# THE SYSTEMATICS AND PHYLOGENY OF THE GENUS DIOLCOGASTER ASHMEAD (HYMENOPTERA: BRACONIDAE: MICROGASTRINAE) WITH A REVISION OF AUSTRALASIAN SPECIES 



Lateral view of female Diolcogaster sons (Wilkinson). Scale $=400 \mu \mathrm{~m}$.

## AZHAR SAEED M. Sc. (Faisalabad)

A thesis submitted for the Degree of Doctor of Philosophy in the Faculty of
Agriculture and Natural Resource Sciences at
The University of Adelaide

July 1996

## Dedicated to my parents

## in recognition of their

love, prayers and patience

## Table of contents

## Contents Page

Summary ..... v
Declaration ..... viii
Acknowledgments ..... ix
Chapter 1: Introduction ..... 1
Chapter 2: Review of Literature ..... 7
2.1 Phylogenetic relations among braconid subfamilies with reference to the Microgastrinae ..... 8
2.2 The Microgastrinae: taxonomy and phylogeny ..... 12
2.2.1 The early period ..... 12
2.2.2 The beginning of the modern era ..... 13
2.2.3 The post war period (1945-1987) ..... 14
2.2.4 The present era ( 1988 to the present) ..... 18
2.2.4.1 Phylogeny of the subfamily ..... 18
2.2.4.2 Taxonomy of the subfamily ..... 23
2.3 The genus Diolcogaster Ashmead ..... 25
2.4 Biology of microgastrines ..... 29
2.5 Host species of Diolcogaster ..... 31
Figures 2.1-2.14 ..... 33
Chapter 3: Materials and Methods ..... 42
3.1 General methods ..... 43
3.2 Collecting techniques ..... 43
3.3 Scanning electron microscopy ..... 44
3.4 Terminology ..... 45
3.5 Institutional abbreviations ..... 45
3.6 Phylogenetic analyses ..... 47
3.6.1 Computers and programs ..... 47
3.6.2 Selection of out-groups and construction of hypothetical ancestor ..... 49
3.6.3 Treatment of quantitative characters ..... 50
3.6.4 Discussion of theoretical phylogenetic methods ..... 53
3.6.5 Methods of measuring information content of phylogenetic analyses ..... 54
3.6.6 Discussion of PAUP features ..... 56
Chapter 4: Morphology of the Microgastrinae, particularly Diolcogaster Ashmead ..... 58
4.1 Introduction ..... 59
4.2 Adult morphology ..... 59
4.2.1 Head ..... 59
4.2.2 Mesosoma ..... 60
4.2.3 Wings ..... 62
4.2.4 Legs ..... 63
4.2.5 Metasoma ..... 64
4.2.6 Female genitalia ..... 65
4.2.7 Male genitalia ..... 65
4.3 General morphology of immature stages ..... 66
Figures 4.1-4.10 ..... 67
Chapter 5: Phylogenetics of Diolcogaster Ashmead ..... 72
5.1 Introduction ..... 73
5.2 Selection of taxa ..... 73
5.2.1 The in-group taxa ..... 73
5.2.2 The out-group taxa ..... 73
5.3 Selection and treatment of characters ..... 74
5.3.1 Selection of characters ..... 74
5.3.2 Treatment of characters ..... 75
5.3.2.1 Polarity of characters ..... 7.5
5.3.2.2 Qualitative characters ..... 75
5.3.2.3 Quantitative characters ..... 92
5.3.2.4 Ordering and scoring of characters ..... 95
5.4 Preliminary Analyses ..... 96
5.4.1 Effect of out-groups ..... 96
5.4.2 Swapping algorithm and addition sequence ..... 97
5.4.3 Effect of inclusion and exclusion of quantitative characters ..... 98
5.4.4 Effect of autapomorphies ..... 100
5.5 Analyses to determine the relationships among Diolcogaster species ..... 100
5.5.1 Analysis with the unpolarised data (Analysis A): comparing the strict consensus and $50 \%$ majority rule trees ..... 101
5.5.2 Analysis with the polarised and ordered data (Analysis B) ..... 103
5.5.3 Comparison of Analysis A and B ..... 103
5.5.4 Level of homoplasy ..... 104
5.6 Classification of Diolcogaster ..... 105
5.6.1 Limitations of Analyses ..... 105
5.6.2 The genus Diolcogaster ..... 106
Figures 5.1-5.33 ..... 108
Chapter 6: Taxonomic Treatment of Diolcogaster Ashmead ..... 127
6.1 Introduction ..... 128
6.2 The genus Diolcogaster Ashmead ..... 128
6.3 Species groups of Diolcogaster ..... 131
6.3.1 alvearius-group ..... 131
6.3.2 basimacula-group ..... 131
6.3.3 connexus-group ..... 132
6.3.4 euterpus-group ..... 132
6.3.5 hadrommatus-group ..... 133
6.3.6 lelaps-group ..... 133
6.3.7 scotica-group ..... 134
6.3.8 spretus-group ..... 134
6.3.9 xanthaspis-group ..... 135
6.4 Key to Australasian species of Diolcogaster ..... 135
6.5 Treatment of Diolcogaster species ..... 141
6.5.1 Diolcogaster adiastola sp. nov. ..... 141
6.5.2 Diolcogaster alkingara sp. nov ..... 143
6.5.3 Diolcogaster ashmeadi sp. nov ..... 146
6.5.4 Diolcogaster dangerfieldi sp. nov. ..... 148
6.5.5 Diolcogaster dichromus sp. nov. ..... 150
6.5.6 Diolcogaster eclectes (Nixon) ..... 152
6.5.7 Diolcogaster euterpus (Nixon) ..... 155
6.5.8 Diolcogaster hadrommatus sp. nov. ..... 157
6.5.9 Diolcogaster harrisi sp. nov. ..... 160
6.5.10 Diolcogaster iqbali sp. nov. ..... 162
6.5.11 Diolcogaster lucindae sp. nov. ..... 164
6.5.12 Diolcogaster masoni sp. nov. ..... 167
6.5.13 Diolcogaster merata sp. nov. ..... 169
6.5.14 Diolcogaster muzaffari sp. nov ..... 171
6.5.15 Diolcogaster naumanni sp. nov. ..... 174
6.5.16 Diolcogaster newguineaensis sp. nov. ..... 176
6.5.17 Diolcogaster nixoni sp. nov ..... 178
6.5.18 Diolcogaster notopecktos sp. nov ..... 180
6.5.19 Diolcogaster perniciosus (Wilkinson) ..... 182
6.5.20 Diolcogaster rixosus (Wilkinson) ..... 185
6.5.21 Diolcogaster robertsi sp. nov. ..... 188
6.5.22 Diolcogaster sons (Wilkinson) ..... 190
6.5.23 Diolcogaster tearae (Wilkinson) ..... 193
6.5.24 Diolcogaster vulpinus (Wilkinson) ..... 196
6.5.25 Diolcogaster walkerae sp. nov. ..... 198
6.5.26 Diolcogaster yousufi sp. nov ..... 200
6.6 The genus Neodiolcogaster gen. nov. ..... 203
6.7 Key to species of Neodiolcogaster gen. nov. ..... 205
6.8 Treatment of Neodiolcogaster species ..... 206
6.8.1 Diolcogaster tegularis (Szépligeti) ..... 206
6.8.2 Diolcogaster whiffieldi sp. nov. ..... 208
6.9 New Genus ..... 210
Figures 6.1-6.60 ..... 212
Chapter 7: General Discussion ..... 233
References ..... 239
Appendices ..... 254
Appendix A1: Means of quantitative characters
Appendix A1.1: Means of quantitative characters 36-39 ..... 256
Appendix A1.2: Means of quantitative characters 40-43 ..... 257
Appendix A2: Graphical representation of quantitative characters
Appendix A2.1: Graphical representation of character 36 ..... 258
Appendix A2.2: Graphical representation of character 37 ..... 259
Appendix A2.3: Graphical representation of character 38 ..... 260
Appendix A2.4: Graphical representation of character 39 ..... 261
Appendix A2.5: Graphical representation of character 40 ..... 262
Appendix A2.6: Graphical representation of character 41 ..... 263
Appendix A2.7: Graphical representation of character 42 ..... 264
Appendix A2.8: Graphical representation of character 43 ..... 265
Appendix A3: Data Matrix ..... 267

## Summary

The braconid wasp subfamily Microgastrinae comprises about 1300 described species world-wide, some of which are important parasitoids of pest Lepidoptera. The genus Diolcogaster Ashmead is one of 52 genera recognised in the subfamily. Previously it has been treated under the generic names, Microgaster Latreille and Protomicroplitis Ashmead but more recently it has been identified as a separate member of the Cotesia-complex of genera. Although relatively easy to identify, Diolcogaster has been postulated to be polyphyletic. Further the Australasian fauna is substantial, although only six species were previously recognised. These two aspects of Diolcogaster, its phylogenetic status within the Cotesia-complex and the Australasian fauna, are the focus of this study.

A brief literature review describes the history of taxonomic and phylogenetic studies on the Microgastrinae and, in particular, the genus Diolcogaster. Although the monophyly of the Microgastrinae is clearly demonstrated, the relationships within the subfamily are not well-resolved and recent studies present conflicting hypotheses. Further, the monophyly of Diolcogaster has been seriously questioned recently and it is possible that the genus is paraphyletic or, more likely, polyphyletic with respect to other Cotesia-complex genera.

A detailed treatment of the external morphology of the genus is presented and explains characters and terminology used in the taxonomic revision and phylogenetic analysis. A section on methodology then follows and describes the techniques used for collection and identification of material, the use of scanning electron microscopy (SEM), environmental scanning electron microscopy (ESEM) and field emission scanning electron microscopy (FESEM). The selection and treatment of phylogenetically important characters and the selection of in-group and out-group taxa is discussed along with the methodology adopted for phylogenetic analyses, and the workings of the parsimony program PAUP (version 3.1.1).

The in-group taxa selected include 26 species of Australasian Diolcogaster, representative species from non-Australasian species-groups, the type species of the genus, Diolcogaster brevicaudus (Provancher), as well as an additional 28 taxa from 20 other microgastrine genera comprising representatives of both cotesiine and non-cotesiine genera. Epsilogaster panama Whitfield and Mason (Mendesellinae), Cardiochiles fuscipennis

Szépligeti, Cardiochiles eremophilasturtiae Dangerfield and Austin (Cardiochilinae), and a hypothetical ancestor were used as out-groups. A data matrix was compiled using MacClade (version 3.02) for these 68 taxa and 43 characters. Eight of these characters were treated quantitatively, and preliminary analyses were undertaken with them included and excluded to assess whether they had a higher level of homoplasy compared with qualitative characters. Analyses were conducted using out-group taxa individually and in all possible combinations. The most parsimonious solution for the data set (i.e. that with the shortest tree(s) and highest consistency index), was obtained when the hypothetical ancestor was used as the out-group and the data treated as unordered. In all other analyses (e.g. using other out-group taxa and ordered data), either the tree length was longer and/or the consistency index was lower.

Based on the phylogenetic analyses conducted, the Cotesia-complex was not resolved as a monophyletic group, although most of the included genera were so resolved, i.e. Buluka De Saeger, Deuterixys Mason, Fornicia Brullé, Microplitis Foerster, and Wilkinsonellus Mason. Further, Diolcogaster was clearly shown to be polyphyletic as indicated by the fact that the basimacula+merata+fasciipennis species-groups, the connexus-group and the euterpus-group of Diolcogaster were resolved as sister-groups to other microgastrine genera. The monophyly of several species groups of Diolcogaster was however confirmed, i.e. the basimacula-group, euterpus-group, hadrommatus-group and the spretus-group. The phylogenetic analyses also indicated that the abdominalis- and scotica-groups form a monophyletic group, while the connexus-group appears to be polyphyletic. However, clear from the analyses undertaken is that the data show an extremely high level of homoplasy as indicated by the fact that only six of 43 characters unequivocally support a single clade consisting of Fornicia species. Further, this level of homoplasy means that the overall pattern of relationships is unstable in that minor changes to either PAUP parameters and/or character coding produced trees of different topology, although the groups discussed above were virtually always resolved.

Even though Diolcogaster is now shown to be polyphyletic, this level of phylogenetic instability make it effectively impossible to reclassify the genus and divide it into smaller systematically stable genera. For this reason Diolcogaster is maintained as a separate working genus until the generic boundaries within the Microgastrinae are better resolved.

Diolcogaster is revised for the Australasian region and recorded for the first time from New Zealand. Based on the above analyses, six species-groups are proposed for the Australasian fauna, a further three species-groups are recognised as extralimital, while the relationships of 10 species were not resolved and, accordingly, they represent monotypic species-groups. A total of 26 species are now known from Australasia of which six were previously described. D. eclectes (Nixon) is record for the first time from the region and 19 species are described as new: Diolcogaster adiastola, D. alkingara, D. ashmeadi, $D$. dangerfieldi, D. dichromus, D. hadrommatus, D. harrisi, D. iqbali, D. lucindae, D. masoni, D. merata, D. muzaffari, D. naumanni, D. newguineaensis, D. nixoni, D. notopecktos, D. robertsi, D. walkerae, and D. yousufi. A new genus, Neodiolcogaster, is erected for the new species D. whitfieldi, while Choeras tegularis (Szépligeti) is also transferred to this new genus. For both genera, an illustrated key to Australasian species based on females is presented, and where possible notes on their biology and host relationships are also given.

The results of this study are discussed in regard to the inadequacy of morphological data to determine phylogenetic relationships within the Microgastrinae, and their potential as biological control agents. Although this study has by no means exhausted the likelihood of finding characters useful for phylogenetic analysis, it is also clear from this and previous work that morphological characters will probably not fully resolve relationships within this subfamily because of the extremely high level of homoplasy. In this respect the role of other data sets, such as those generated by molecular systematics, is discussed as a means of solving generic-level relationships with the subfamily. Finally, the role of Diolcogaster species in biological control is discussed along with their host relationships, and general importance in regulating host populations.

## 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 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.

## Acknowledgments

The past four and half years of my life have changed me a lot, the completion of a PhD has opened many new horizons for my life. At the start of my studies in Australia I was a bit shy, but eager to learn about a new subject, the new culture and meet people. I think I have done all that successfully. After four years, I feel myself to be much more confident. I know many things about the Aussie culture, I have made many new international friends, and, above all, I have learned a new subject, the subject of hymenopteran systematics. The completion of this degree has made my life more purposeful, I realise many of the responsibilities of being a member of the systematists community are upon my shoulders. Now at the start of a new life, I have set many goals for the future, and I hope I will be able to fulfil these goals in the coming years of my life.

I thank my principal supervisor, Dr Andrew Donald Austin, Associate Professor in Crop Protection, for his untiring efforts in helping me to make this project successful. Regular meetings with him proved to be an excellent stimulant to get through this subject. He has been both a multi-dimensional teacher and a friend. He taught me the subject of hymenopteran systematics, made innumerable spelling and grammar corrections, even in my personal letters, has invited me for many barbecues at his home, rarely teased me about cricket (when Pakistan lost to Australia), and took me to my first ever basketball game. Thanks Andy for everything.

