.7	dissimulator	4.2	deetoo	8	Coded 3	
deetoo	8	fuscipeniis	4.2	pollinator	8	pollinator	2.0
explorator	8	sp. Indet.	4.2	latipes	8	subflavus	2.1
mexicanus	8	philippensis	4.2	saltator	8	mulrii	3
abnormipes	8	Coded 4		ruficollis	8	Epsilogaster	3.
Coded5		rubricollis	5	Coded 4		latipes	3.
acutus	9.5	Coded 5		nlgripennis	9	callemondah	3.
		macula	5.6	rubricollis	g	Coded 5	
		fasciipennis	5.9			tobiasi	5.
						Coded 6	
						toxopeusi	6

41. T2 medial field		42. Ovipositor length		43. ovipositor dimensions		
	0.53		0.52		0.28	
	0.23		0.32		0.17	
Coded 0		Coded 0		Coded 0		
pollinator	0.1	latipes	0.08	Epsilogaster	0.05	
toxopeusi	0.2	bubbur	0.1	macula	0.07	
exlevae	0.2	naumanni	0.1	saeedi	0.1	
pedis	0.21	nockatungensis	0.1	Coded 1		
fasciipennis	0.29	noongarensis	0.1	lasciipennis	0.11	
rubricollis	0.29	mulrii	0.1	A. minutus	0.11	
Coded 1		tobiasl	0.11	magnus	0.12	
callemondah	0.3	Microplitis	0.12	explorator	0.13	
deetoo	0.3	subflavus	0.14	enderleini	0.14	
eremophilasturtiae	0.3	acutus	0.15	Prasmadon	0.15	
gwenae	0.3	rubidum	0.19	turneri	0.16	
sumatranus	0.3	toxopeusi	0.2	pedis	0.16	
diaphaniae	0.31	abnormipes	0.2	sumatranus	0.16	
sp. indet.	0.32	Coded 1		mexicanus	0.16	
Prasmadon	0.36	rubicundus	0.3	dilatus	0.17	
areyongensis	0.4	bicolor	0.3	minutus	0.17	
evelinae	0.4	niariceps	0.34	atricornis	0.18	
rufator	0.4	rasl	0.35	nigripennis	0.18	
saeedi	0.4	seminiger	0.39	evelinae	0.19	
enderleini	0.4	inhali	0.4	semininer	0.19	
ruficollie	0.4	morulus	0.4	arevongensis	0.10	
A minutus	0.4	rutator	0.4	dissimulator	0.2	
A. minutus	0.43	rulator	0.4		0.2	
toblasi	0.43	minutus	0.45	ruscipeniis	0.2	
lurneri	0.45	hymeniae	0.47	gwenae	0.2	
hymeniae	0.45	nigripennis	0.48	uniformis	0.2	
tibiator	0.47	rubricollis	0.48	verticalis	0.2	
goosei	0.5	saltator	0.48	philippensis	0.2	
iqball	0.5	callemondah	0.5	rubricollis	0.2	
occidentalis	0.5	evelinae	0.5	diaphaniae	0.2	
rasi	0.5	goosei	0.5	rubicundus	0.2	
scotti	0.5	pollinator	0.5	viator	0.21	
uniformis	0.5	scotti	0.5	nigromaculata	0.21	
verticalis	0.5	verticalis	0.5	hymeniae	0.24	
Coded 2		Prasmadon	0.5	eremophilasturtiae	0.25	
minutus	0.53	Coded 2		evievae	0.25	
saltator	0.55	viator	0.53	tibiator	0.26	
mexicanus	0.59	tibiator	0.54	rubidum	0.20	
nexicands	0.50	diaphopian	0.54	Coded 2	0.27	
magnia	0.0	dilatua	0.57		0.00	
macula	0.0		0.58	DICOIOF	0.28	
dilatus	0.62	nigromaculata	0.59	rasi	0.29	
atricornis	0.63	uniformis	0.6	callemondah	0.3	
nigromaculata	0.65	atricornis	0.6	goosei	0.3	
viator	0.69	mexicanus	0.64	iqbali	0.3	
dissimulator	0.7	dissimulator	0.7	morulus	0.3	
fuscipeniis	0.7	eremophllasturtiae	0.7	occidentalis	0.3	
philippensis	0.7	fuscipeniis	0.7	rufator	0.3	
bicolor	0.7	gwenae	0.7	scottl	0.3	
Code 3		occidentalis	0.7	nigriceps	0.3	
latipes	0.77	phillppensis	0.7	saltator	0.33	
magnus	0.78	pedls	0.75	Microplitis	0.4	
acutus	0.8	sumatranus	0.75	toxopeusi	0.4	
rubidum	0.83	explorator	0.75		0.4	
abnormines	0.00	exlevae	0.70	acutus	0.4	
nigricens	0.00	turneri	0.0	tobiasi	0.4	
ngnooparansis	1	Coded 2	0.0	Coded 2	0.43	
semininer	1	mannue	0.00	obueu 3	0.45	
Coded A	1	niagilus	0.89	aunomipes	0.45	
	10	areyongensis	0.9	oubour	0.5	
uubbur	1.2	Saleeoi	0.9	nockatungensis	0.5	
	-	rascilpennis	0.93	noongarensis	0.5	
		A. minutus	1.07	subflavus	0.57	
		Epsilogaster	1.1	latipes	0.57	
		enderleini	1.1	Coded 4		
		Coded 4		mulrii	0.75	
		macula	1.4	Coded 6		
				naumanni	1	
- Appendix A4. The data matrix of characters and states for 59 species of Cardiochilinae and four outgroups: *Epsilogaster*, *Prasmadon*, *Microplitis demolitor*, and the hypothetical ancestor. The characters, their state assignments, and the corresponding state codes are given in Section 5.4 and the taxa are listed in more detail in Table 5.1.2 and Chapter 6. The characters 1 43 are as follows:
- 1. Eye pilosity
- 2. Clypeal margin shape
- 3. Clypeal tubercles
- 4. Malar carina
- 5. Shape of glossa
- 6. Glossal elongation
- 7. Galeae dimensions
- 8. Maxillary palp segmentation
- 9. Mandibular dentation
- 10. Notauli
- 11. Scutal medial carina
- 12. Apical scutellar cup
- 13. Propodeal areola
- 14. Propodeal medial longitudinal furrow
- 15. Epicnemial carina