My special thanks are also due to Dr. Paul C. Dangerfield, my friend and colleague. Throughout the four years of this project Paul proved to be a best mate and an excellent teacher. His guidance started on the very first day of my arrival at the Waite when he showed me around this campus. From that day forth his guidance never ended. He was my teacher in drawing, scanning electron microscopy, and the computer program PAUP. He was an integral part of every discussion on these and other projects. He also gave me great social support, invited me to parties, took me to pubs in town, introduced me to a lot of people, and above all he was always there when I need him. Thank you very much Paul for everything, without your support this project would have been very difficult for me to complete.

My thanks are also due to Dr Mike Keller, my second supervisor for regularly asking me about the progress of project and in this way keeping me on my toes.

I am highly thankful to Dr James B. Whitfield for helping me at a critical stage by providing the character codings for D. brevicaudus (Provancher). Thank you for sending much needed literature on microgastrines, solving important nomenclatural problems, and advising on the selection and discussion of phylogenetically important characters. Jim was supportive in all situations, sometimes responding to as many as four email messages per day.

The micrographs 5.6, 5.11, 5.12, 5.15 and 5.17 are taken from Austin (1987, 1989 and 1990) and Dangerfield and Austin (1995) and were originally taken by Dr P. C. Dangerfield, while the line drawings 5.22, 5.23 and 5.26 are from Austin (1987) and Dangerfield and Austin (1995) and are adopted from figures originally drawn by Dr P. C. Dangerfield. I thank him sincerely for allowing me to access these illustrations.

I wish to thank Stuart Maclure from CSIRO, and John Terlet and Lynn Waterhouse from CEMMSA, for their assistance with scanning electron microscopy. I would also like to thank the following people for lending material of Diolcogaster and other microgastrines and/or much needed reprints of their work: Kees van Achterberg, Jo Berry, Jo Cardale, Marlene Elson-Harris, Murray Fletcher, Gary Gibson, Terry Houston, Tom Huddleston, Max Moulds, Ian Naumann, Jenö Papp, Donald Quicke, Margaret Scneider, Mike Sharkey, David Smith, David Wahl, Annette Walker, Ken Walker, Bob Wharton, Margaret Williams and Jim Whitfield.

My special thanks are also due to all Rotarians across the world. Without the financial support of the Rotary Foundation of Rotary International, the completion of this project would have been impossible. I would especially like to say thanks to Rotarians A.Q. Alvi, Sheikh Abdul Rauf, Bashir Ahmed, and other members of the Rotary Club of Faisalabad, which was my sponsoring club; John Roberts, Beth Roberts, Allan Pointon, Meva Pointon, and all other members of the West Torrens Rotary Club, Adelaide which was my host club; and Branco Franco and Rosa Franco of the Rotary Club of Port Lincoln, South Australia. All these people supported me in one way or another. Most importantly, I am short of words to express my heartiest thanks to my host counsellor Mr. John Roberts and his wife Beth Roberts. The Roberts family were the first to receive me at the Adelaide airport on my arrival in 1992. Since then their support never ended, and they cared for my every need like real
parents, helped me to cope with a very big culture shock, and inviting me for many dinner parties at their home. As a result of their kindness I never felt away from my parents and home. Thanks John and Beth. I would also like to thank all my co-ordinators at the One Rotary Centre, Evanston who have been always very helpful and understanding during my scholarship period.

I lived at the Kathleen Lumley College, a residential college of the University of Adelaide, during my stay in Adelaide. This was an excellent place to live. I lived with many people from all corners of the world, made innumerable friends, and had a wonderful time. In the last four years the only thing permanent in this college, except its buildings, was the staff of this college. I would like to thank them for making my stay very comfortable and enjoyable, especially Rachel, Marylin, Soula, Marci and Trudy.

My heartiest thanks also go to my friend Iqbal and his wife Mussarat Iqbal. Iqbal was a part of my life for eight years before I left for Australia, and the one whom I used to miss the most. He joined me in Adelaide midway through my candidature. Mussarat joined us one year later. Their presence in Adelaide was a great comfort to me, as I always had someone to talk to and share with, and a place to eat and relax. They were always there when I needed them and made me felt very special. Thank you very much Miq and Mussie.

I am also thankful to Pakistani community living in Adelaide, and in particular the Khalid and Dawood families for being my good friends and being a great social support during my stay in Adelaide.

My special thanks are also due for Ms. Lucinda Deane, who joined the small group of my very best friends in the last few months of my candidature, for being my wonderful and special friend, and for taking care of my 'articles' hungry thesis.

I would like to thank my family: my parents for being courageous enough to allow me to stay more than four years away from them and complete my studies, for their encouragement, prayers for my success and health, and for patiently waiting for my return; my brother Mazhar Saeed and his family who made me feel that 'no worries, I will be there whenever you need me', and for regularly arranging telephone contact with my parents; and most importantly, my eldest brother Muzaffar Saeed and his family for his fatherly love, wise guidance and for financing my studies since I was at high school. I am really proud of to be a
member of such a wonderful, co-operative, caring and understanding family, and I have always felt myself very lucky to be a part of them. Thanks to every body in my family.

Last, but not least, are my heartiest thanks to all those friends, known or forgotten, who came into my life, loved me or I loved them. For without their friendship, I would not have been where I am today. It would not have been possible for me to rise so high, do this PhD and fulfil my dreams. By writing these few words I acknowledge from the depths of my heart that without their eternal influence on my life, all this would not have been possible. Thanks every one.

## Chapter 1

## Introduction

The Hymenoptera is one of the largest assemblages of insects and consist of more than 115,000 described species world wide, but the true size of the order has been conseaty estimated 300,000 species (Goulet and Huber 1993). Members of the order are present in virtually every type of habitat, from arid deserts to swamps and from tropical rainforests to aquatic environments, while some apterous ichneumonids (e.g. Gelis spp.) occur almost to the snow line in temperate mountainous regions (LaSalle 1993). They are diurnal as well as nocturnal. The Hymenoptera also have a diverse array of biologies (Gauld and Bolton 1988; LaSalle and Gauld 1993). The sawflies and woodwasps, which together form the paraphyletic Symphyta (Whitfield 1992), are virtually all phytophagous, their caterpillar-like larva feeding on leaves or wood and sometimes causing serious economic damage. The remaining Hymenoptera comprise the highly speciose Apocrita, which is further divided into parasitic superfamilies and the Aculeates. The Aculeates mostly consist of the bees and solitary and social wasps, while the parasitic groups exploit insects and other arthropods as prey or hosts for their parasitic immature stages. Some highly derived members within several of these parasitic superfamilies have also become secondarily phytophagous (Gauld and Bolton 1988).

The parasitic Hymenoptera represent the largest proportion of the order, about $75 \%$, although they are taxonomically the poorest known (LaSalle 1993). Their larvae feed primarily on endopterygote insects, e.g. Lepidoptera, Coleoptera and Diptera. However, many also attack exopterygote insects, e.g. Hemiptera, Orthoptera, as well as Araneae and other arthropods. Apart from being poorly known taxonomically, the biology of few species has been worked out compared with the size of the group. There are probably many reasons for this, but the small size of many species, the cryptic behaviour of adults, short life cycle, and the reclusive habits of many parasitic species, undoubtedly have made them difficult to study compared with other insects.

The parasitic Hymenoptera are particularly important as biological control agents of various agricultural pests and, thus, are responsible for substantial economic and environmental benefits (LaSalle 1993). They have been used far more often than general predators in this way and have contributed more than $87 \%$ of all biological control importations (Greathead 1986). The environmental benefits of parasitic Hymenoptera are also of considerable importance as they have been responsible for a decreased use in
pesticides. World-wide hundreds of millions of dollars have been saved directly or indirectly by biological control projects using hymenopteran parasitoids. Further, the biodiversity of the parasitic Hymenoptera have an actual value in the control they provide because, from observations of host/parasitoid relationship in the nature, it is clear that phytophagous insects are rarely attacked by a single species of parasitoid, but rather by a complex of species (Memmot and Godfray 1993). According to Waage (1991), it is fundamentally important to conserve a large reservoir of parasitoid diversity, regardless of what we know about their taxonomy, because it cannot be predicted what pests may emerge in the future and, therefore, what parasitoids might be useful in controlling them. In a related way, the number of parasitoid species used in a biological control projects can be a contributing factor to the degree of success achieved. For instance, different parasitoid species are often more effective at different times of the year, or on different host plants, or at different population densities, or at the same time but on different host life stages (LaSalle 1993).

The ability of many parasitic Hymenoptera to respond in a density dependent manner to host numbers often allows them to maintain a host population at a certain level. This in turn may result in conserving an ecosystem and contribute to the diversity of other organisms (LaSalle 1993). Further evidence of their importance in terrestrial ecosystems comes from the fact that 1) they are an important element in many food chains, 2) they are highly speciated, 3) they often display complex behavioural and physiological adaptations for dealing with their host(s), and 4) the removal of a parasitoid can cause an explosive outbreak in a pest population resulting in substantial economic and environmental damage (LaSalle 1993).

The success of parasitic Hymenoptera as biological control agents, apart from resulting in huge savings, both in economic and human terms, has also stimulated much research on the group (Godfray 1994). Similarly, in recent years an awareness and need to develop sustainable environmental friendly agriculture and to conserve the world's dwindling biodiversity, has caused an upsurge in taxonomic research of insects in general, including the Hymenoptera (e.g. Hanson and Gauld 1995). However, it is probable that at least $75 \%$ of parasitic Hymenoptera species have yet to be described, while it is widely appreciated that many described species (particularly in the older taxonomic literature) are poorly diagnosed and are not recognisable (LaSalle 1993).

Although the taxonomy of the parasitic Hymenoptera has been long regarded as an integral part of biological control studies, there remain many critical groups, such as genera in the Braconidae, Aphelinidae, Encyrtidae and Eulophidae which are poorly studied, particularly for the Australasian region. A recent example which serves to highlight this situation is a recent study by Austin et al. (1994) reviewing the taxonomy of the parasitoids of the eucalypt longicorn beetles, Phoracantha spp. One species in this genus is now regarded as a serious pest on eucalyptus in the Mediterranean, South Africa and western USA. In this study, which supported an effort by workers in California to introduce likely biological control agents, four species were found to be new, three represented a new genus, and a further two species could not be identified further than genus level. The same taxonomic problems also often exist with pest species, and when this important first stage of any biological control project is not properly undertaken, the loss in time and money can be great. The fiasco that surrounded the misidentification of the casava mealybug, Phenacoccus manihoti Matile-Ferrero and subsequent search for prospective biological control agents in the wrong place, serves as a recent topical example (Noyes and Hayat 1994).

Taxonomic studies will always be an integral part of biological control programs, however, in recent years biodiversity studies have provided a new impetus for taxonomic research, and justification for undertaking taxonomic revisions of highly diverse groups such as the parasitic Hymenoptera. Much of this effort to document biodiversity is focused on tropical forests where incredible numbers of parasitoid species have been recorded (e.g. Noyes 1989; Askew 1990; Naumann et al. 1991; Iqbal and Austin in press). If this biodiversity is to be rationally interpreted, it will be essential for the species collected to be identified at least to the level of functional groups (usually genera), and the number of species present estimated as accurately as possible. For this to happen a comparable taxonomic research effect will be required, similar to the enormous project currently underway for the Costa Rican insect fauna (Gámez and Gauld 1993).

Underpinning taxonomic studies relevant to both biological control and biodiversity studies is the need for parallel research on the phylogenetic relationships among groups. Such studies aim to produce natural classifications which can have a powerful predictive value, for instance in estimating relationships of newly discovered taxa, and their likely biology. For the parasitic Hymenoptera, the current knowledge of their evolutionary
relationships is relatively poor and the classifications used are often historical rather than phylogenetically-based. The classification of tribes and genera for the Scelionidae and many families of chalcidoids are relevant examples of this. Even groups that have been exposed to substantial phylogenetic analysis, such as the Braconidae, do not necessarily have stable classifications (e.g. van Achterberg 1984, 1988; Quicke and van Achterberg 1990; van Achterberg and Quicke 1992; Wharton et al. 1992). However, these studies at least result in working hypotheses that highlight which relationships are thought to be stable and those which are contentious.

This project focuses on one subfamily of the Braconidae, the Microgastrinae, which have been exposed to extensive taxonomic (e.g. Wilkinson 1927-1945; Nixon 1961-76; Papp 1978-90; Austin and Dangerfield 1992; Whitfield 1995a) and some phylogenetic studies (e.g. Mason 1981; Walker et al. 1990). As a group the microgastrines are the largest subfamily of Braconidae (Goulet and Huber 1993), and consist of about 1300 described species world-wide (Shaw and Huddleston 1991) but conservatively may comprise 13,00015,000 species. Microgastrines are all endoparasitoids of lepidopteran larvae. Mason (1981) generated the first phylogenetic treatment of the subfamily, and divided it into five tribes and 51 genera. However, his hypothesis of relationships was later seriously questioned by Walker et al. (1990) and, thus, like braconid subfamily relationships, many aspects of the microgastrine classification remain unclear or contentious.

Within the Microgastrinae is a recognisable group of 19 genera referred as the Cotesiacomplex, which has previously been recognised as a monophyletic assemblage, based on a group of partially host-related characters (Mason 1981; Walker et al. 1990). Diolcogaster Ashmead, the main focus of this study and one of the member genera of this group, is not particularly large in number of species relative to other taxa such as Microplitis Foerster, Cotesia Cameron and Glyptapanteles Ashmead. However, it is a critical group in that it may render other genera within the complex paraphyletic or polyphyletic and, thus, substantially affect the generic level classification of the Cotesia-complex.

This study takes a cladistic approach, using morphological characters derived from females, in an attempt to resolve the phylogenetic relationships among genera within the Cotesia-complex and among species of Diolcogaster. In addition to this phylogenetic work, a taxonomic revision of Diolcogaster is undertaken for the Australasian region to make the
fauna of the region better known. The species-level study also provides the basis for a detailed examination of characters and character states for the phylogenetic analysis, and means to test the robustness of characters used by previous workers to separate species. It also allows for the richness of the genus to be assessed for a region that is known to harbour a large but mostly unstudied microgastrine fauna. Thus, the diversity of Diolcogaster can be compared with other genera for Australasia and with other zoogeographic regions, at least in a preliminary way.

The present study is structured so that Chapter 2 reviews the literature pertinent to all parts of the project, Chapter 3 covers the methods employed, Chapter 4 discusses the morphology of microgastrines with particular emphasis on Diolcogaster, Chapter 5 details the phylogenetic results of the project, while Chapter 6 revises the Australasian fauna of the genus. Finally, in Chapter 7, the General Discussion, several facets of the project have been selected for broader analysis and discussions.

## Chapter 2

## Review of Literature

2.1 Phylogenetic relations among braconid subfamilies with reference to the Microgastrinae 2.2 The Microgastrinae: taxonomy and phylogeny
2.2.1 The early period
2.2.2 The beginning of the modern era
2.2.3 The post war period (1945-1987)
2.2.4 The present era ( 1988 to the present)
2.2.4.1 Phylogeny of the subfamily
2.2.4.2 Taxonomy of the subfamily
2.3 The genus Diolcogaster Ashmead
2.4 Biology of microgastrines
2.5 Host species of Diolcogaster

Figures 2.1-2.14

### 2.1 Phylogenetic relations among braconid subfamilies with reference to the Microgastrinae

The study of the phylogenetics of braconid subfamilies began in the late 1960's and, after passing through various stages, the broad relationships among about half of the 40 or so recognised subfamilies are now moderately well understood (see below). The subfamily Microgastrinae has been placed with various subfamilies by different workers, but always within a lineage of advanced endoparasitic groups. Nixon (1965) recognised this, at least in part, by associating together the Microgastrinae, Miracinae, Adelinae, Cardiochilinae and some unplaced genera, but his main contribution was in recognising many new characters that were subsequently used by later workers in more formal phylogenetic studies.

Tobias (1967) discussed 17 morphological and biological trends within the Braconidae, emphasising reduction in wing venation, male genitalia and characters which he postulated were associated with host selection. He placed the Microgastrinae with the Cheloninae, Adeliinae and Ichneutinae, which in turn were included in a largely unresolved assemblage of endoparasitic subfamilies, referred to as the helconoid group (Fig. 2.1).

Mason (1983) described a new subfamily, the Khoikhoiinae, and to determine its relationships with the Cardiochilinae, Miracinae and Microgastrinae he examined 32 characters deemed to be of phylogenetic significance. Nine of these were synapomorphies for all four subfamilies combined, 10 characters were autapomorphic, leaving only 13 useful characters for internal analysis. Of these, Mason highlighted five characters. A straight or concave clypeal margin and first metasomal tergite with completely delimited sides he used to define the group Khoikhoiinae+Microgastrinae+Miracinae. A constant number of flagellomeres and ventral ridge on the hind basitarsus were used to link the Microgastrinae+Miracinae, however a propodeum with medial carinae was considered of doubtful value as a synapomorphy because of its occurrence in the Khoikhoiinae, Miracinae and some specialised genera within the Microgastrinae and Cardiochilinae. He coined the term "Microgastri" for these four subfamilies (Fig. 2.2), which he proposed formed a monophyletic group based on the following synapomorphies: 1) occipital carina absent, 2) first metasomal tergite with a Y-shaped dorsal groove and membranous area between the arms of the Y spiracles of first metasomal tergite located on the folded underside part of tergum, 3) lateral membranes of basal metasomal segments covered with closely parallel
striations, 4) metasomal sternite one with basal and distal sections fused to form a single rectangular plate, 5) spiracles of metasomal tergite seven absent, 6) 2 nd CU vein of hind wing absent, and 7) 3-RS of fore wing convex anteriorly. However, the relationships proposed by Mason (1983) for these four subfamilies (Fig. 2.2) was intuitive and, as discussed below, was later changed after parsimony-based analyses.

Van Achterberg (1984) presented a phylogeny for the Braconidae based on biological and morphological characters of larvae and adults, which discussed the putative synapomorphies found in each subfamily and groups of subfamilies. He employed a number of new or lesser known characters in his discussion, such as ecto- versus endoparasitism, pupation in or outside the host or its cocoon, situation of the spiracles on the second metasomal tergite, development of a dorsope, pronope and posterior flange of propleuron. In this study the Khoikhoiinae were placed as the sister-group to the Microgastrinae in "GroupIVa" along with the Cardiochilinae, Neoneurinae and Cheloninae, while the Miracinae were placed in "Group-II" as the sister-group to the Acaelinae (Fig. 2.3). Soon after this, van Achterberg (1988) discussed the need for character weighting and the problem of parallelism within the Braconidae. He identified more than 20 characters that he proposed had evolved in parallel, including several he employed in his 1984 study. To explain this phenomenon he used data modified from van Achterberg (1984) and, after reinterpretation, added the Ecnominae to his "Group-IVa" between the Cheloninae and Neoneurinae, but retained the Miracinae and Acaelinae in "Group-II" (Fig. 2.4). However, van Achterberg's (1984, 1988) hypotheses were intuitive assessments of braconid subfamily relationships and his splitting of Mason's (1983) "microgastri" was not well supported on both morphological and biological grounds.

Quicke and van Achterberg (1990) conducted the first parsimony-based analysis of relationships among the subfamilies of Braconidae. A total of 96 characters, including external and internal morphological characters of both larvae and adults and some biological characters, were used. They were polarised on the basis of an hierarchical system of outgroups, with Ichneumonidae and Symphyta used as the main out-groups. The analysis showed that the Braconidae can be divided in to three separate groups (Figs 2.5, 2.6); a large paraphyletic basal assemblage consisting of the ectoparasitic cyclostomes and relatives, and two monophyletic groups, the 'helconoid assemblage' and 'microgastroid assemblage',
comprising advanced-endoparasitoids. Quicke and van Achterberg's (1990) study generated a number of competing hypotheses, depending on how they had analysed the data but, of the two trees they preferred, the relationships among subfamilies around the Microgastrinae different substantially. The first tree, generated by Hennig86 (Fig. 2.5), placed the Microgastrinae as the sister-group to the Cardiochilinae+Khoikhoiinae, while these three subfamilies together formed the sister-group to the Neoneurinae+Ichneutinae s.l. The Miracinae Adeliinae, Cheloninae and Dirrhopinae then formed a paraphyletic clade to these two groups of subfamilies (Fig. 2.5). In the second tree, generated using PAUP (Fig. 2.6), the Microgastrinae were again placed as the sister-group to the Cardiochilinae+Khoikhoiinae, while the Miracinae, Adeliinae and Cheloninae were paraphyletic to these three, and the Ichneutinae s.l., Neoneurinae and Dirrhopinae were place further away. This detailed treatment by Quicke and van Achterberg (1990) intensified the interest of braconid workers in the phylogenetic relationships among subfamilies and it generated a chain of discussions, both published and unpublished.

Wharton et al. (1992) presented a reassessment of Quicke and van Achterberg's (1990) findings and they were highly critical of several aspects of the work. In particular, they noted 1) the inconsistent way in which out-group comparisons were employed for polarity decisions, 2 ) over $20 \%$ of character coding in the data matrix were treated as missing, 3) six characters were unresolved in half the taxa, 4) several potentially important characters, viz. reduction in the number of labial or maxillary palpal segments, loss of fore wing vein $r-m$, and formation of a metasomal carapace were not included, 5 ); there was a $2-5 \%$ error rate in character coding and 6) no list of the taxa examined was provided. Further, Wharton et al. (1992) reanalysed the data and found several shorter trees that were substantially different in structure from the results presented in Quicke and van Achterberg's original paper. In summary, Wharton et al. (1992) concluded that braconid subfamily relationships are far from resolved and that much can be done in the future through improved selection and taxa, character exploration and polarisation, and improved methods of analysis. Van Achterberg and Quicke (1992) attempted to counter some of the criticisms made about their work by Wharton et al. (1992), but generally the problems raised by the latter authors are straightforward and difficult to argue against.

Whitfield (1992) examined the polyphyletic origin of endoparasitism in the cyclostome lineage of the Braconidae. He used 36 morphological and biological characters for the analysis and the results indicated that endoparasitism has arisen twice within this assemblage, once in the Rogadinae and once in a group including the Gnamptodontinae, Opiinae and Alysiinae. This work partly contradicts that of Quicke and van Achterberg (1990), in that the latter study postulates a single origin for endoparasitism within the cyclostomes, a proposition that is further expounded by Quicke (1993a). Although Whitfield's (1992) study does not bear directly on the relationships within the microgastroid complex, it does serve as an example of how phylogenetic studies can assist in explaining the evolution of biological characters.

Van Achterberg (1993) published an illustrated key to braconid subfamilies and presented a consensus tree for relationships among the subfamilies, generated using PAUP 3.1 from the data matrix in Quicke and van Achterberg (1990), modified to include corrections and additional characters from Quicke et al. (1992) and Wharton et al. (1992) (Fig. 2.7). The tree shows a different set of relationships among the microgastroid subfamilies compared with some of the above studies. However, the terminal sister-group relationship of ((Cardiochilinae+Khoikhoiinae)+Microgastrinae)+ Miracinae, resolved in one of Quicke and van Achterberg's (1990) trees (Fig. 2.6), was maintained.

Whitfield and Mason (1994) described a new subfamily, the Mendesellinae, comprising two genera and nine species from the New World. They examined relationships within the microgastroid complex (sensu Quicke and van Achterberg 1990), but mainly to obtain an outgroup perspective for character distribution and polarity and to assess the status and relationships of the new subfamily. Analysis of 21 characters indicated that the Mendesellinae was the sister-group to the Cardiochilinae+(Microgastrinae+ (Miracinae + Khoikhoiinae)) (Fig. 2.8), thus reversing the position of the Miracinae and Cardiochilinae as proposed by Quicke and Van Achterberg (1990). Whitfield and Mason's (1994) results further showed that the Adeliinae, Cheloninae and Dirrhopinae were basal within the complex, and that the Ichneutinae s.l. and Neoneurinae were more distantly placed.

In summary, the studies undertaken on the relationships among braconid subfamilies to date have consistently resolved a small monophyletic group that includes the Microgastrinae. The relationships proposed by Whitfield and Mason (1994), although preliminary in nature,
provide the most likely set of relationships around the Microgastrinae. However, evident from the competing hypotheses presented by various authors is that the relationships outside of the group comprising the Cardiochilinae, Microgastrinae, Miracinae and Khoikhoiinae are blurred, although it seems likely that the Adeliinae, Cheloninae and Dirrhopinae fall out just below this group.

### 2.2 The Microgastrinae: taxonomy and phylogeny

### 2.2.1 The early period

The first member of the subfamily was described under the genus Microgaster Latreille (1804), and until 1862 all microgastrine species were described under this name. Forster (1862) described two additional genera, Apanteles Foerster and Microplitis, to accommodate other microgastrine species. However, little taxonomic work was undertaken on the group until the latter part of the nineteenth century and the first 20 years of the twentieth century, during which time there was an explosion in the description of new microgastrine species. For example, Ashmead (1900b) described Parapanteles Ashmead and Hypomicrogaster Ashmead during his treatment of the Ichneumonoidea, and Cameron (1891) described Cotesia while treating the parasitic Hymenoptera of India associated with pests insects. Ashmead's (1900b) revision of the Ichneumonoidea, in which he accommodated the Evaniidae, Agriotypidae, Ichneumonidae, Alysiidae, Braconidae and Stephanidae, first recognised the Microgastrinae as a separate subfamily close to the Cardiochilinae and Agathidinae. He suggested three probable tribes within the Microgastrinae with Neoneurus Haliday and Elasmosoma Ruthe forming one tribe; Mirax Haliday and allies forming another tribe; and Microgaster, Apanteles and others, which Ashmead termed the "genuine microgastrines", forming a third tribe. He provided a key to the then 19 recognised genera of Microgastrinae and included the salient characters of three new genera, Diolcogaster, Parapanteles and Hypomicrogaster. However, no formal description of these genera were given.

Viereck $(1910,1912)$ described several species of ichneumonids and braconids based on material in the United States National Museum, including new species of Protapanteles Ashmead and Pseudapanteles Ashmead and a new subgenus of Apanteles, viz. Dolichogenidea Viereck.

### 2.2.2 The beginning of the modern era (1927-45)

The taxonomy of microgastrines between 1927 and 1945 was dominated by D. S. Wilkinson, who described a large number of new species from various regions but particularly the Oriental, Australasian and African regions, based on material held in the British Museum (Natural History). Most of the species he described were placed in Apanteles s.l., and to a lesser extent, Microgaster and Microplitis (Wilkinson 1927, 1928a, 1928b), with many having been reared from known hosts. Wilkinson did not agree with the generic names proposed by Ashmead and Viereck and suggested that "Apanteles may not be susceptible of division into distinct smaller groups". Soon after, Wilkinson (1929) recognised an important new character, specialised sensilla on the ovipositor sheaths (called "the processes"), and proposed that the species with these sensilla may be separated as a new subgenus or genus. However, he refrained from doing so, apparently believing that such a change would have been premature and potentially lead to a cascade of generic division.

Table. 2.1: Microgastrine species treated by Wilkinson between 1927 and 1945.

| Year of <br> publication | Genus | Total <br> species | New <br> species | Region |
| :--- | :--- | :---: | :---: | :--- |
| 1927 | Microgaster | 9 | 4 | Indo-Malaya |
| 1928a | Apanteles | 38 | 17 | Indo-Australia |
| 1928 b | Apanteles | 36 | 18 | Indo-Australia |
| 1929 | Microgaster | 24 | 12 | Indo-Australia, Africa |
| 1930 | Microplitis | 12 | - | Indo-Australia |
| 1932 | Apanteles | 49 | 9 | Africa |
| 1934a | Microgaster, | 2 | 2 | Africa, Australia |
| 1934b | Microplitis | Apanteles | 18 | 6 |
| 1935 | Apanteles |  |  | Palaearctic, Oriental, |
| 1936a | Apanteles, | 2 | 2 | Africa, New Zealand |
|  | Microgaster |  | 4 | Madagascar, Fiji |
| 1936b | Apanteles | 1 |  | Madagascar, Algeria, |
| 1936c | Apanteles | 2 | 1 | Papua New Guinea |
| 1937 | Apanteles | 2 | 1 | Pritain |
| 1938a | Apanteles | 1 |  | Palaearctic |
| 1938b | Apanteles | 1 | 1 | - |
| 1938c | Apanteles | 2 | 2 | South Africa |
| 1939 | Apanteles | 2 | 1 | Palaearctic |
| 1940a | Apanteles | 2 | 2 | Europe |
| 1940b | Apanteles | 2 | 1 | - |
| 1941a | Apanteles | 2 | 2 | Europe |
| 1941b | Apanteles | 3 | 2 | Europe |
| 1945 | Apanteles | 50 | - | Europe |
|  |  |  | Palaearctic |  |

Because of the increasing number of Apanteles species, Wilkinson (1932) attempted to divide the genus in to a number of groups. He first recognised five groups and designated them using arbitrary letters; $\mathrm{M}, \mathrm{A}, \mathrm{F}, \mathrm{U}$ and S , which approximated, at least in part, Marshall's (1885) system of dividing the Microgastrinae into sections. Some of the salient characters of these groups were as follows:

Group A - propodeum with or without medial longitudinal carina but never with an areola, first metasomal tergite (T1) parallel-sided or narrow at apex (equivalent to Marshall's section IV).

Group F - second metasomal tergite (T2) as long as third (T3), propodeum with or without medial longitudinal carina but never with an areola, T1 parallel-sided or broader at apex, ovipositor sheaths short (equivalent to Marshall's sections I and II).

Group $U-\mathrm{T} 2$ much shorter than T3, propodeum with or without an areola but never with a medial longitudinal carina, costulae never present (equivalent to Marshall's sections II with costulae absent).