- 16. Hind tibial apical projection
- 17. Hind basitarsus flattening
- 18. Tarsal claw pectination
- 19. 1r in fore wing
- 20. 3r in fore wing
- 21. Discal cell elongation
- 22. Shape of Rs in fore wing
- 23. 2r-m in hind wing
- 24. 2-1A in hind wing
- 25. Ovipositor sheath setosity
- 26. Hypopygial medial sclerotisation
- 27. Hypopygial apical sclerotisation
- 28. Hypopygial apical shape
- 29. Ovipositor curvature
- 30. Clypeal dimensions
- 31. Facial dimensions

- 32. Eye to temple ratio
- 33. Occipital depth
- 34. Scape dimensions
- 35. Antennal separation
- 36. Antennal segmentation
- 37. Scutellar sulcus dimensions
- 38. Stigmal dimensions
- 39. Hamuli number
- 40. Shape of T1
- 41. Median field of T2
- 42. Ovipositor sheath length
- 43. Ovipositor sheath dimensions

	3	x 2 13 14 15 16 17, 18 19, 110 111 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133, 134, 135, 36, 137, 38, 139, 140, 141, 142, 143,
-	Facilitation	
	Epswogaster	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
2	Prasmacon	0 1 0 1 1 0 0 1 0 0 1 0 0 1 0 0 1 0 0 1 0 0 0 1 0 0 0 2 1 0 0 0 0
3	Mic. demolitor	
4	Hyp. Ancestor	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
5	Icropeusi	
6	areyongensis	
7	bubbur	
1.	callemondah	
9	deeloo	
10	dissimulator	
11	eremophilasturtiae	
12	evelinae	
13	exlevae	
14	fuscipennis	
15	goosei	0 0 1 1 2 1 2 0 0 1 0 0 0 1 0 0 0 1 1 1 2 0 0 0 0
16	owenae	0 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 1 0 1 0 0 0 1 0 0 0 1 0 0 0 1 0
17	igbali	0 0 1 1 2 1 2 0 0 0 0 0 0 1 0 0 0 1 1 2 0 0 0 0
11	morulus	6 0 1 0 0 0 1 0 0 1 1 0 0 0 0 1 0 0 1 1 1 2 0 0 0 1 0 1
110	naumann	1 0 0 1 1 0 1 0 0 0 0 0 0 0 0 0 1 2 0 2 1 0 1 1 0 1 0
20	nockatunoensis	1 0 0 1 - 0 - 0 0 0 0 0 2 0 1 0 0 2 1 0 1 1 0 1 0 0 1 0 1
21	noongarensis	3 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
22	occidentalis	
1 2 2	pollinator	
1	pontinetor	
24	rest	
25	rutator	0 0 1 1 2 1 2 0 0 0 1 0 0 0 1 0 0 0 1 1 1 2 0 0 0 0
26	saeeo	
27	scoth	
21	turneri	
28	uniformis	
30	verticalis	
31	sp indet.	
32	atricornis	
33	pedia	
14	philopensis	
35	subliavus	1 0 1 1 7 0 7 0 0 1 0 1 0 0 0 0 0 0 1 0 1
3.6	latipes	
37	muitri	
3.8	sumatranus	
19	macula	2 0 0 1 0 0 1 0 0 0 0 0 3 1 1 0 0 2 1 0 0 1 0 1 0 0 0 0 2 2 1 0 2 1 3 1 2 1 2 1 2 1 2 1 2 1 2 1 2 1 2 1
40	lascigennis	2 0 0 1 0 0 1 0 0 0 0 0 3 1 1 0 0 0 1 0 1
41	nipripennis	2 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
42	tubricollis	2 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
43	daphanae	0 0 1 1 2 0 0 0 0 1 0 0 0 0 1 0 0 0 1 1 0 0 1 1 1 1 2 0 1 0 0 0 0
11	dilatus	1 0 0 1 0 0 0 0 0 1 0 0 0 1 1 0 0 1 1 0 0 1 0 1 2 0 1 1 0 0 1 0 4 3 2 - 3 4 2 1 1 1 1 2 2 1
11	explorator	
11	manhus	1 0 0 1 2 1 2 0 0 1 0 1 4 0 1 1 0 0 1 0 1 2 0 0 1 0 6 2 2 1 3 3 - 2 0 1 1 3 3 1
1.	manusa	
11	mexicanus	<u> </u>
48	minutus	
4.9	rupicungus	
50	libialor	
51	rubidum	
52	nigriceos	
53	seminiget	
54	bicolot	1 1 0 1 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 1 1 2 0 1 1 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 1 0
55	vialct	1 0 0 1 2 1 2 0 0 1 0 1 0 0 1 1 0 0 1 0 1
56	enserleini	
57	nipromaculata	0 0 1 1 2 1 1 0 0 1 0 0 0 1 0 0 1 0 0 1 1 1 1
58	hymeniae	0 0 1 1 2 1 2 0 0 1 0 0 0 1 0 0 1 0 0 1 1 1 1
59	A.minutus	1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 1 0
6.0	lobiasi	0 0 0 1 0 0 1 1 1 1 0 1 0 0 0 0 1 1 0 0 0 0 2 1 1 2 3 2 3 5 3 0 1 1 5 1 0 2
1	acelus	1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 2 1 0 1 1 0 0 0 0
100	collator	
102	salialut	
100	Curiconis	
164	abnormibes	La

Appendix A5. Dangerfield, P. C. and Austin, A. D. (1990). Revision of the Oriental genus *Hartemita* Cameron (Hymenoptera: Braconidae: Cardiochilinae). *Journal of Natural History* 24, 137-158. A reprint of this publication is attached to the inside back cover of the thesis.

REFERENCES

Abdinbekova, A. A. (1975). Braconids of Azerbaidjan. Elm, Baku 1975, 1-323.

Achterberg, C. van (1976). A Preliminary key to the subfamilies of the Braconidae (Hymenoptera). *Tijdschrift voor Entomologie* **119**, 33-78.

Achterberg, C. van (1979). A revision of the Subfamily Zelinae auct. (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* **122**, 241-479.

Achterberg, C. van (1980). Notes on some species of Braconidae (Hymenoptera) described by Hedwig from Iran and Afghanistan. *Entomologische Berichten, Deel* 40, 25-31.