Group $S$ - propodeum with complete areola, costulae present.
Group $M$ - all species not fitting into any of the above mentioned groups.
Wilkinson (1934b) described a sixth group of Apanteles which he called the G group, defined by having a dorso-ventrally flattened body. However, the untimely death of Wilkinson in 1941 during World War II left his intention to publish a monograph of the Palaearctic species of Apanteles incomplete. However, he had already undertaken most of the work for this project, and it was completed by G. E. J. Nixon and published in 1945. The species and genera of microgastrines treated by Wilkinson are summarised in Table 2.1.

In total, Wilkinson covered 264 species of Microgastrinae and described 89 new species and, by the time of his death, had made the group truly well-known on a world wide base. Further, he made a significant contribution in documenting the hosts of many species.

### 2.2.3 The post war period (1945-1987)

Short (1954) classified 33 species of Apanteles from the Palaearctic region on the basis of larval characters, and included information on the form of the mandibles, the number of setae on the prelabium and maxilla, and the degree of sclerotization of the skin and head
sclerites. However, it was only the form of mandibles which appeared to be of any taxonomic significance, and he grouped species in a similar way to that of Wilkinson (1945).

After Wilkinson's death, G. E. J. Nixon was appointed to his position at the British Museum (Natural History) and he set out to continue Wilkinson's mission of making the taxonomy of microgastrine wasps better known. Nixon published a series of papers between 1961 and 1976 which re-evaluated the internal classification of the subfamily, described a large number of species and documented a significant amount of new host data.

Table. 2.2: Microgastrine species treated by Nixon between 1961 and 1976.

| Year | Genus or Apanteles s.l. species-group | Total spp. | New spp. | Region |
| :---: | :---: | :---: | :---: | :---: |
| 1961 | Apanteles | 2 | 2 | Palaearctic |
| 1965 | Microgastrinae | 360 | 229 | World fauna |
| 1967 | ultor-group | 43 | 23 | Indo-Australia |
| 1968 | Microgaster | 46 | 14 | Nearctic, Palaearctic, IndoAustralia |
| 1970 | Microplitis | 28 | 8 | north-western Europe |
| 1972 | laevigatus-group | 43 | 20 | north-western Europe |
| 1973 | vitripennis-, pallipes-, octonarius-, triangulator-, fraternus-, formosus-, parasitellae-, metacarpalis-, circumscriptus-groups | 65 | 24 | north-western Europe |
| 1974 | glomeratus-group | 64 | 23 | north-western Europe |
| 1976 | merula-, lacteus-, vipio-, ultor-, ater-, butalidis-, carbonarius-, validus-groups | 50 | 10 | north-western Europe |

Nixon (1965) presented the most comprehensive treatment of the subfamily, and it is this work that has had a substantial and long term influence on all subsequent taxonomic research on the Microgastrinae. He restricted the subfamily to two tribes, the Cardiochilini and Microgastrini, and one genus, Mirax, which he held separately but did not place in a separate tribe. He defined the subfamily on the presence of spiracles on the lateral membranous parts of the first metasomal tergite, and the Microgastrini by the hind wing second submarginal cell being closed, and the hind wing vannal lobe being distinct. Nixon
treated 19 genera within the Microgastrini and presented a comprehensive key to them. Eight of these genera, Semionis Nixon, Miropotes Nixon, Philoplitis Nixon, Alloplitis Nixon, Prasmodon Nixon, Larissimus Nixon, Parenion Nixon and Sendaphne Nixon, were described as new, and three genera, Hypomicrogaster, Protomicroplitis Ashmead, and Xanthomicrogaster Cameron, were taken out of synonymy to provide a more restricted definition and clearer limits to Microgaster. Apanteles s.l., the most problematic genus because of its size, was divided into 44 species-groups, based on characters that Nixon did not think were sharp enough to justify the recognition of separate genera. He revised the species of 19 of these species-groups and, as well, divided Promicrogaster Brues and Richardson into two species-groups, Hypomicrogaster into eight species-groups, and Protomicroplitis into 20 species-groups, 10 of which were keyed to species level. In total, Nixon (1965) treated 360 species of microgastrines of which 229 were described as new.

Nixon (1967) revised the ultor-group of Apanteles from the Indo-Australian region, which he had previously diagnosed (Nixon 1965) on the basis of three characters; the punctation of scutum, the shape of postero-lateral field of propodeum, and the general appearance of the vannal lobe of hind wing. To accommodate the new species described, he modified this definition to include the restricted lateral shape of the ovipositor. Soon after, Nixon (1968) revised Microgaster (sensu Nixon 1965) from the Nearctic, Palaearctic and Indo-Australian regions and recognised several new characters for the genus, including the presence of teeth or a lobe on the claws , and the degree of sclerotization of the hypopygium. However, even using these characters, Nixon realised that identification of many species of Microgaster remained problematic. In the same vein, Nixon (1970) revised Microplitis for north-western Europe, and in so doing he again stated that few significant characters could be found to separate the species, thus highlighting a problem experienced to the present day, that undertaking species-level taxonomic studies on many microgastrine groups is a difficult enterprise.

Between 1970 and 1976 Nixon revised several microgastrine genera from north-western Europe and all of the species-groups of Apanteles s.l. In so doing he discovered several new characters associated with the glomeratus-group of Apanteles (Nixon 1974), the largest and taxonomically the most difficult group in the genus. Two of these, the exposure of the phragma of scutellum and pilosity of the hind wing vannal lobe, have now been recognised to
be taxonomically important to a broader range of microgastrine genera. Importantly, Nixon (1972) in his treatment of the species-groups of Apanteles s.l., reiterated more clearly his sentiments expressed in 1965, that Apanteles was polyphyletic and the hundreds of species in the genus shared only a single character, the open areolet of fore wing. Implicit in this statement and clearly expressed by Nixon was that many species-groups of Apanteles show closer affinities with species-groups of other microgastrine genera than they do with each other. Nixon's publications treating the species-groups of Apanteles and other microgastrine genera are summarised in Table 2.2.

Table. 2.3: Microgastrine species treated by Papp between 1978 and 1990.

| Year | Genus or Apanteles s.l. species-group | $\begin{gathered} \hline \text { Total } \\ \text { species } \end{gathered}$ | $\begin{aligned} & \text { New } \\ & \text { species } \end{aligned}$ | Region |
| :---: | :---: | :---: | :---: | :---: |
| 1978 | laevigatus-group | 71 | - | Europe, North Africa, East Palaearctic, Nearctic |
| 1979 | laevigatus-group | 28 | - | Palaearctic, Nearctic |
| 1980a | lineipes-, obscurus-, ater-groups | ? | - | Palaearctic |
| 1980b | Fornicia | 10 | 2 | Oriental |
| 1981 | lacteus-, ultor-, longipalpis-, vipio-, butalids-groups | 41 | - |  |
| 1982 | laspeyresiella-, merula-, falcatus-, validus-groups | 23 | - | Europe, East Palaearctic, Nearctic, Africa |
| 1983a | carbonarius-, circumscriptus-, fraternus-, pallipes-, parasitellae-, liparidis-, octonarius-, thompsoni-group | 66 | 5 | Europe, East Palaearctic, Nearctic, Oriental |
| 1983b | Apanteles s.l. | 43 | - | Hungary and adjacent countries |
| 1984a | Apanteles s.l. | 37 | - | Hungary and adjacent countries |
| 1984b | Microgaster | 68 | 7 | Palaearctic |
| 1984c | metacarpalis-, formosus-, popularis-, <br> suevus-groups | 51 | 3 | Europe, Eastern Palaearctic, Nearctic |
| 1986a | glomeratus-group | 36 | - | Europe, Eastern Palaearctic |
| 1986b | Glabromicroplitis | 5 | - | Holarctic |
| 1987 | glomeratus-, cultellus-groups | 103 | 1 | Europe, Eastern Palaearctic, Nearctic |
| 1990 | Apanteles s.str. | 9 | - | Europe |
| Total |  | 18 |  |  |

Where Wilkinson's main contribution was in describing new species, Nixon's legacy, apart from describing a large number of species and documenting many new host records, was his discovery of many new characters that have proven to be important, both for taxonomic and phylogenetic studies. It is Nixon's thoughtful treatment of the subfamily that has provided a solid basis for much of the work of subsequent authors.

Following Nixon's treatment of the European fauna of Apanteles s.l., Papp continued to explore the microgastrine fauna of Europe between 1976 and 1990. Primarily, Papp built on Nixon's revisions and extended them to cover the fauna of the western Palaearctic region. He surveyed all of the species-groups of Apanteles (Papp 1978, 1979, 1980a, 1981, 1982, 1983a, 1983b, 1984a, 1984c, 1986a, 1987 and 1990) and, as well, treated several other microgastrine genera, i.e. Fornicia Brullé (Papp 1980b), Microgaster (Papp 1984b) and Glabromicroplitis Papp (Papp 1986b) (Table 2.3). Most recently, Papp (1988) placed the European species of Apanteles s.l. according to Mason's (1981) reclassification of the subfamily (see below).

### 2.2.4 The present era ( 1988 to the present)

### 2.2.4.1 Phylogeny of the subfamily

Although the relationships among the microgastroid subfamilies are moderately wellunderstood, the relationships among genera within the Microgastrinae remain poorly resolved, despite several detailed studies. Mason (1981) presented the first attempt to resolve relationships within the subfamily in a formal cladistic way which resulted in reclassifying the genera and dividing Apanteles s.l. into 23 separate genera. He introduced a number of new character systems, including larval and antennal features. However, the main focus of the study was on a host-associated character complex termed the "Macrolepidoptera suite" of characters (Table 2.4).

Mason could not find any strong synapomorphies to unite Mirax, Cardiochiles Nees and the Microgastrini (sensu Nixon) into one subfamily and he maintained them as separate. He defined the Microgastrinae on the basis of the following apomorphic characters: 1) flagellum 16 -segmented, 2) flagellar segments with placodes in two ranks giving the appearance of a transverse constriction, 3) areolet of fore wing absent or small, 4) apical margin of the clypeus concave, 5) first metasomal segment with a strongly defined tergite, 6) first metasomal

Table. 2.4: The "Macrolepidoptera suite" of characters used by Mason (1981) in his phylogenetic analysis of the Microgastrinae.

| Character | Plesiomorphic state | Apomorphic state |
| :---: | :---: | :---: |
| Characters of female genitalia |  |  |
| Height/Length of tergite 9 | 2.4-4.0 | 1.0-2.0 |
| Anterior apodeme of tergite 9 | Weak | Prominent |
| Apex of 2nd valvifer | Tapered | Widened |
| Origin of 3rd valvulae | On distal half, usually near apex of 2nd valvifer | Near base of 2nd valvifer |
| Length of 3rd valvulae | Medium to long, seldom shorter than | Short, rarely extending beyond apex of abdomen apex of abdomen |
| Hairs of 3rd valvulae | Many, hairy throughout the entire length | Few, near apex only |
| Length of 2nd valvulae | Almost always extending beyond apex of tergite 9 | Rarely extending beyond apex of tergite 9 |
| Taper of 2nd valvulae | Evenly tapered | Abruptly narrowed at apical 0.6-0.7 |
| Hypopygium | Usually medially desclerotised in fan-like folds or sometimes sharply folded medially | Evenly sclerotised, without sharp median fold except at apical 0.1 |
| Characters of both sexes |  |  |
| Antero-lateral margin of metanotum | Usually with more or less conspicuous lobe bearing setae in a tuft | Evenly curved and often without a tuft of setae |
| Characters of immatures |  |  |
| Skin of last instar larvae | Small papules each bearing a spinule that is as long as the papulae | Papules smooth or bearing short spinules |
| Mandibles of instar | Blade completely set, about 18-25 teeth | Blade with tiny teeth, too difficult to count; or teeth fewer than 15 , confined to apical half; or no teeth |
| Propagation | Larva usually solitary | Larva usually gregarious, seldom solitary |
| Choice of host | mostly Microlepidoptera | Macrolepidoptera, rarely <br> Microlepidoptera |

spiracle present on the laterotergite, and 7) hind tarsus with a medial ventral ridge formed by a single row of closely appressed or connate hairs. He also discussed a number of characters and presented transformation series for some of them. In particular, the character systems which he treated in detail were the "Macrolepidoptera suite" (see Table 2.4), and the reductional pathways associated with the loss of sculpturing on the propodeum (see Figs $5.21 \mathrm{a}-1)$ and the fore wing areolet. However, these characters are complex and remain difficult to interpret (Walker et al. 1990). Mason (1981) discussed over 50 characters and defined the plesiomorphic and apomorphic states for each. However, his phylogenetic hypothesis (Fig. 2.9) was an intuitive approximation of relationships and was not based on a parsimony analysis. He recognised five tribes forming two major groups: the Apantelini+Microgastrini and the Microplitini+(Fornicini+Cotesiini). The latter group comprised the largest number of genera and was defined by the "Macrolepidoptera suite" of characters (Table 2.4), in particular in having a short ovipositor and evenly sclerotised hypopygium. Within this clade, the Diolcogaster-group of genera was placed as the sistergroup to Wilkinsonellus Mason. Mason (1981) used genus-groups as the basis for his analysis rather than genera but he did not explicitly state what genera were contained in each group. These were later presented in Walker et al. (1990) (see Table 2.5).

Table. 2.5: Genus-groups of Microgastrine and their respective component genera recognised by Mason (1981), after Walker et al. (1990).

| Genus-group | Component genera |
| :--- | :--- |
| Alloplitis-group | Alloplitis, Philoplitis |
| Apanteles-group | Apanteles, Papanteles, Alphomelon, Dasylagon |
| Choeras-group | Choeras, Sathon, Iconella, Hygroplitis |
| Cotesia-group | Cotesia, Protapanteles, Glyptapanteles, Nyreria |
| Diolcogaster-group | Diolcogaster, Exix, Parenion, Buluka |
| Dolichogenidea-group | Dolichogenidea, ?Exoryza |
| Microgaster-group | Microgaster, Rhygoplitis |
| Microplitis-group | Microplitis, Snellenius |
| Miropotes-group | Miropotes, Exulonyx |
| Pholetesor-group | Pholetesor, Teremys |
| Prasmodon-group | Prasmodon, Paroplitis, Clarkinella |
| Promicrogaster-group | Promicrogaster, Sendaphne |
| Pseudapanteles-group | Pseudapanteles, Xanthomicrogaster |
| Rasivalva-group | Rasivalva, Distatrix |
| Venanus-group | Venanus, Venanides |
|  |  |

In total Mason treated 51 genera, of which 23 were new. His reclassification retained several large genera but, importantly, it split Apanteles s.l. into numerous genera most of which correspond to the species-groups of Apanteles previously recognised by Nixon (1965), as listed in Mason (1981) and Papp (1988) (Table 2.6). He also predicted that future detailed studies of Dolichogenidea, Apanteles, Choeras Mason, Glyptapanteles, Promicrogaster, Microplitis and Diolcogaster would probably result in further splitting of these genera, i.e. they are possibly polyphyletic.