Achterberg, C. van (1984). Essay on the phylogeny of Braconidae (Hymenoptera: Ichneumonoidea). Entomologisk Tidskrift 105, 41-58.

Achterberg, C. van (1988). Parallelisms in the Braconidae (Hymenoptera) with special reference to the biology. Advances in Hymenoptera Research 1988, 85-115.

Achterberg, C. van (1990). Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen Leiden 258, 1-180.

Achterberg, C. van (1993). Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen Leiden 283, 1-189.

- Anderberg, A. and Tehler, A. (1990). Consensus trees, a necessity in taxonomic practice. *Cladistics* 6, 399-402.
- Archie, J. W. (1985). Methods for coding variable morphological features for numerical taxonomic analysis. Systematic Zoology 34, 326-345.
- Archie, J. W. (1989). A Randomization Test for Phylogenetic Information in Systematic Data. Systematic Zoology 38, 239-252.
- Arnett, R. H. Jr, Samuelson, G. A., Heppner, J. B., Nishida, G. M., Watt, J. C. and Woodruff, R. E. (1986). *Insect and Spider Collections of the World*. 220 pp. (E. J. Brille: Gainesville).

Ashmead, W. H. (1894). Synopsis of the North American species of Toxoneura, Say. Proceedings of the U. S. national Museum 3, 47-53.

Ashmead, W. H. ((1899) 1900). Insects of New Jersey. Report of the New Jersey Bd Agriculture: Supplement 1899, 1-755.

Ashmead, W. H. (1905). New Hymenoptera from the Philippines. Proceedings of the U. S. national Museum 29, 107-117.

Austin, A. D. (1990). Revision of the Australian genus *Miropotes* Nixon (Hymenoptera: Braconidae: Microgastrinae), with comments on the

phylogenetic importance of the female ovipositor system. Systematic Entomology 15, 43-68.

- Austin, A. D. and Allen, G. (1989). Parasitoids of Uraba lugens Walker (Lepidoptera: Noctuidae) in South Australia, with description of new species of Braconidae. Transactions of the Royal Society of South Australia 113(4), 169-184.
- Austin, A. D. and Dangerfield, P. C. (1992). Synopsis of Australasian Microgastrinae (Hymenoptera: Braconidae), with a key to genera and description of new taxa. *Invertebrate Taxonomy* 6, 1-76.
- Austin, A. D. and Dangerfield, P. C. (1993). Systematics of Australian and New Guinean *Microplitis* Foerster and *Snellenius* Westwood (Hymenoptera: Braconidae: Microgastrinae), with a Review of Their Biology and Host Relationships. *Invertebrate Taxonomy* 7, 1097-1166.
- Austin, A. D. and Faulds, W. (1989). Two new Australian species of *Bracon F*. (Hymenoptera: Braconidae) parasitic on *Phylacteophaga spp*. (Hymenoptera: Pergidae). Journal of the Australian entomological Society 28, 207-213.
- Austin, A. D. and Wharton, R. A. (1992). New records of subfamilies, tribes and genera of Braconidae (Insecta: Hymenoptera) from Australia, with description of seven new species. *Transactions of the Royal Society of South Australia* 116(2), 41-63.
- Baltazar, C. R. (1966). A Catalogue of Philippine Hymenoptera. *Pacific Insects* Monograph 8, 1-488.
- Beeson, C. F. C. (1941). Ecology and Control of the Forest Insects of India and the Neighbouring Countries. 767pp. (Forest Research Institute and Colleges: Government of India).
- Beeson, C. F. C. and Chatterjee, S. N. (1935). On the Biology of the Braconidae. *Indian Forest Records* 1, 105-138.
- Belokobylskij, S. A. (1987). A new genus in the subfamily Cardiochilinae (Hym: Brac.) from the Soviet Far East. Zoologicheskii Zhurnal 66(2), 302-304. [In Russian]
- Berfield, S. (1993). *Speedometer 3.23*. A computer program in 'Think C'. (Berfield: Hayward, California).
- Boucek, Z. (1988). Australasian Chalcidoidea (Hymenoptera): A biosystematic revision of genera of fourteen families, with a reclassification of species. 832pp. (CAB International, The Cambrian News Ltd: Aberystwyth, UK).
- Brooks, D. R., O'Grady, T., and Wiley, E. O. (1986). A measure of the information content of phylogenetic trees, and its use as an optimality criterion. *Systematic Zoology* 35, 571-581.
- Brown, R. W. (1954). Composition of Scientific Words. 882pp. (George W. King Printing Co.: Baltimore).

- Brues, C. T. (1918). Parasitic Hymenoptera from the British Solomon Islands collected by Dr W. M. Mann. Bulletin of the Museum of Comparative Zoology, Harvard 62, 96-132.
- Brues, C. T. (1924). Some South African parasitic Hymenoptera of the families Evaniidae, Braconidae, Alysiidae, and Plumariidae in the South African museum with a catalogue of known species. Annals of the South African Museum 19, 1-150.
- Brues, C. T. (1926). Studies on Ethiopian Braconidae, with a catalogue of the African species. Proceedings of the American Academy of Arts and Sciences 61, 205-436.
- Brues, C. T. (1933). The parasitic Hymenoptera of the Baltic Amber. Bernstein-Fortschritte 3, 4-178.
- Brullé, A. (1846). Suites á Buffon: Histoire naturelle des insects: Hyménoptéres. Paris Roret 4, 1-689.
- Cameron, P. (1887). Notes on Hymenoptera with description of new species. Biologia of central-American Hymenoptera 1, 412.
- Cameron, P. (1902). Descriptions of new genera and species of Hymenoptera collected by Major C. S. Nurse at Deesa, Simla and Ferozepore. Journal of the Bombay natural History Society 14, 419-449.
- Cameron, P. (1904). Descriptions of new genera and species of Hymenoptera from Dunbrody, Cape Colony. *Record of the Albany Museum, Grahamstown* 1, 125-160.
- Cameron, P. (1905). On the phytophagous and parasitic Hymenoptera collected by MrE. Ernest Green in Ceylon. Spolia Zeylanica, Columbia 3, 67-97.
- Cameron, P. (1906). On the Tenthredinidae and parasitic Hymenoptera collected in Baluchistan by Major C. G. Nurse. Part 1. Journal of Bombay natural History Society 17, 89-107.
- Cameron, P. (1907). Descriptions of two new genera and four new species of Indian parasitic Hymenoptera. Zeitschrift für Systematische Hymenopterologie und Dipterologie 7, 462-466.
- Cameron, P. (1910). On some asiatic species of the subfamilies Spathinae, Doryctinae, Rhogadinae, Cardiochilinae and Macrocentrinae in the Royal Berlin Zoological Museum. Wiener Entomologische Zeitung 29, 93-100.
- Cameron, P. (1912). On the Hymenoptera of the Belgian Congo in the Congo Museum Tervueren. Annales de la Société Entomologique de Belgique 56, 357-401.
- Cameron, P. (1913). On the Hymenoptera (exclusive of the Anthophila and Formicidae) collected by Mrs De Beaufort in the Papuan Islands of Waigeu and Saonek. Bijdragen tot de Dierkunde 19, 75-86.

- Cameron, S. A., Derr, J. N., Austin, A. D., Wooley, J. B. and Wharton, R. A. (1992).
 The application of nucleotide sequence data to phylogeny of the Hymenoptera: a review. *Journal of Hymenoptera Research* 1(1), 63-79.
- Carpenter, J. M. (1988). Choosing among multiple equally parsimonious cladograms. *Cladistics* 4, 291-296.
- Carpenter, J. M. (1992). Random cladistics. Cladistics 8, 147-153.
- Ceballos, G. (1943). Las trubus de los himenópteros de Espana. Madrid, Instituto Espanol de Entomologia 1-420.
- Chappill, J. A. (1989). Quantitative characters in phylogenetic analysis. *Cladistics* 5, 217-234.
- Colless, D. H. (1980). Congruence between morphometric and allozyme data for Menidia species: a reappraisal. Systematic Zoology 29, 288-299.
- Colless, D. H. (1981). Predictivity and stability in classifications: some comments on recent studies. *Systematic Zoology* **30**, 325-331.
- Common, I. F. B. (1990). *Moths of Australia*. 535 pp. (Melbourne University Press: Melbourne).
- Cresson, E. T. (1865). Catalogue of the Hymenoptera in the collection of the Entomological Society of Philadelphia, from the Colorado Territory. Proceedings of the Entomological Society of Philadelphia 4, 242-313.
- Cresson, E. T. (1873). Descriptions of North American Hymenoptera. Canadian Entomologist 5, 66-69.
- Cresson, E. T. (1887). Synopsis of the families and genera of the Hymenoptera of America, North of Mexico together with a catalogue of the described species, and bibliography. *Transactions of the American Entomological Society* Supplementary volume 1887, 1-350..
- Crowe, T. M. (1994). Morphometrics, phylogenetic models and cladistics: means to an end or much ado about nothing? *Cladistics* 10, 77-84.
- Dalla Torre, C. G. (1898). Catalogus Hymenopterorum. 4. Braconidae. 323pp (G. Engelmann: Leipzig).
- Dangerfield, P. C. and Austin, A. D. (1990). Revision of the Oriental genus Hartemita Cameron (Hymenoptera: Braconidae: Cardiochilinae). Journal of Natural History 24, 137-158.
- Dangerfield, P. C. and Austin, A. D. (1995). Revision of the Australasian species of Cardiochilinae (Hymenoptera: Braconidae). *Invertebrate Taxonomy* in press.
- Danks, H. V., Rabb, R. L. and Southern, P. S. (1979). Biology of the insect parasites of *Heliothis* larvae in North Carolina. *Journal of the Georgia entomological Society* 14, 36-63.
- de Gaulle, J. (1907). Catalogue systématique et biologique des Hyménoptères de France. Fam. VIII Braconidae. *Feuille des Jeunes Naturalistes, Paris* **38**, 187.

- De Saeger, H. (1948). Cardiochilinae et Sigalphinae (Hymenoptera, Apocrita) Fam. Braconidae. Exploration du Parc National Albert Mission G. F. de Witte 53, 1-272.
- Docavo, Alberti, I. (1960). Especies nuevas Braconinae de Espana (Hym. Braconidae). Eos 36, 25-39.
- Dowton, M. and Austin, A. D. (1994). Molecular phylogeny of the insect order Hymenoptera: Apocritan relationships. *Proceedings of the National Academy* of Sciences, USA **91**, 9911-9915.
- Dowton, M. and Austin, A. D. (in press). The origin of parasitism in the wasps inferred from mitochondrial DNA sequences. *Molecular Biology and Evolution*.
- Dudarenko, G. P. (1974). The formation of the abdominal test in Braconidae (Hymenoptera) and some problems. *Entomologische Obozrkunde* **53**(1), 14-129.
- Eady, R. D. (1968). Some illustrations of microsculpture in the Hymenoptera. Proceedings of the Royal Entomological Society, London, Series A 43, 66-72.
- Eady, R. D. (1974). The present state of nomenclature of wing venation in the Braconidae (Hymenoptera); its origins and comparison with related groups. *Journal of Entomology* 43, 63-72.
- Enderlein, G. (1905). Neue Braconiden aus dem indischen und afrikanischen Gebeit. *Stettiner Entomologische Zeitung* 66, 227-236.
- Enderlein, G. (1906). Die Indo-australischen und Afrikanischen Cardiochilinen. Stettiner Entomologische Zeitung 67, 245-252.
- Enderlein, G. (1912). Neue Gattungen und Arten von Braconiden. Archiv für Naturgeschichte, Berlin 78, 94-100.
- Fabricius, J. C. (1781). In Species Insectorum. 1, 552 pp. (Bohn: Hamburg).
- Faith, D. F. (1991). Cladistic Permutation Tests for Monophyly and Nonmonophyly. *Systematic Zoology* **40**, 366-375.
- Faith, D. F. and Ballard, J. W. O. (1994). Length differences and topology-dependent tests: A response to Källersjö et al. *Cladistics* **10**, 57-64.
- Faith. D. F. and Cranston, P. S. (1991). Could a cladogram this short have arisen by chance alone?: On permutation tests for cladistic structure. *Cladistics* 7, 1-28.
- Faith, D. F. and Cranston, P. S. (1992). Probability, Parsimony and Popper. Systematic Biology 41, 252-257.
- Farris, J. S. (1970). Methods for computing Wagner trees. Systematic Zoology 19, 83-92.
- Farris, J. S. (1972). Estimating phylogenetic trees from distance matrices. American Naturalist 106, 645-668.
- Farris, J. S. (1979). The Information Content of the Phylogenetic System. Systematic Zoology 28, 483-519.