Table. 2.6: Species-groups of Apanteles and the genera they now represent (after Mason 1981; Papp 1988).

| Genus | Species-groups of Apanteles s.l. |
| :---: | :---: |
| Apanteles s.str. | ater-, metacarpalis-, crassicornis- (part), taeniaticornis-, mycetophilus-, trifasciatus-caesar-, grandiculus- and obscurus-groups |
| Choeras | parasitellae- and validus-groups |
| Cotesia | pistrinariae- and glomeratus-groups |
| Deuterixys | carbonarius-group |
| Distatrix | formosus-group |
| Dolichogenidea | lacteus-, laevigatus-, lineipes-, longipalpis-and ultorgroups |
| Glyptapanteles | fraternus-, liparidis-, octonarius-, triangulator-, pallipes- thompsoni- and vitripennis-groups |
| Iconella | merula- and sundanus-groups |
| Illidops | butalidis-, suevus- and vipio-group |
| Nyreria | mlanje-groups |
| Parapanteles | paradoxus-, ultor-, laevigatus-, longipalpis-groups |
| Pholetesor | bucculatricis- and circumscriptus-groups |
| Protapanteles | popularis-group |
| Pseudapanteles | nerion- (part) and annulicornis-groups |
| Sathon | falcatus-group |
| Wilkinsonellus | henicopus- and daira-groups |
| Venanides | congoensis-group |

Although Mason's (1981) study suffered from some shortcomings it remains a benchmark for all subsequent research, and the most important single contribution to date on the generic relationships within the Microgastrinae. Further, he recognised a number of new characters, which have proved useful in subsequent phylogenetic analyses of microgastrine genera, and even those aspects of his work that have been criticised, have fostered rigorous debate and spurred substantial research (e.g. Austin 1989, 1990; Walker et al. 1990; Whitfield and Mason 1994).

Williams (1985), in erecting a new genus, Lathrapanteles Williams for Sathon papaipemae Muesebeck and three new species, examined the relationships of some genera
that possess the "Macrolepidoptera" characters. The phylogeny of the genus was reconstructed using only seven characters, and a generalised out-group constructed from Apanteles, Choeras, Cotesia, Diolcogaster, Glyptapanteles and Sathon Mason. One species, L. ampyx Williams fell outside the genus, and this small study, once again, raised the possibility of the polyphyletic nature of some microgastrine genera, in this case the ChoerasSathon complex.

Walker et al. (1990) reanalysed Mason's (1981) data and showed that his intuitive tree was not the most parsimonious solution to the data, that it was far less resolved in structure (compare Figs 2.9 and 2.10), and was little affected by the character weightings employed by Mason. Further, to investigate the possible monophyly of Apanteles (s.l.), Walker et al. (1990) weighted the loss of fore wing vein r-m 10 times to force the monophyly of the genus. This analysis resulted in a tree many steps longer than the results obtained with the data unweighted. They went on to reinterpret several of Mason's characters and transformation series, and analysed 34 characters, polarised using the Cardiochilinae, Miracinae and Khoikhoiinae as out-groups. These data yielded 512 equally parsimonious trees, the consensus of which (Fig. 2.11) had little structure but did resolve the Cotesia-complex (viz. Forniciini +Cotesini+Microplitini sensu Mason), and the Apanteles + Dolichogenidea+ Pholetesor group, but not the Apantelini or Microgastrini. In discussing most of Mason's characters in detail, Walker et al. (1990) selected three for special consideration. These were the propodeal carination, fore wing areolet, and the presence of an anterior medial groove on the first metasomal tergite. They postulated that these were complex characters which could not be scored with confidence, and when they were removed from the reinterpreted data set, little structure was lost from the tree (compare Figs 2.11 and 2.12). Further analysis showed that within this group of 512 trees there were two major topologies which differed only in the placement of basal groups: one placed the Miropotes-group as the most basal because of the loss of hind wing vein $2 \mathrm{r}-\mathrm{m}$ (Fig. 2.13), and the other placed the Prasmodon-group and Xenogaster as unresolved sister-groups to the remaining Microgastrinae because of the form of the hypopygium (Fig. 2.14). Walker et al. (1990) favoured the second of these trees as representing the likely relationships of the group after employing successive weighting of the data, and considering the polarity discussion of the membranous hypopygium presented in Austin (1990).

Since Walker et al. (1990), no further studies have been published on the phylogenetic relationships within the Microgastrinae. Their study did little more than show up the inadequacies of Mason's (1981) phylogeny, and in relying on Mason's data they made no contribution to finding new characters. Further, they accepted the genera and generic grouping employed by Mason. However, Mason himself recognised the several genera (see above), including Diolcogaster, probably needed to be further divided. However, Walker et al. (1990) in reanalysing Mason's work showed his hypothesis was not tenable, and this has acted as a check on its possible widespread acceptance.

### 2.2.4.2 Taxonomy of the subfamily

Williams (1988) revised the genus Sathon, which is differentiated from other Microgastrini sensu Nixon by the possession of an exposed scutellar phragma and reduced lateral metanotal lobes. He described five new species and presented a key to the Holarctic and Neotropical species.

Austin (1989), in revising Buluka De Saeger, showed that several characters, such as a smooth vertex and areolet shape were not important in defining this genus, as claimed by the previous workers (i.e. Nixon 1965; Mason 1981), while several others viz. length of carapace, width of face, and eye convergence, were found to be sexually dimorphic. He also discussed the relationships among Buluka and other genera and highlighted three major problems in resolving microgastrine relationships. These were the large number of species in the subfamily; the high degree of morphological convergence among genera and species; and the presence of many reductional characters in the group. Austin (1989) noted that Buluka shares a number of synapomorphies with Diolcogaster, viz. short and evenly sclerotised hypopygium, a complete medial longitudinal carina on the propodeum, maxillary palps being 3-segmented, absence of an epicnemial carina, presence of a basal medial groove on T1, enlarged hind coxa, presence of elongate flattened sensilla on the tip of the ovipositor sheaths, and the presence of specialised sensilla on ventral surface of antennae. However, he also pointed out that the exact position of Buluka could not be confirmed until a detailed study of the genera in the Cotesiini, including the species groups of Diolcogaster, was undertaken. Austin (1990) revised the Australasian genus Miropotes and surveyed the ovipositor system across various genera of microgastrines and the related subfamilies

Cardiochilinae, Miracinae, Khoikhoiinae, Cheloninae and Neoneurinae. The characters examined in this system were the sclerotisation of hypopygium, the length of hypopygium, the length of ovipositor sheaths (expressed as a proportion of hind tibia), and the hairs on the exposed parts of the ovipositor sheaths. He discussed the relationships among Miropotes and other microgastrine genera, especially in regard to the structure of the ovipositor and hypopygium, and suggested that the polarity of a number of characters in Mason's (1981) "Macrolepidoptera suite" should be changed. The most significant of these was the reversal of and evenly sclerotised and inflexible hypopygium from an apomorphic to a plesiomorphic state.

Table. 2.7: Microgastrine species treated by various workers between 1989 and 1995.

| Publication | Taxa treated | Total species | $\begin{aligned} & \text { New } \\ & \text { species } \end{aligned}$ | Region |
| :---: | :---: | :---: | :---: | :---: |
| Austin 1989 | Buluka | 7 | 5 | World fauna |
| Austin \& Dangerfield 1989 | Apanteles, Microgaster, Cotesia | 12 | 1 | New world Diatraea parasites |
| Austin 1990 | Miropotes | 10 | 8 | Australia |
| Austin \& Dangerfield 1992 | Microgastrinae | 164 | 15 | Australasia |
| Austin \& Dangerfield 1993 | Microplitis, Snellenius | 30 | 23 | Australia, New Guinea |
| Whitfield 1985 | Deuterixys | 3 | 3 | North America |
| Whitfield 1995a | Microgastrinae | 281 | - | North American checklist |
| Whitfield 1995b | Xanthapanteles | 1 | 1 | Neotropics |
| Whitfield (in press) | Pholetesor | 21 | 11 | Nearctic fauna |
| Whitfield \& Scaccia (in press) | Distatrix | 1 | 1 | North America |
| Total |  |  | 57 |  |

Austin and Dangerfield (1992) published a detailed synopsis of the microgastrines of the Australasian region. They recognised 22 genera and, in addition, described a new genus, Austrocotesia Austin and Dangerfield, and 15 new species. In this study three genera, Parapanteles, Fornicia and Deuterixys Mason, were recorded for the first time from the region, while four genera, Buluka, Parenion, Snellenius Westwood and Wilkinsonellus were recorded from mainland Australia for the first time. They also complied a detailed host-
parasitoid list and presented a short discussion on the biology of the subfamily. Austin and Dangerfield (1993) revised Microplitis and Snellenius from Australia and New Guinea (Table 2.7) and in so doing, placed Glabromicroplitis as a junior synonym of Microplitis. They also reviewed the biology and host relationships of both genera on a world-wide basis and provided a list of the host families.

Whitfield (in press) revised Pholetesor Mason for the Nearctic region, analysed the phylogenetic relationships among species and, based on the results obtained, proposed eight species-groups. Whitfield (1995a) published an annotated checklist of the Microgastrinae for North America which covered 281 species and 32 genera, several of which were overlooked by Mason (1981). Eight species of Diolcogaster were listed for the region. Whitfield (1995b) described a new genus, Xanthapanteles Whitfield, and presented a comparison of the several characters with other microgastrine genera, 1) the arrangement of antennal placodes, 2) the fore wing areolet 3) the propodeal carination, 4) the shape of first metasomal tergite, 5) the sculpturing of metasomal tergites, and 6) the sclerotization of the hypopygium.

Recent taxonomic research by Huddleston and Walker (1988), Dangerfield and Austin (1990, 1995) and Dangerfield, Whitfield and Austin (in press) has provided a solid background on the morphology, species limits and internal relationships of the Cardiochilinae, the nominal sister-group to the Microgastrinae. This work will undoubtedly play an important role in the future, as it has done in this study, in helping to understand the inner workings of the microgastrines.

### 2.3 The genus Diolcogaster Ashmead

Diolcogaster was first described by Ashmead (1900a) with Microgaster brevicaudus Provancher designated as the type species of the genus. However, in his substantial publication on the Ichneumonoidea, published in the same year, Ashmead (1900b) listed a different species, Microgaster melligaster Provancher, as the type species of Diolcogaster. In neither work was there a formal description given for the genus, although in Ashmead (1900b) Diolcogaster was separated from Hygroplitis Thomson and Microgaster on the basis of three characters: the second metasomal tergite being poorly separated from the third; the second tergite appearing trilobed due to two nearly parallel longitudinal grooves; and the ovipositor being very short. Because of the earlier designation of Microgaster brevicaudus as
the type species of Diolcogaster (published in March, 1900) as compared to that of Microgaster melligaster (October, 1900), the former species has priority and is the true type species of the genus. Since the work of Ashmead, 48 species of Diolcogaster have been described (not including the new species described here - see Chapter 6) by 20 authors in various genera viz. Ichneumon L., Zadiolcogaster Viereck, Protomicroplitis, Hygroplitis, Apanteles s.l. and Microgaster (Table 2.8)

Nixon (1965) rationalised much of the confusion that existed among the non-Apanteles s.l. genera recognised at the time by removing Protomicroplitis, Hypomicrogaster and Xanthomicrogaster from synonymy under Microgaster, diagnosing Protomicroplitis and dividing it into 22 species-groups, comprising 44 species ( 19 of which were new). Shenefelt (1973) followed Nixon's arrangement of microgastrine genera and catalogued the 44 species of world Protomicroplitis.

Mason (1981) re-established the genus Diolcogaster, and redescribed it in detail based on the type species Microgaster brevicaudus. He included most the species-groups of Protomicroplitis (sensu Nixon) in Diolcogaster, listing 24 species, but excluded the calceata, marginata-, lepelleyi,- calliptera- and schunkei-groups which he retained in Protomicroplitis s.str. Mason (1981) separated Protomicroplitis from Diolcogaster on the basis of the latter genus having an evenly curved usually rugose propodeum (not angled), the first metasomal tergite almost twice as long as wide (not three to four times), and antennal flagellomeres having longitudinal placodes distributed in regular rows so that a median constriction on most flagellomeres is clearly visible. Mason also recognised that several species-groups of Diolcogaster probably represents artificial segregates of what might be a polyphyletic assemblage.

Tobias (1986) listed 10 species of Diolcogaster from the European part of the USSR, of which five were new combinations. Austin and Dangerfield (1992) listed six species of Diolcogaster from Australasia and they estimated that the regions fauna was about 70+ species. Austin and Dangerfield (1992) further strengthened the conclusion of Mason (1981) that Diolcogaster was not a monophyletic group and they suggested that the genus is better considered to be paraphyletic without the inclusion of genera such as Parenion, Wilkinsonellus and Buluka.

Table. 2.8: World species of Diolcogaster Ashmead and summary of their taxonomic history.
Diolcogaster abdominalis (Nees von Esenbeck): Microgaster abdominalis Nees von Esenbeck, 1834: 163. Microplitis abdominalis Szépligeti, 1899: 100. Hygroplitis abdominalis Lyle, 1918: 130. Microgaster deprimator Wesmael, 1837: 10. Protomicroplitis abdominalis Nixon, 1965: 254. Diolcogaster abdominalis Mason, 1981: 114.

Diolcogaster alce (Nixon): Protomicroplitis alce Nixon, 1965: 247. Diolcogaster alce Mason, 1981: 114.

Diolcogaster alveariaus (Fabricius): Ichneumon alveariaus Fabricius, 1798: 232. Cryptus alveariaus Fabricius, 1804: 90. Ichneumon alveariaus Walckenaer, 1802: 110. Bracon alveariaus Zetterstedt, 1840: 398. Microplitis alveariaus Marshall, 1872: 107. Protomicroplitis alveariaus Nixon, 1965: 250. Diolcogaster alveariaus Mason, 1981: 114.
Diolcogaster anomus (Viereck): Zadiolcogaster anomus Viereck, 1913: 367. Microgaster anomus Muesebeck and Walkley, 1951: 135. Diolcogaster anomus Mason, 1981: 114.
Diolcogaster auripes (Provancher): Microgaster auripes Provancher, 1886: 141. Protomicroplitis auripes Nixon, 1965: 252. Diolcogaster auripes Mason, 1981: 114.
Diolcogaster austrina (Wilkinson): Microgaster austrina Wilkinson, 1929: 119. Protomicroplitis austrina Nixon, 1965: 256. Diolcogaster austrina Mason, 1981: 114.
Diolcogaster bakeri (Muesebeck): Microgaster bakeri Muesebeck, 1922: 29. Diolcogaster bakeri Mason, 1981: 114.
Diolcogaster basimacula (Cameron): Apanteles basimacula Cameron, 1904: 173. Microgaster basimacula Wilkinson, 1929: 101. Protomicroplitis basimacula Nixon, 1965: 246. Diolcogaster basimacula Mason, 1981: 114.
Diolcogaster brevicaudus (Provancher): Microgaster brevicaudus Provancher, 1886: 140. Diolcogaster brevicauda Ashmead, 1900: 594a. Microgaster (Diolcogaster) brevicaudus Viereck, 1911: 96. Diolcogaster brevicauda Mason, 1981: 114.
Diolcogaster coenonymphae (Watanabe): Microgaster coenonymphae Watanabe, 1937: 101. Protomicroplitis coenonymphae Nixon, 1965: 258. Diolcogaster coenonymphae Mason, 1981: 114.

Diolcogaster connexus (Nees von Esenbeck): Microgaster connexus Nees von Esenbeck, 1834: 174. Microplitis connexa (-us) Marshall, 1872: 118. Protomicroplitis connexus Nixon, 1965: 248. Diolcogaster connexus Mason, 1981: 114.

Diolcogaster curticornis (Granger): Microgaster curticornis Granger, 1949: 221. Diolcogaster curticornis Mason, 1981: 114.
Diolcogaster duris (Nixon): Protomicroplitis duris Nixon, 1965: 263. Diolcogaster duris Mason, 1981: 114.
Diolcogaster eclectes (Nixon): Protomicroplitis eclectes Nixon, 1965: 246. Diolcogaster eclectes Mason, 1981: 114.
Diolcogaster erro (Nixon): Protomicroplitis erro Nixon, 1965: 248. Diolcogaster erro Mason, 1981: 114.
Diolcogaster euterpus (Nixon): Protomicroplitis euterpe Nixon, 1965: 250. Diolcogaster euterpe Mason, 1981: 114. Diolcogaster euterpus Austin and Dangerfield, 1992: 27.
Diolcogaster facetosa (Weed): Microgaster facetosus Weed, 1888: 296. Microgaster (Diolcogaster) solidaginis Viereck, 1917: 202. Protomicroplitis facetosa Nixon, 1965: 252. Diolcogaster facetosa Mason, 1981: 114.
Diolcogaster fasciipennis (Gahan): Microgaster fasciipennis Gahan, 1918: 587. Protomicroplitis fasciipennis Nixon, 1965: 244. Diolcogaster fasciipennis Mason, 1981: 114.
Diolcogaster garmani (Ashmead): Protomicroplitis germani Ashmead, 1900a: 132. Microgaster garmani Muesebeck, 1922: 26. Diolcogaster germani Whitfield, 1995: 250.
Diolcogaster glaphyra (De Saeger): Microgaster glaphyra De Saeger, 1944: 81. Protomicroplitis glaphyra Nixon, 1965: 246. Diolcogaster glaphyra Mason, 1981: 114.
Diolcogaster hinzi (Nixon): Protomicroplitis hinzi Nixon, 1965: 252. Diolcogaster hinzi Mason, 1981: 114.
Diolcogaster integra (Wilkinson): Microgaster integra Wilkinson, 1929: 103. Protomicroplitis integra Nixon, 1965: 246. Diolcogaster integra Mason, 1981: 114.
Diolcogaster ippis (Nixon): Protomicroplitis ippis Nixon, 1965: 263. Diolcogaster ippis Mason, 1981: 114.
Diolcogaster iridescens (Cresson): Microgaster iridescens Cresson, 1865: 68. Microgaster indescens Szépligeti, 1904: 113. Urogaster iridescens Ashmead, 1900a: 277. Diolcogaster iridescens Mason, 1981: 114.
Diolcogaster kasachstanica (Tobias): Hygroplitis kasachstanica Tobias, 1964: 208. Protomicroplitis kasachstanica Nixon, 1968: 69. Diolcogaster kasachstanica Tobias, 1986: 368.
Diolcogaster lelaps (Nixon): Protomicroplitis lelaps Nixon, 1965: 263. Diolcogaster lelaps Mason, 1981: 114.
Diolcogaster mayae (Shestakov): Microgaster mayae Shestakov, 1932: 260. Diolcogaster mayae Mason, 1981: 114.

Diolcogaster medon (Nixon): Protomicroplitis medon Nixon, 1965: 243. Diolcogaster medon Mason, 1981: 114.
Diolcogaster meges (Nixon): Protomicroplitis meges Nixon, 1965: 251. Diolcogaster meges Mason, 1981: 114.
Diolcogaster melleus (Nixon): Protomicroplitis melleus Nixon, 1965: 243. Diolcogaster melleus Mason, 1981: 114.
Diolcogaster minuta (Reinhard): Microgaster minuta Reinhard, 1880: 357. Protomicroplitis minuta Nixon, 1965: 250. Diolcogaster minuta Mason, 1981: 114.
Diolcogaster nephele (Nixon): Protomicroplitis nephele Nixon, 1965: 247. Diolcogaster nephele Mason, 1981: 114.
Diolcogaster orontes (Nixon): Protomicroplitis orontes Nixon, 1965: 254. Diolcogaster orontes Mason, 1981: 114.
Diolcogaster pariander (Nixon): Protomicroplitis pariander Nixon, 1965: 240. Diolcogaster pariander Mason, 1981: 114.
Diolcogaster perniciosus (Wilkinson): Microgaster perniciosa Wilkinson, 1929: 112. Protomicroplitis perniciosa Nixon, 1965: 248. Diolcogaster perniciosa Mason, 1981: 114. Diolcogaster perniciosus Austin and Dangerfield, 1992: 27.
Diolcogaster pyrene (Nixon): Protomicroplitis pyrene Nixon, 1965: 242. Diolcogaster pyrene Mason, 1981: 114.
Diolcogaster reales (Nixon): Protomicroplitis reales Nixon, 1965: 239. Diolcogaster reales Mason, 1981: 114.
Diolcogaster rixosus (Wilkinson): Microgaster rixosa Wilkinson, 1929: 108. Diolcogaster rixosus Austin and Dangerfield, 1992: 27.
Diolcogaster schizurae (Muesebeck): Microgaster schizurae Muesebeck, 1922: 30. Diolcogaster schizurae Mason, 1981: 114.
Diolcogaster scotica (Marshall): Microgaster scoticus Marshall, 1885: 251. Protomicroplitis scotica Nixon, 1965: 252. Diolcogaster scotica Mason, 1981: 114.
Diolcogaster seriphus (Nixon): Protomicroplitis seriphus Nixon, 1965: 243. Diolcogaster seriphus Mason, 1981: 114.
Diolcogaster sons (Wilkinson): Microgaster sons Wilkinson, 1932b: 87. Protomicroplitis sons Nixon, 1965: 247. Diolcogaster sons Mason, 1981: 114. Diolcogaster sons Austin and Dangerfield, 1992: 27.
Diolcogaster spretus (Marshall): Microgaster spretus Marshall, 1885: 259. Microgaster (Lissogaster) spreta Fahringer, 1937: 329. Protomicroplitis spretus Nixon, 1965: 225. Diolcogaster spretus Mason, 1981: 114. Diolcogaster spreta Tobias, 1986: 367.
Diolcogaster stepposa (Tobias): Hygroplitis stepposa Tobias, 1964: 209. Protomicroplitis stepposa Nixon, 1968: 69. Diolcogaster stepposa Mason, 1981: 114-Diolcogaster stepposa Tobias, 1986: 368. Diolcogaster tearae (Wilkinson): Microgaster tearae Wilkinson, 1929: 107. Diolcogaster tearae Austin and Dangerfield, 1992: 27.
Diolcogaster tomentosa (Wilkinson): Microgastertomentosa Wilkinson, 1930b: 282. Protomicroplitis tomentosa Nixon, 1965: 255. Diolcogaster tomentosa Mason, 1981: 114.
Diolcogaster urios (Nixon): Protomicroplitis urios Nixon, 1965: 243. Diolcogaster urios Mason, 1981: 114.
Diolcogaster vulpinus (Wilkinson): Microgaster vulpina Wilkinson, 1929: 109. Diolcogaster vulpinus Austin and Dangerfield, 1992: 27.
Diolcogaster xanthaspis (Ashmead): Apanteles xanthaspis Ashmead, 1900a: 280. Microgaster xanthaspis Muesebeck, 1922: 28. Protomicroplitis xanthaspis Nixon, 1965: 242. Diolcogaster xanthaspis Mason, 1981: 114.

Stoltz and Whitfield (1992) recorded polydnaviruses in Diolcogaster facetosa (Weed) which had individually enveloped nucleocapsids, and which were unlike those recorded from other genera of the Cotesiini sensu Mason, which had multiple-enveloped nucleocapsids. Based on this restricted, but nonetheless interesting, observation they questioned the position of the genus within the Cotesiini and suggested it should be reconsidered.

### 2.4 Biology of microgastrines

Shaw and Huddleston (1991) give a detailed account of the biology of microgastrines. Members of the subfamily are endoparasitoids of lepidopteran larvae and are among the most important components of the parasitoid complex of this host group. Although they mostly attack the exposed larvae some species have long ovipositors with which they reach concealed hosts in flower heads, leaf rolls and fungi, while others are specialised to parasitise leaf-mining Lepidoptera. Most microgastrines have a narrow host range, and they mostly oviposit into early or middle instar hosts. However, there are many exceptions, for example, a few species of Diolcogaster and Cotesia are known to oviposit into host embryos (Johansson 1951; Tadic 1958; Wilbert 1960). Gregarious development in microgastrines has been found in most genera. In gregarious species, eggs are mostly deposited in a single ovipositor insertion, however, in some cases repeated insertions have been observed (De Saeger 1937). The broods generally consist of 10-40 larvae. The winter is generally passed as a cocooned pre-pupa, or as a first instar larva, while in some gregarious species as a second instar larva (Laving and Levin 1982). However, such observations are based almost exclusively on temperate species, and it is likely that species from warmer climates overwinter as adults. Most microgastrines overwinter only in one way, however, in a few species of Cotesia both modes have been observed in the same species (Parker 1935; Allen 1958; Laving and Levin 1982). Variable feeding habits have been observed in the subfamily. For example, Microgaster species with exerted ovipositors are mostly solitary parasitoids and attack the early instars of moderately large silk-spinning microlepidoptera, and they probably represent the ancestral end of the subfamily. Whereas, Microplitis with very short ovipositors attack exposed macrolepidopterans and feed on haemolymph and body fats, and they constitute, biologically, the most advanced microgastrines. Most other microgastrine species range between these two extremes.

As lepidopteran parasitoids, the subfamily has been widely used in biological control, mostly involving advanced groups which feed on haemolymph and body fats and attack exposed hosts, e.g. members of Microplitis and Cotesia. In many studies the hosts of microgastrines have been found to suffer a brief spell of paralysis after attack. Eggs laid in the host haemocoel have in some cases been found to adhere loosely to internal organs by the terminal parts of their pedicels (King et al. 1969), and they swell before hatching (Vance

1931; Fallis 1942; Allen 1958; Sato 1980; Arthur and Mason 1986). Teratocytes are liberated as the egg hatches (Tower 1915), and in some cases the serosal cells surround the first instar larva for several weeks (Vance 1931). The teratocytes absorb nutrients and are later consumed (Arakawa and Kitano 1989), but they have also been considered to have secretory functions by several authors (e.g. Stoltz 1986). Four instars may occur in some Microplitis (Hegazi and Fuhrer 1985; Strand et al. 1988) and at least in one species of Apanteles (Porter 1983). However, mostly Apanteles s.l. and other microgastrines including Microplitis (Lewis 1970; Puttler and Thewke 1970) have three instars. First instar larvae are mandibulate and aggressive. The larvae are caudate initially but soon develop an anal vesicle which may have a respiratory function (Muesebeck 1918; Gatenby 1919), though Edson and Vinson (1976, 1977) doubted this and considered it to be an excretory and nutrient absorption organ. Second instar larvae have greatly reduced mandibles but generally appear to feed on the fat body in addition to haemolymph. The final instar has more powerful and, usually at least partially, serrate mandibles used to scrape through the host integument and, in groups with a final ectophagous stage, strongly serrate mandibles to consume the remaining tissues. Open spiracles and a developed tracheal system are not present until the third instar. Cocoon structure is extremely variable in the group but always a neat circular cap is cut by the emerging adult. Like Microplitis, some species of Apanteles s.l. have interesting cocoon forming habits. One solitary species attacking conifer-feeding geometrids always forms its yellow-brown cocoon at the very tip of the needle, in contrast to the host's usual resting place towards the needle base. Diolcogaster species which attack large geometrids cause the host to arch as the parasitoids emerge. They form a neat honeycomb of pinkish-brown cocoons in a semicircular space between the host and the twig on which it rested. Most of the solitary species make plain white cocoons, sometimes in semiconcealments.

Diolcogaster species generally feed gregariously on macrolepidopterans and are also haemolymph and fat-body feeders. The possess individually enveloped polydnavirus nucleocapsids which have been found to disrupt the host's immune response (Stoltz and Whitfield, 1992).

### 2.5 Host species of Diolcogaster

Of the 50 described species of Diolcogaster 18 have known host associations (Table 2.9) comprising at least 14 lepidopterous families, viz. Arctiidae, Geometridae, Hemerophilidae, Lasiocampidae, Limacodidae, Lymatriidae, Noctuidae, Notodontidae, Nymphalidae, Phycitidae, Pyralidae, Satyridae, Thaumetopoeidae and Tortricidae. Biological information on the genus is scant and is limited mostly to incidental observations and that extrapolated from other microgastrine genera (see above). The fact that some species have been reared from known pest Lepidoptera indicates that they could be potentially important as biological control agents. Although host data are limited, several species appear to have relationships associated with particular host families. For instance, D. perniciosus (Wilkinson) is apparently mostly restricted to arctiid hosts, D. rixosus (Wilkinson) to limacodids, D. tomentosa (Wilkinson) to pyralids, and D. schizurae (Muesebeck) to notodontids. Other species seem to utilise hosts from several families, e.g. D. alvearius (F.), D. connexus (Nees) and D. facetosa.

Table. 2.9: List of hosts of Diolcogaster Ashmead species.

| Host | Diolcogaster species |
| :---: | :---: |
| Anthelidae unknown spp. | Diolcogaster perniciosus (Wilkinson) |
| Arctiidae |  |
| Arctia caja L. | Diolcogaster connexus (Nees) |
| Ardices glatignyi Le Guillemot | Diolcogaster perniciosus (Wilkinson) |
| Nyctemera amica (White) | Diolcogaster perniciosus (Wilkinson) |
| Nyctemera annulata (Boisduval) | Diolcogaster perniciosus (Wilkinson) |
| Nyctemera apicalis (Walker) | Diolcogaster fasciipennis (Gahan) |
| Phragmatobia fuliginosa L. | Diolcogaster connexus (Nees) |
| Spilosoma glatignyi Le Guillemot | Diolcogaster perniciosus (Wilkinson) |
| Choreutidae |  |
| Brenthia leptocosma Meyrick | Diolcogaster curticornis (Granger) |
| Geometridae |  |
| Biston betularia L. | Diolcogaster alvearius (F.) |
| Boarmia perfumaria Newman | Diolcogaster alvearius (F.) |
| Boarmia repandata L. | Diolcogaster alvearius (F.) |
| Boarmia rhomboidaria Schiffermüller | Diolcogaster alvearius (F.) |
| Boarmia rhomboidaria Schiffermüller | Diolcogaster alvearius (F.) |
| Boarmia sp. | Diolcogaster alvearius (F.) |
| Cleora jubata Thunberg | Diolcogaster minuta (Reinhard) |
| Deilinia pusaria L. | Diolcogaster hinzi (Nixon) |
| Odontoptera bidentata (Clerck) | Diolcogaster alvearius (F.) |
| Opisthograptis luteolata L. | Diolcogaster alvearius (F.) |
| Rumia crataegaria F . | Diolcogaster alvearius (F.) |
| Synopsia abruptaria Thunberg | Diolcogaster alvearius (F.) |
| Urapteryx sambucaria L. | Diolcogaster alvearius (F.) |
| Lasiocampidae |  |
| Malacosoma neustria L. | Diolcogaster connexus (Nees) |

## Limacodidae

Doratifera oxleyi (Newman)
Doratifera sp.