Farris, J. S. (1988). Hennig86 version 1.5 manual; software and MSDOS program.

- Farris, J. S. (1991a). Excess Homoplasy Ratios. Cladistics 7, 81-91.
- Farris, J. S. (1991b). Cladistic permutation tests. Systematic Zoology 40, 366-375.
- Farris, J. S., Källersjö, M., Kluge, A. G. and Bult, C. (1994). Permutations. *Cladistics* **10**, 65-76.
- Faulds, W. (1990). Introduction into New Zealand of Bracon phylacteophagus, a biocontrol agent of Phylacteophaga froggatti, Eucalyptus leaf-mining sawfly. New Zealand Journal of Forestry Science 20, 54-64.
- Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783-791.
- Fischer, M. (1958). Neue Cardiochiles Arten aus Ägypten (Hymenoptera: Braconidae). Polskie Pismo Entomologiczne 28, 33-37.
- Fischer, M. and Parshad, B. (1968). A new reared braconid-fly (Hymenoptera) from India. *Polskie Pismo Entomologiczne* **38**, 807-810.
- Fullaway, D. T. (1919). New genera and species of Braconidae mostly Malayan. Journal of the Straits Branch of the Royal Asiatic Society 80, 39-61.
- Gardner, T. R. (1957). Collection and distribution of beneficial insects in the Pacific area and south-east Asia. *Proceedings of the 8th Pacific Science Congress* **3A**, 1475-1478.
- Gauld, I. D. (1983). The classification, evolution and distribution of the Labeninae, and ancient southern group of Ichneumonidae (Hymenoptera). Systematic Entomology 8, 167-178.
- Gauld, I. D. (1984). An introduction to the Ichneumonidae of Australia. British Museum of Natural History no. 895, 413pp. (The Chameleon Press: London).
- Gauld, I. D. (1985). The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). Bulletin of the British Museum (Natural History) 51 (2), 61-185.
- Gauld, I. and Bolton, B. (1988). *The Hymenoptera*. 332pp. (Oxford University press: New York).
- Gauld, I. D. and Holloway, G. A. (1986). Australian ichneumonids of the tribes Labenini and Poecilocryptini. Bulletin of the British Museum (Natural History)(Ent.) 53 (2), 107-149.
- Gibson, G. A. (1985). Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. *Canadian Entomologist* **117**, 1395-1443.
- Godfray, H. C. J. (1993). *Parasitoids: Behavioral and Evolutionary Ecology*. 473pp. (Princeton University Press: Princeton, New Jersey).
- Goloboff, P. A. (1991a). Homoplasy and the Choice among Cladograms. *Cladistics* 7, 215-232.

Goloboff, P. A. (1991b). Random Data, Homoplasy and Information. *Cladistics* 7, 395-406.

- Goloboff, P. A. (1993). Character optimization and calculation of tree lengths. *Cladistics* 9, 433-436.
- Goulet, H. and Huber, J. T. (1993). Hymenoptera of the world: An identification guide to families. 668pp. (Agriculture Canada: Canada).
- Granger, C. (1949). Braconides de Madagascar. Memoirs of the Institute of science, Madagascar 2, 1-428.
- Handlirsch, A. (1925). Handbuch der Entomologie 3, 741-754.
- Harris, R. A. (1979). A glossary of surface sculpturing. Occasional papers in Entomology 28, 1-31.
- Hauser, D. L. and Presch, W. (1991). The effect of ordered characters on phylogenetic reconstruction. *Cladistics* 7, 243-265.

Hedwig, K. (1957). Ichneumonidae und Braconiden aus Iran 1954 (Hym.). Jahresheft des Vereins für Vaterlandische Naturkunde in Württemberg **112**, 104-117.

Hennig, W. (1981). Insect Phylogeny. 514pp. (Chichester: Wiley).

- Huddleston, T. and Walker, A. K. (1988). Cardiochiles (Hymenoptera: Braconidae), a parasitoid of lepidopterous larvae, in the Sahel of Africa, with a review of the biology and host relationships of the genus. Bulletin of entomological Research 78, 435-461.
- Johnson, N. F. (1988). Midcoxal Articulations and the Phylogeny of the Order Hymenoptera. Annals of the Entomological Society of America 81(6), 870-881.
- Klompen, J. S. H. and Oliver, J. H. Jr (1993). Systematic relationships in the soft ticks (Acari: Ixodida: Argasidae). Systematic Entomology 18, 313-331.
- Kluge, A. and Farris, J. (1969). Quantitative phyletics in the evolution of anurans. *Systematic Zoology* **18**, 1-32.
- Knight, W. J. and Webb, M. D. (1993). The phylogenetic relationships between virus vectors and other genera of macrosteline leafhoppers, including descriptions of new taxa (Homoptera: Cicadellidae: Deltocephalinae). Systematic Entomology 18, 11-55.
- Kokoujev, N. (1895). Fragments Braconologiques. Trudy Russkago Entomologicheskago Obshchestva 34, 24-35.
- Kokoujev, N. (1904). Hymenoptera asiatic nova. Verhandlung Entomologicheskoe Obozrenie 4, 213-215.
- Königsmann, E. (1977). Das phylogenetische System der Hemenoptera. Teil 2: "Symphyta." Deutsche Entomologische Zeitschrift 24, 1-40.
- Kriechbaumer, J. (1894). Hymenoptera ichneumonidea a medico nautico Dr Joh.
 Brauns in itinere ad oras Africae occidentalis lecta. Berliner Entomologische Zeitschrift 39, 43-68.

- LaSalle, J. and Gauld, I. D. (1993). *Hymenoptera and Biodiversity*. 348pp. (C.A.B. International: Wallingford, UK).
- Lewis, W. J., Sparks, A. N., Jones, R. L. and Barras, D. J. (1972). Efficiency of Cardiochiles nigriceps as a parasite of Heliothis virescens on cotton. Environmental Entomology 1, 468-471.
- Lynn, D. C. and Vinson, S. B. (1977). Effects of temperature, host age, and hormones upon the encapsulation of *Cardiochiles nigriceps* eggs by *Heliothis* spp. *Journal of Invertebrate Pathology* **29**, 50-55.
- Maddison, W. P. and Maddison, D. R. (1992). MacClade: Analysis of Phylogeny and Character Evolution. Version 3. 398pp. (Sinauer Associates Inc.: Massachusetts, U.S.A).
- Mangel, M. and Clarke, W. C. (1988). Dynamic modelling in behavioural ecology. 308pp. (Princeton University Press: Princeton).
- Mao, Y. T. (1945). Three new species of Laminitarsus Fullaway from Singapore and the Philippines (Hymenoptera: Braconidae). Journal of the Washington Academy of Sciences 35, 189-192.
- Mao, Y. T. (1949). The species of Ichneumon-flies of the genus Cardiochiles occurring in America north of Mexico. Proceedings of the U.S. National Museum 99, 229-268.
- Marsh, P. M. (1986). A new species of Cardiochiles (Hym. Brac.) introduced into Florida to control Diaphania spp. (Lep. Pyralidae). Proceedings of the Entomological Society of Washington 88(1), 131-133.
- Marshall, T. A. (1901). Description de deux espéces nouvelles de Braconides. Bulletin of the Museum of Natural History, Paris 6, 363-364.
- Mason, W. R. M. (1981). The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): a phylogeny and reclassification of Microgastrinae. *Memoirs of the Entomological Society of Canada* **115**, 1-147.
- Mason, W. R. M. (1983). A new South African subfamily related to Cardiochilinae (Hymenoptera: Braconidae). Contributions to the American Entomological Institute 20, 49-62.
- Messenger, P. S. (1974). Procedures for conducting a biological control program against *Heliothis armigera*. *Plant Protection Service Technical Bulletin* **19**, 1-17.
- Mickevich, M. F. and Platnick, N. I. (1989). On the information content of classifications. *Cladistics* 5, 33-47.
- Miyamoto, M. M. (1985). Consensus cladograms and general classification. *Cladistics* 1, 186-189.
- Morley, C. (1909). Notes on the Braconidae of Marshall's collection. *Entomologist* **42**, 61-62.

Muesebeck, C. F. W. (1949). Two new genera and three new species of Braconidae. Proceedings of the Entomological Society of Washington 52, 77-81.

- Naumann, I. D. (1982). Systematics of the Australasian Ambositrinae (Hymenoptera: Diapriidae), with a synopsis on non-Australian genera of the subfamily. Australian Journal of Zoology, Supplement Series **85**, 1-239.
- Naumann, I. D. (1991). Chapter 42, Hymenoptera in *Insects of Australia*. 2nd edition, 1137pp. (Melbourne University Press: Melbourne).
- Nees ab Esenbeck (1818). Appendix ad J. L. C. Gravenhorst conspectum generum et familiarum Ichneumonidum, genera et familias Ichneumonidum adscitorum exhibens. *Nova Acta Leopoldina* 9, 299-310.
- Nees ab Esenbeck (1834). Hymenopterorum Ichneumonibus Affinium Monographiae, Genera Europaea et species illustrantes. 320 (pt. 1) & 448 (pt. 2) pp. (Cotta: Stuttgart).
- Nixon, G. E. J. (1965). A reclassification of the Tribe Microgasterini (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History) Entomology, Supplement 2, 1-284.
- Noyes, J. S. and Hayat, M. (1994). Oriental Mealybug Parasitoids of the Anagyrini (Hymenoptera: Encyrtidae). 554pp. (C.A.B. International: Wallingford, London).
- Page, R. D. M. (1992). Comments on the information content of classifications. *Cladistics* 8, 87-95.
- Parrott, A. W. (1953). A Systematic Catalogue of Australian Braconidae. Pacific Science 7, 193-218.
- Pimental, R. A. and Riggins, R. (1987). The nature of cladistic data. *Cladistics* 3(3), 201-209.
- Qin, T. -K., Gullan, P. J., Beattie, G. A. C., Truemann, J. W. H., Cranston, P. S., Fletcher, M. J. and Sands, D. P. A. (1994). The current distribution and geographical origin of the scale insect pest *Ceroplastes sinensis* (Hemiptera: Coccidae). *Bulletin of Entomological Research* 84(4), 541-550.
- Quicke, D. L. J. and Achterberg, C. van (1990). Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandlingen Leiden 258, 1-95.
- Rasnitsyn, A. P. (1969). Origin and Evolution of the Lower Hymenoptera. *Trudy* Paleontologicheskogo Instituta 123, 1-196.
- Rasnitsyn, A. P. (1980). The Origin and Evolution of Hymenoptera. Trudy Paleontologicheskogo Instituta 174, 1-190.
- Rasnitsyn, A. P. (1988). An Outline of Evolution of the Hymenopterous Insects (Order Vespida). Oriental Insects 22, 115-145.
- Reed, A. W. (1981). Aboriginal Words and Place Names. 286pp. (Rigby: Adelaide).