## Lymantriidae

Euproctis chrysorrohoea Hübner
Euproctis similis Fuessly
Nygmia phaeorrhoea L.
Prothesia auriflua F.
Prothesia sp.

## Noctuidae

Acronycta tridens Schiffermüller
Earias sp.
Elaphria versicolor (Grote)
Euparthenos nubilis (Hübner)
Faronta difusa (Walker)
Neleucania albilinea Hübner
Orthosia revicta (Morrison.)
Pseudaletia unipancta (Haworth)

## Notodontidae

Dicentria lignicolor Walker
Heterocampa manteo Doubleday
Plathypena scabra F.
Protoleucania albilinea Hübner
Schizura concinna Abbot \& Smith Schizura leptinoides Grote
Schizura unicornis Abbot \& Smith
Nymphalidae
Vanessa atalanta (L.)
Coenonympha oedippus F.

## Pyralidae

Dioryctria palumbella F .
Euzophera consociella Hübner
Lamida carbonifera Meyrick
Macalla sp.
Macalla sp.
Marasmia grisealis Ghesquiére
Marasmia trapezalis (Guenée)
Rhodophaea advenella (Zincken)
Sylepta gordialis (Guenée)
unknown genus

## Thaumetopoeidae

Epicoma tristis (Donovan) or
?Teara tristis Lewin

## Tortricidae

Argyrotaenia velutinana (Walker)
Croesia septentrionalis Spinola

Diolcogaster rixosus (Wilkinson)
Diolcogaster rixosus (Wilkinson)

Diolcogaster connexus (Nees)
Diolcogaster connexus (Nees)
Diolcogaster connexus (Nees)
Diolcogaster connexus (Nees)
Diolcogaster connexus (Nees)

Diolcogaster connexus (Nees)
Diolcogaster fasciipennis (Gahan)
Diolcogaster facetosa (Weed)
Diolcogaster facetosa (Weed)
Diolcogaster auripes (Provancher)
Diolcogaster auripes (Provancher)
Diolcogaster facetosa (Weed)
Diolcogaster auripes (Provancher)

Diolcogaster schizurae (Muesebeck)
Diolcogaster schizurae (Muesebeck)
Diolcogaster facetosa (Weed)
Diolcogaster auripes (Provancher)
Diolcogaster schizurae (Muesebeck)
Diolcogaster schizurae (Muesebeck)
Diolcogaster schizurae (Muesebeck)

Diolcogaster abdominalis (Nees)
Diolcogaster coenonymphae (Watanabe)

Diolcogaster spretus (Marshall)
Diolcogaster spretus (Marshall)
Diolcogaster tomentosa (Wilkinson)
Diolcogaster curticornis (Granger)
Diolcogaster tomentosa (Wilkinson)
Diolcogaster austrina (Wilkinson)
Diolcogaster austrina (Wilkinson)
Diolcogaster spretus (Marshall)
Diolcogaster iridescens (Cresson)
Diolcogaster tomentosa (Wilkinson)

Diolcogaster tearae (Wilkinson)

Diolcogaster facetosa (Weed)
Diolcogaster alvearius (F.)


Fig. 2.1: Phylogenetic scheme of braconid subfamilies after Tobias (1967). The bracket shows the subfamilies proposed to be related to the Microgastrinae.


Fig. 2.2: Phylogenetic relationships among the 'Microgastri' proposed by Mason (1983).


Fig. 2.3: Relationships among braconid subfamilies after van Achterberg (1984), with those in group IVa which includes the Microgastrinae indicated by the bracket.


Fig. 2.4: van Achterberg's (1988) scheme for phylogenetic relationships of braconid subfamilies showing modifications to proposed relationships within and near group IVa which is indicated by the bracket.


Fig. 2.5: Consensus tree of 15 equally shortest trees generated by Hennig86 for braconid subfamily relationships, after Quicke and van Achterberg (1990)


Fig. 2.6: A consensus tree generated by PAUP showing braconid subfamily relationships, using unweighted data, after Quicke and van Achterberg (1990).


Fig. 2.7: Phylogenetic relationships among braconid subfamilies after van Achterberg (1993), based on a modified version of the data matrix of Quicke and van Achterberg (1990). The microgastroid complex is indicated by the bracket.


Fig. 2.8: Relationships among the among the microgastroid subfamilies (in bracket) with the indication of the Mendesellinae, after Whitfield and Mason (1994).


Fig. 2.9: Phylogenetic relationships within the Microgastrinae after Mason (1981) (see Table 2.5 for explanation of generic groups).


Fig. 2.10: Strict consensus tree of seven equally parsimonious trees for microgastrine relationships generated from Mason's (1981) original data, after Walker et al. (1990).


Fig. 2.11: Strict consensus tree of 185 equally parsimonious trees for microgastrine relationships generated from the reinterpreted data set of Walker et al. (1990), with the three characters propodeal sculpturing, forewing areolet and medial groove on T 1 included.


Fig. 2.12: Strict consensus tree of 512 equally parsimonious trees for microgastrine relationships from the reinterpreted data set of Walker et al. (1990), with the three characters, propodeal sculpturing, forewing areolet and medial groove of T1 excluded.


Fig. 2.13: The strict consensus tree for microgastrine relationships from Fig. 2.11 showing one of the two conflicting topologies with the Miropotes-group in the basal position, based on the absence of hindwing vein $2 \mathrm{r}-\mathrm{m}$, after Walker et al. (1990).


Fig. 2.14: The strict consensus tree for microgastrine relationships from Fig. 2.12 showing one of the two conflicting topologies with the Miropotes-group included in a clade with the Apanteles and other groups, based on the presence of ventro-medially membranous, folded and expandable hypopygium, after Walker et al. (1990).

## 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 Selection of out-groups and construction of hypothetical ancestor
3.6.3 Treatment of quantitative characters
3.6.4 Discussion of theoretical phylogenetic methods
3.6.5 Methods of measuring information content of phylogenetic analyses
3.6.6 Discussion of PAUP features

### 3.1 General methods

All available material of Australasian Diolcogaster, representatives of non-Australasian species-groups of Diolcogaster and other microgastrine genera, were borrowed from Australian and world collections as listed in Table 3.3. Colour-coded labels were used to keep track of specimens from each collection. Label data on specimens as well as published information were used to compile information on geographic distributions and host relationships of species. External morphology was studied using a Zeiss DR stereomicroscope with $10 \mathrm{x} / 125$ eye-pieces, and $2 \mathrm{x}, 4 \mathrm{x}$, and 8 x objective lenses. Detailed study of minute characters, such as antennal placodes and sensilla was undertaken using one of several types of scanning electron microscopes (SEM) available at the University of Adelaide.

Measurements for body characters were taken using a 100 division calibrated ocular micrometer. Drawings of body parts were undertaken freehand after measuring the proportions of various structures with the ocular micrometer. Drawings of wings and male genitalia were done using the following procedure: wings were separated from the body, kept for 48 h in $95 \%$ alcohol and then mounted on microscope slides in Canada Balsam. For male genitalia, specimens were soaked in water for 24 h and then dissected under a stereomicroscope. Genitalia were partially cleared in warm $10 \% \mathrm{KOH}$, washed in distilled water, transferred to an alcohol series and mounted on slides in Canada Balsam. All prepared slides were dried in an oven for 72 h at $38-40 \mathrm{C}^{\circ}$. Slides were placed in a slide projector modified to take microscope slides and an image projected onto a drawing table through a split prism. Wings and genitalia were traced and detail was later filled in after further microscopic examination.

### 3.2 Collecting techniques

Malaise traps were set up at various sites in the Adelaide region at various times during the project, as well as during specific field trips to the Flinders Ranges (September (1994) and Kangaroo Island (February 1995). However, these traps yielded only a single specimen of Diolcogaster tearae (Wilkinson). Data labels on Diolcogaster specimens from Australasia show that Malaise trapping is the commonest way by which material has been actively collected for this genus, but that the largest proportion of specimens have been obtained by
rearing them from parasitised lepidopteran larvae (Table 3.1).

Table 3.1: Comparison of collecting techniques shown on data labels of Australasian specimens of Diolcogaster ( $n=1870$ ).

| Technique | \% of specimens |
| :--- | :---: |
| Unknown | 49 |
| Reared | 39 |
| Malaise trap | 10 |
| Others (sweeping, pan traps, light trap) | 2 |

### 3.3 Scanning Electron Microscopy

Specimens for scanning electron microscopy were cleaned in a dilute pure soap solution (5\%), soaked and rinsed thoroughly in distilled water and dehydrated in an alcohol series. They were then dried in an Emscope CPD 750 critical point drier, mounted on card-points with water based seccotine glue, and cards then secured to SEM stubs with carbon-based plasticine (Leitz-C-Plast). Specimens were coated in an Emscope SB38 sputter-coater with 40 nm of gold at 0.08 Tor and 15 milliamps for 4 min and examined under a Cambridge Stereoscan 250 (MK 3B) using secondary electron imaging at 20 kv and a spot size of seven. It was found that sputter coating in an argon atmosphere gave better results than evaporative coating in air, presumably because sputter coating gave a more even layer of gold. Sometimes uneven coating, even with sputter coating, provided problems with charging specimens and poor image quality because of the shape and pilosity of specimens. When this occurred, specimens were examined at a lower voltage (i.e. $10-15 \mathrm{kv}$ ), or the back-scattered electron detector was used, or the specimens were re-coated.

When only two to three specimens were available of a species (or for holotypes), they were examined uncoated under an Electroscan E3 environmental scanning electron microscope (ESEM) at 15 kv and variable ( $6-13 \mathrm{~mm}$ ) working distance. This technique was especially useful for scoring the presence or absence of fluted bent-tipped sensilla, and the arrangement of placodes on antennae when little material was available. However, in these cases the images obtained were generally of poorer quality (compare Figs 5.18 and 5.19). However, in the latter half of this project a Philips XL30 field emission electron microscope (FESEM) became available and this proved superior to the ESEM in specimen manipulation and generation of high quality images of uncoated specimens.

### 3.4 Terminology

Terms for wing venation are based on the modified Comstock-Needham system (see Eady 1974; van Achterberg 1979) and follow Austin and Dangerfield (1992) but with some modifications based on Wharton and Marsh (in press). Terms for wing cells follow Austin and Dangerfield (1992) and van Achterberg (1979, 1993) (Figs 4.4, 4.5). Terms for general morphology are detailed in Chapter 4, and follow van Achterberg (1979, 1993), Austin and Dangerfield (1992, 1993), Dangerfield and Austin (1995); those for male genitalia follow Gauld and Bolton (1993), and those for antennal sensilla follow Norton and Vinson (1974). A list of these terms and their abbreviations (or symbols) are given in Table 3.2. 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 epicnemium, not the prepectus. Also the term sternaulus is used instead of precoxal groove following Dangerfield and Austin (1995) (Fig. 4.3). The apical triangular area of the propodeum is referred to here as the nucha (Fig. 4.2). This term has not been used before in braconids, however it is adopted here from Masner and Huggert (1989), where it has been used for platygastroids and defined as the "postero-median neck-like constricted part of propodeum". The apical bridge of the first tergite of the metasoma ( T 1 ) is used here for the first time: this is the apical one-third (or less) of T 1 which is not cut by the medial longitudinal groove (Figs 6.8, 6.37). Terminology for surface sculpturing follows Eady (1968) and Harris (1979). Terminology and measurements taken for various parts of the body and wing venation are illustrated in Figures 4.1-4.10. Names for some of the new species described in Chapter 6 were derived using Brown (1954) and Reed (1988).

### 3.5 Institutional abbreviations

Abbreviations used in the text for institutions follow Arnett et al. (1986). Those not listed in this reference are indicated by an asterisk. People responsible for institutional loans are acknowledged in the acknowledgments section.

Table 3.2: Abbreviations used for terminology.

| Abbreviation | n Term | Abbreviation | Term |
| :---: | :---: | :---: | :---: |
| General terminology |  | pa | parameres <br> phragma of scutellum |
| ab ap | apical bridge of T1 | ph |  |
| ad a | aedeagus | pl | placodes |
| ada a | aedeagal apodemes | pn1 | dorsal pronotum |
| an a | antero-medial node of T2 | pn2 | lateral pronotum |
| ap a | anterior tentorial pits | pp | propodeum |
| ar p | propodeal areola | ppl | propleuron |
| as a | antennal sockets | pplf | propleural flange |
| bts fl | fluted bent-tipped | $\begin{aligned} & \mathrm{ps} \\ & \mathrm{~S} 7 \end{aligned}$ | pleural suture |
| cl cl | clypeus | S8 | sternite eight |
| cp c | carapace | sc | scutum |
| cs cos | costulae | scl1 | dorsal scutellum |
| cup | cusps | scl2 | lateral scutellum |
| di di | digitus | scl3 | lateral band of scutellum |
| ds d | dorsellum | scl4 | medial posterior band of |
| ef e | epicnemial furrow |  | scutellum |
| es e | epistomal scrobe | sp | spiracles |
| fa f | face | ss | specialised sensilla of |
| fc m | medial longitudinal carina of face | sss | ovipositor sheaths scuto-scutellar sulcus |
| fl fl | flagellomeres | st | sternulus |
| fr fr | frons | T1 | first metasomal tergite |
| gc g | gonocordo | T2 | second metasomal tergite |
| hb $\quad \mathrm{h}$ | hind basitarsus | T3 | third metasomal tergite |
| ht $\quad \mathrm{h}$ | hind tibia | tc | transverse lateral carinae |
| hx h | hind coxa |  | of propodeum |
| hy hyp | hypopygium | tm | temples |
| ihts in | inner hind tibial spur | va | volsellar apodemes |
| $\mathrm{lb} \quad \mathrm{l}$ | labrum | vo | volsellae |
| lf1 | lateral field of propodeum | Measure | nts |
| $1 \mathrm{2} 2 \quad 1$ | lateral field of T2 | AL | length of antenna |
| 1 mt la | lateral band of | CW | clypeus width |
|  | metanotum | CH | clypeus height |
| $\mathrm{lp} \quad$ la | labial palps | EH | eye height |
| lpg la | lateral pronotum groove | EW | eye width |
| It la | laterotergite | FW | facial width |
| mf1 m | median field of T2 | FH | facial height |
| mf 2 m | median field of T3 | HBL | length of hind basitarsus |
| $\mathrm{mg} \quad \mathrm{m}$ | medial longitudinal groove of T1 | $\mathrm{HL}$ HTL | head length length of hind tibia |
| mlc p | propodeal longitudinal | HW | head width |
|  | carina | HXL | length of hind coxa |
| mp m | maxillary palps | HXW | width of hind coxa |
| msp m | mesopleuron | HYL | hypopygial length |
| mt m | metanotum | IHTSL | length of inner hind |
| $\mathrm{mtm} \quad \mathrm{m}$ | metepimeron |  | tibial spur |
| $\mathrm{mtp} \quad \mathrm{m}$ | metapleuron | OHTSL | length of outer hind |
| mts m | metepisternum |  | tibial spur |
| no no | notauli | OOL | distance from outer margin |
| nu nuch | nucha |  | of lateral ocellus to edge |
| oc oce | ocelli |  | of eye |
| ohts ous | outer hind tibial spur | OSL | length of ovipositor |
| op oct | occiput |  | sheaths |
| os ovis | ovipositor sheaths | POL | distance between inner |
| ov ous | ovipositor |  | margins of lateral ocelli |