- Riley, C. V. and Howard, L. O. (1890). Some of the bred parasitic Hymenoptera in the National Collection. *Insect Life* 2, 348-353.
- Rohlf, F. J. (1982). Consensus indices for comparing classifications. *Mathematical Biosciences* 59, 131-144.
- Rohwer, S. A. (1920). Descriptions of twenty-six new species of North American Hymenoptera. *Proceedings of the U.S. National Museum* 57, 209-231.
- Rondani, C. (1876). Repertorio degli insetti parasitti e delle loro vittime. Supplemento. Bollettino della Societa Entomologica Italiana 8, 54-70.
- Roman, A. (1910). Notizen zur Schlupfwespensammlung des Schwedischen Reichsmuseum. *Entomologisk Tidskrift* **31**, 109-196.
- Roman, A. (1915). Results of Dr E. Mjobergs Swedish Scientific Expeditions to Australia 1910-13. 1. Schlupfwespen. Arkiv fur zoologi 9, 1-18.
- Ross, H. H. (1936). The ancestry and wing venation of the Hymenoptera. Annals of the Entomological Society of America **29**, 99-111.
- Say, T. (1836). Descriptions of new species of North American Hymenoptera, and observations on some already described. *Boston Journal of Natural History* 1, 209-305.
- Schulz, W. A. (1906). Die Hymenopteren der Insel Fernando Po. In: Spolia Hymenopterologica. 356pp (Jungfermann: Paderborn).
- Schulz, W. A. (1911). Zweihundert alte Hymenopteren. Zoologische Annalen 4, 1-220.
- Sharkey, M. J. and Mason, W. R. M. (1986). The generic validity of Aenigmostomus and Asiacardiochiles (Hymenoptera: Braconidae). Proceedings of the Entomological Society, Washington 88, 300-302.
- Shenefelt, R. D. (1973). Braconidae 5. Microgasterinae & Ichneutinae. In Hymenopterorum Catalogus. (Eds J. van der Vecht and R. D. Shenefelt.) Part 9, pp. 669-812. (Dr W. Junk: Gravenhage).
- Shenefelt, R. D. (1978). Braconidae 10. Braconinae, Gnathobraconinae, Mesotoinae, Pseudodicrogeniinae, Telengainae, Ypsistocerinae. *Hymenopterorum Catalogus* (Eds J. van der Vecht and R. D. Shenefelt.) Part 15, pp. 1425-1872. (Dr W. Junk: Gravenhage).
- Smith, H. A., Capinera, J. L., Pena, J. E. and Linbo-Terhaar, B. (1994). Parasitism of pickleworm and melonworm (Lepidoptera: Pyralidae) by *Cardiochiles diaphaniae* (Hymenoptera: Braconidae). *Environmental entomology* 23, 1283-1293.
- Spinola, M. (1851). Historia fisica y politica de Chile. Paris, Maulde y Renon 6, 1-572.
- Stoltz, D. and Whitfield, J. B. (1992). Viruses and virus-like entities in the parasitic Hymenoptera. Journal of Hymenoptera Research 1(1), 125-139.

- Swofford, D. L. (1993). PAUP: Phylogenetic Analysis Using Parsimony. Version 3.1.1. (Computer program distributed by the Illinois Natural History Survey: Champaign, Illinois).
- Swofford, D. L. and Begle, D. P., (1993). PAUP Phylogenetic Analysis Using Parsimony: User's Manual. 257pp. (Laboratory of Molecular Systematics, Smithsonian Institution: Washington).
- Szépligeti, G. V. (1896). Adatok a Magyar fauna Braconidáinak ismeretéhez. Természetrajzi Füzetek 19, 165-186.
- Szépligeti, G. V. (1900). Braconiden aus Neu-Guinea in der Sammlung des Ungarischen National-Museums. *Természetrajzi Füzetek* 23, 49-65.
- Szépligeti, G. V. (1901). Braconiden aus Syrien und Palästina. Természetrajzi Füzetek 24, 151-152.
- Szépligeti, G. V. (1902). Tropische Cenocoeliden und Braconiden aus der Sammlung des Ungarischen National-Museums. *Természetrajzi Füzetek* **25**, 39-84.
- Szépligeti, G. V. (1904). Hymenoptera Fam. Braconiden. (Premiere partie). Genera Insectorum 22, 23, 1-253.
- Szépligeti, G. V. (1908). Braconiden aus der Sammlung des Ungarischen National Museums. Annales Historico-Naturales Musei Nationalis Hungarici, Budapest 6, 297-427.
- Szépligeti, G. V. (1911). Braconidae der I. Zental-Afrika-Expedition.
 Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika Expedition 1907-1908 1911, 393-418
- Szépligeti, G. V. (1913). Neue afrikanische Braconiden aus der Sammlung des ungarischen National-Museums. Annales Historico-Naturales Musei Nationalis Hungarici, Budapest 11, 592-608.
- Szépligeti, G. V. (1914). Central-Afrikanische Braconiden des Congo-Museums. *Review of Zoology of Africa* 3, 403-420.
- Telenga, N. A. (1949). A survey of the fauna of the family Braconidae (Hymenoptera) of Tadzikistan. *Entomologicheskoe Obozrenie* **30**, 381-388.
- Telenga, N. A. (1955). Hymenoptera. Fam. Braconidae. Subfam. Microgasterinae, subfam. Agathidinae. Fauna SSSR 5, 1-312. [In Russian]
- Thompson, W. R. (1953). A Catalogue of the Parasites and Predators of Insect Pests: Section 2, Part 2, Hosts of the Hymenoptera (Agaonidae to Braconidae). (The Commonwealth Institute of Biological Control: Ottawa, Canada).
- Thorpe, R. S. (1984). Coding morphometric characters for constructing distance Wagner networks. *Evolution* **38**, 244-355.
- Thumlert, T. A. and Austin, A. D. (1994). Biology of *Phylacteophaga froggatti* Riek (Hymenoptera: Pergidae) and its parasitoids in South Australia. *Transactions of the Royal Society of South Australia* **118**(2), 99-113.

- Tobias, V. I. (1954). Data relating to the fauna and biology of Braconidae of western Kazakhstan. *Trudy Zoologicheskogo Instituta Leningrad* **16**, 417-426. [In Russian]
- Tobias, V. I. (1967). Review of the System, Phylogenesis, and Evolution of the Family Braconidae (Hymenoptera). *Entomologicheskoe Obozrenie* **46**(3), 645-669.
- Tobias, V. I. and Alexeev, J. I. (1977). Contribution to the knowledge of Braconidae of the genus *Cardiochiles* Nees (Hym.) species with black body coloration. *Trudy Zoologicheskogo Instituta Leningrad* 71, 94-104. [In Russian]
- Tobias, V. I., Belokobylskij, S. A. and Kotenko, A. G. (1986). Identification of Insects of European USSR. 3(4), (Publishing House of Science: Leningrad). [In Russian]
- Trueman, J. W. H. (1993). Randomization confounded: A response to Carpenter. *Cladistics* 9, 101-109.
- Turner, R. E. (1918). Notes on the Braconidae in the British Museum 2. On the Australian species of Cardiochilinae and Doryctinae. Annals and Magazine of Natural History 9(1), 49-57.
- Viereck, H. L. (1905). Notes and descriptions of Hymenoptera from the western United States, in the collection of the University of Kansas. Transactions of the Kansas Academic Society 19, 264-326.
- Viereck, H. L. (1912). Descriptions of five new genera and twenty-six new species of Ichneumon-flies. *Proceedings of the U. S. National Museum* 42, 139-153.
- Viereck, H. L. (1914). Type species of the genera of ichneumon-flies (monograph only). Bulletin of the United States National Museum 83, 1-186.
- Viereck, H. L. (1918). A list of families and subfamilies of Ichneumon-flies or the super-family Ichneumonoidea (Hymenoptera). Proceedings of the Biological Society of Washington 31, 69-74.
- Vinson, S. B. (1975). Biochemical coevolution between parasitoids and their hosts. 14-18, in Price, P. W. (Ed). Evolutionary strategies of parasitic insects and mites. 224pp. (Plenum: New York).
- Vinson, S. B. and Iwantsch, G. F. (1980). Host suitability for insect parasitoids. Annual Review of Entomology 25, 397-419.
- von Neumann, J. and Morgenstern, O. (1947). Theory of games and economic behaviour. 2nd edition. (Princeton University Press: Princeton, New Jersey).
- Wahl D. B. (1986). Larval structures of oxytirines and their significance for the higher classification of some Ichneumonidae (Hymenoptera). Systematic Entomology 11, 117-127.

- Wahl, D. B. (1988). A review of the mature larvae of the banchini and their phylogenetic significance, with comments on the Stilbopinae (Hymenoptera: Ichneumonidae). Advances in Parasitic Hymenoptera Research 1988, 147-161.
- Wahl, D. B. (1990). A review of the mature larvae of Diplazontinae, with notes on larvae of Acaenitinae and Orthocentrinae and proposal of two new subfamilies (Insecta: Hymenoptera, Ichneumonidae). *Journal of Natural History* 24, 27-52.
- Wahl, D. B. (1991). The status of *Rhimphoctona*, with special reference to the higher categories within Campoleginae and the relationships of the subfamily (Hymenoptera: Ichneumonidae). *Transactions of the American Entomological Society* 117, 193-213.
- Walker, A. K., Kitching, I. J and Austin, A. D. (1990). A reassessment of the phylogenetic relationships within the Microgastrinae (Hymenoptera: Braconidae). *Cladistics* 6, 291-306.
- Wallace, A. R. (1876). The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface. Vol. 1, 503pp. (Macmillan: London).
- Watanabe, C. (1934). On some species of Braconidae from Formosa and the Philippines in the Deutsches Entomologisches Museum. *Insecta Matsumarana* 8, 119-123.
- Watanabe, C. (1937). A contribution to the knowledge of the braconid fauna of the Empire of Japan. Journal of the Faculty of Agriculture, Hokaido University 42, 1-188.
- Watrous, L. E. and Wheeler, Q. D. (1981). The out-group comparison method of character analysis. *Systematic Zoology* **30**(1), 1-11.
- Weller, S. T., Friedlander, T. P., Martin, J. A. and Pashley, D. P. (1992) Phylogenetic studies of ribosomal RNA variation in higher moths and butterflies (Lepidoptera: Ditrysia). *Molecular phylogenetics and evolution* 1(4), 312-337.
- Wharton, R. A., Shaw, S. R., Sharkey, M. J., Wahl, D. B., Wooley, J. B., Whitfield, J. B., Marsh, P. M. and Johnson, J. W. (1992). Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea): a reassessment. *Cladistics* 8, 199-235.
- Whitfield, J. B. (1992). The polyphyletic origin of endoparasitism in the cyclostome lineages of Braconidae (Hymenoptera). *Systematic Entomology* **17**, 273-286.
- Whitfield, J. B., Johnson, N. F. and Hamerski, M. R. (1989). Identity and Phylogenetic Significance of the metapostnotum in Nonaculeate Hymenoptera. Annals of the Entomological Society of America 82(6), 663-673.

- Whitfield, J. B. and Mason, W. R. M. (1994). Mendesellinae, a new subfamily of braconid wasps (Hymenoptera, Braconidae) with a review of relationships within the microgastroid assemblage. Systematic Entomology 19, 61-76.
- Wiley, E. O., Siegel-Causey, D., Brooks, D. R. and Funk, V. A. (1991). The Complete Cladist A Primer of Phylogenetic Procedures. 158pp. (The University of Kansas, Museum of Natural History, Special Publications: Kansas).

Wilkinson, M. (1992). Ordered versus unordered characters. Cladistics 8, 375-385.

Wilkinson, D. S. (1930). New species and host records of Braconidae. Bulletin of entomological Research 21, 481-487.

Yeates, D. (1992). Why remove autapomorphies? Cladistics 8, 387-389.

Dangerfield, P. C. & Austin, A. D. (1990). Revision of the Oriental genus Hartemita Cameron (Hymenoptera: Braconidae: Cardiochilinae). *Journal of Natural History*, 24(1), p.137-158.

> NOTE: This publication is included in the print copy of the thesis held in the University of Adelaide Library.

It is also available online to authorised users at: <u>http://dx.doi.org/10.1080/00222939000770091</u>

ERRATUM

1182

Throughout text "Prasmadon" should read Prasmodon.

p. x. The abbreviation "it's" is incorrect and should read "its".

p. 6. The term "palpi" should read "palps".

p. 9. lines 11-13. To correct the grammar of this sentence these lines should read "Quicke and Achterberg's (1990) data, like Mason's (1981), must be treated with caution as few undefined species were used to score characters."

p. 17. "Malaise traps" are named after the entomologist R. Malaise and therefore the word Malaise should be capitalised.

pp. 19 and 38. Sections "3.4. Terminology" and "4.4.3. Wings" should refer to "Sharkey, M. 1994. Another look at wing vein/cell nomenclature. *Ichnews* **14**, 2-5".

p. 40. The term "adeagus" should read"aedeagus".

pp. 50 and 65. The author for *Epsilogaster* is incorrectly given as "Whitfield" and should read "Whitfield and Mason".

p. 51. line 8. "Flagellomere segments" should read "flagellomeres".

P. 72. lines 4 and 6. The references to "figure 5.5" are incorrect and should read "figure 5.4".

p. 128. line 6. "(UQIC)" should read "(ANIC)".

p. 135. line 7. The locality "south-east Queensland" should read "south-east and central Queensland".

p. 140. The species Aust. pollinator also occurs in the north coast of N.S.W.