| Abbreviation | n Term | Abbreviation | Term |
| :---: | :---: | :---: | :---: |
|  |  | 3-1A | 3rd 1st Anal |
| PPW w | width of propodeum | 3-CU | 3rd Cubitus |
| SCL s | scutum length | 3-M | 3rd Medius |
| SCW s | scutum width | 3-RS | 3rd Radial Sector |
| SL s | scutellum length | 4-RS | 4th Radial Sector |
| SSL s | scuto-scutellar sulcus | art | areolet |
|  | length | $\mathrm{C}+\mathrm{SC}+\mathrm{R}$ | Costa |
| SSW s | scuto-scutellar sulcus | $\mathrm{M}+\mathrm{CU}$ | Medius+Cubitus |
|  | width | m -cu | 1 st medial-cubital cross-vein |
| STL stigh | stigmal length | pa | parastigmal |
| STW st | stigmal width | r | radial-radial sector cross- |
| SW s | scutellum width |  | vein |
| T1L le | length of first | r-m | radial-medial cross-vein |
|  | metasomal tergite T1 | st | stigma |
| T1W | width of first metasomal tergite (T1) | Hind wing | (hw) |
| T2L | length of second | 1-1A | 1st Anal |
|  | metasomal tergite (T2) | 1-M | 1st Medius |
| T2W | width of second | 1-RS | 1st Radial Sector |
|  | metasomal tergite (T2) | $1-\mathrm{SC}+\mathrm{R}$ | 1st Subcosta+Radius |
| T3L | length of third | $1 \mathrm{r}-\mathrm{m}$ | 1st radial-medial cross-vein |
|  | metasomal tergite (T3) | 2-Ma | 2nd 1st Medius |
| T3W | width of third | $2-\mathrm{Mb}$ | 2nd Medius |
|  | metasomal tergite (T3) | 2-RS | 2nd Radial Sector |
| TW | temples width | $2-\mathrm{SC}+\mathrm{R}$ | 2nd Subcosta+Radius |
|  |  | 2A | 2nd Anal |
| Wing venation |  | 2r-m | 2nd radial-medial cross-vein |
| Fore wing (fw) |  | $\mathrm{C}+\mathrm{SC}+\mathrm{R}$ | Costa+Subcosta+Radius |
| 1-1A | 1st Anal | cu-a | cubital-anal cross-vein |
| $\begin{aligned} & \text { 1-CUa, } \\ & \text { 1-CUb } \end{aligned}$ |  | $\mathrm{M}+\mathrm{CU}$ | Medius+Cubitus |
|  | 1st Cubitus divided by 1cu-a | r | radial-radial sector crossvein |
| 1-M | 1st Medius | R1 | Radius 1 |
| 1-R1 | 1st Radius 1 | va | vannal lobe |
| 1-RS | 1st Radial Sector |  |  |
| 1-RS+M | 1st Radial Sector+Medius | Wing cells |  |
| 1 a | 1st anal cross-vein | 1 | Marginal cell |
| $1 \mathrm{cu}-\mathrm{a}$ | 1st cubital-anal cross-vein | 2 | Sub-marginal cell |
| 2-1A | 2nd 1st Anal | 3 | Discal cell |
| 2-CU | 2nd Cubitus | 4 | Sub-discal cell |
| 2-cua | 2nd cubital-anal cross-vein | 5 | Costal cell |
| 2-M | Second Medius | 6 | Basal cell |
| 2-RS | 2nd Radial Sector | 7 | Sub-basal cell |
| 2-RSa | 2nd 1st Radial Sector | 8 | Plical cell |
| 2-RSb | 2nd 2nd Radial Sector |  | $\mathrm{a}, \mathrm{b}$ and c represent 1st, 2nd |
| 2-RS+M | 2nd Radial Sector+Medius |  | and 3rd cells, respectively |

### 3.6 Phylogenetic analyses

### 3.6.1 Computers and programs

The following software was used for preparing this thesis and for data analysis.
Microsoft Word 5.1a (1987-1993) was used for word processing and for creation of
tables and figures. Microsoft Excel 4.0 was used to manipulate morphometric data and create

Table 3.3: Abbreviations used for institutional collections.

| Abbreviation | Collection |
| :--- | :--- |
| AEIC | American Entomological Institute, Gainesville. |
| ANIC | Australian National Insect Collection, Canberra. |
| AMSA | Entomology Department, Australian Museum, Sydney. |
| BMNH | The Natural History Museum, London. |
| CNCI | Canadian National Collection, Ottawa. |
| HNHM | Hungarian Natural History Museum, Budapest. |
| MCZC | Museum of Comparative Zoology, Harvard University, |
|  | Cambridge, Massachusetts. |
| MVMA | Museum of Victoria, Melbourne. |
| NSWA | New South Wales Department of Agriculture, Sydney. |
| QDPI* | Queensland Department of Primary Industries, Brisbane. |
| RMNH | Rijksmuseum van Natuurlijke Historie, Leiden. |
| TDPI* | Tasmania Department of Primary Industries, Hobart. |
| UQBA | Department of Entomology, University of Queensland, |
|  | Brisbane. |
| USNM | Smithsonian Institution, Washington, D. C. |
| WAMP | Western Australian Museum, Perth. |
| WARI* | Duncan Swan Insect Collection, The University of Adelaide, |
|  | Adelaide. |

graphs for the quantitative characters (see Appendices A1 and A2). PAUP 3.1.1 (Swofford 1993) was used for all parsimony-based phylogenetic analyses, while MacClade was used to input the data matrix in spreadsheet format (see Appendix A3). This data matrix was then converted to NEXUS format when opened in PAUP 3.1.1.

Several models of Apple Macintosh computers were used during this study. They vary in the speed at which they ran PAUP and this depended on the size of their Random Assess Memory (RAM) and the processor they employ, as discussed by Dangerfield (1995). The machines used were a Power Macintosh (Power PC) $7500 / 100$ with 100 MHz speed, 16 MB RAM and 601 processor, a Power Macintosh (Power PC) 6200/75 with 75 MHz speed, 8 MB RAM and 603 processor, a Apple Macintosh LCIII, with 25 MHz speed, 8 MB RAM and 030 processor, and a Apple Macintosh LC, with 16 MHz speed, 10 MB RAM and 020 processor.

Watrous and Wheeler (1981) and Wharton et al. (1992) discuss the correct application of out-group criterion for making polarity decisions. The multiple out-group comparison format used in this study was based on the procedures of these authors, as follows:

1) Commonality of a character does not equate to it being primitive.
2) An out-group is a relatively closely related group of organisms to the in-group taxa; the most closely related out-group is the sister-group.
3) For an in-group, the character state found in the out-group is considered to be the plesiomorphic state.
4) When a character is variable within the most immediate out-group, the character state found in the more distantly related taxa was assumed to be plesiomorphic.
5) Any exceptions to the above must be supported with well-stated justifications and explicit arguments.
6) In cases of uncertain relationships among potential out-groups taxa, parsimony arguments were generally not applied.

Based on these procedures, polarity decisions for characters used in this study (see Section 5.3.2.1) were made as follows: Whitfield and Mason (1994) discussed relationships among braconid subfamilies (see Section 2.1) and showed that the Microgastrinae is the sister-group to Khoikhoiinae+Miracinae and the Cardiochilinae is the sister-group to these three subfamilies together, while the Mendesellinae is the sister-group to these four, i.e. $($ Microgastrinae $+($ Khoikhoiinae + Miracinae $))+$ Cardiochilinae.

For the analyses undertaken in this study (see Section 5.4-5.5) three taxa were chosen as out-groups, i.e. Cardiochiles fuscipennis Szépligeti and Car. eremophilasturtiae Dangerfield and Austin (Cardiochilinae) and Epsilogaster panama Whitfield and Mason (Mendesellinae).

All characters were polarised by multiple out-group comparison and, if a character state was the same for the two cardiochiline species, it was assumed to be the plesiomorphic state. However, if a character was variable between the two cardiochilines, the state found in the mendeselline was assumed to be the plesiomorphic state. A hypothetical ancestor was constructed by using the plesiomorphic states of characters determined by these three outgroup species.

### 3.6.3 Treatment of quantitative characters

Quantitative (morphometric) characters consist of continuous measurements, and such data have always posed problems in that they are difficult to divide into discrete states. However, quantitative characters can not be ignored as they can carry a substantial amount of phylogenetic information. Unfortunately, many phylogenetic studies tend to limit or leave out quantitative characters and the results obtained must therefore be considered inferior, or they are incorrectly divided into discrete states, often in an arbitrary way. Previous workers have used different methods in an attempt to objectively divide such data into discrete states (e.g. Kluge and Farris 1969; Mickevich and Johnson 1976; Simon 1983; Almeida and Bisby 1984; Thorpe 1984; Archie 1985 and Chappill, 1989). In this study, eight characters (characters 36-43; see Chapter 5) were treated as quantitative and three methods of coding, simple gap-coding (Mickevich and Johnson 1976), generalised gap-coding (Archie 1985), and segment-coding (Chappill 1989) were tested for the data obtained. The first two methods have several shortcomings in that 1) they do not reflect the proportional differences between taxa, 2) they do not have the ability to discriminate between divergent taxa equally, 3) the number of states produced are not proportional to the variability of character, and 4) the addition of new taxa reduces the possible discrimination between original taxa (Chappill 1989). In this study, the third method, segment-coding, was adopted because it does not suffer from the above problems. In addition, segment coding appears to 'massage' data the least, and the number of states produced are directly related to the amount of variability in the character (Chappill 1989).

The size of the sample used for measurements was at least five specimens and, in cases where less than five specimens were available, all specimens were measured. The procedure adopted for each character is explained here using character 36 (length of hind wing vein $\mathrm{M}+\mathrm{CU}$ to vein 1-M) as an example.

The length of $\mathrm{M}+\mathrm{CU}$ and 1-M were measured; measurements were converted into ratios and, if they were taken for more than one specimen, the ratios were averaged for a species to obtain a mean value, otherwise for a single specimen the ratio was thereafter accepted in place of a mean. Each taxon was treated in this way; a table of mean values for all taxa was then prepared (to 2 decimal places) in ascending order, and the standard deviation (SD) calculated (see Table 3.4).

| Taxon | Mean | Taxon | Mean |
| :--- | :--- | :--- | :--- |
| Neodiolcogaster whitfieldi | 0.57 | Wilkinsonellus striatus | 0.88 |
| Diolcogaster euterpus | 0.59 | Diolcogaster rixosus | 0.88 |
| Diolcogaster nixoni | 0.64 | Diolcogaster perniciosus | 0.88 |
| Buluka straeleni | 0.65 | Diolcogaster robertsi | 0.88 |
| Parenion beelaronga | 0.67 | Diolcogaster scotica | 0.89 |
| Diolcogaster alkingara | 0.67 | Diolcogaster tearae | 0.90 |
| Diolcogaster dangerfieldi | 0.68 | Neodiolcogaster tegularis | 0.90 |
| Diolcogaster merata | 0.70 | Diolcogaster iqbali | 0.90 |
| Buluka achterbergi | 0.71 | Glyptapanteles alticola | 0.91 |
| Diolcogaster periander | 0.71 | Wilkinsonellus amplus | 0.92 |
| Microplitis murrayi | 0.72 | Dolichogenidea eucalypti | 0.93 |
| Diolcogaster harrisi | 0.73 | Fornicia ceylonica | 0.93 |
| Prasmodon sp. | 0.75 | Microplitis demolitor | 0.94 |
| Miropotes chookolis | 0.76 | New genus | 0.95 |
| Diolcogaster muzaffari | 0.78 | Diolcogaster yousufi | 0.95 |
| Cotesia glomerata | 0.79 | Protomicroplitis calliptera | 0.95 |
| Cardiochiles fuscipennis | 0.80 | Protapanteles popularis | 0.96 |
| Diolcogaster newguineaensis | 0.80 | Deuterixys carbonaria | 0.98 |
| Diolcogaster reales | 0.80 | Deuterixys anica | 1.00 |
| Diolcogaster vulpinus | 0.81 | Diolcogaster brevicaudus | 1.00 |
| Diolcogaster adiastola | 0.81 | Diolcogaster dichromus | 1.00 |
| Diolcogaster sons | 0.82 | Diolcogaster duris | 1.00 |
| Diolcogaster eclectes | 0.83 | Diolcogaster fasciipennis | 1.00 |
| Diolcogaster alvearius | 0.83 | Diolcogaster naumanni | 1.00 |
| Diolcogaster lucindae | 0.83 | Diolcogaster orontes | 1.00 |
| Xenogaster insolens | 0.83 | Distatrix formosus | 1.00 |
| Diolcogaster ippis | 0.84 | Fornicia muluensis | 1.00 |
| Diolcogaster hadrommatus | 0.85 | Rasivalva stigmatica | 1.00 |
| Diolcogaster masoni | 0.85 | Glyptapanteles deliasa | 1.07 |
| Diolcogaster notopecktos | 0.86 | Microgaster kuchingensis | 1.10 |
| Diolcogaster walkerae | 0.86 | Card. eremophilasturtiae | 1.11 |
| Apanteles ippeus | 0.86 | Diolcogaster abdominalis | 1.22 |
| Diolcogaster ashmeadi | 0.87 | Epsilogaster panama | 1.43 |
| Diolcogaster coenonymphae | 0.88 | Standard Deviation | $\mathbf{0 . 1 5}$ |
|  |  |  |  |
|  |  |  |  |

The standard deviation ( 0.15 in this case) was then added to the minimum mean ( 0.57 ) in the table, and all mean values less than or equal to the resultant value (0.72) were coded into this segment (the first one being 0 ); the standard deviation was then added to the next mean value ( 0.73 ) and all the mean values less than or equal to the resultant value ( 0.87 ) were given the next code (1). This process was continued (i.e. coding means into the states $0,1,2$,

3, etc.) until the last mean value (1.43) was allotted to a segment (state 5) (Table 3.5). The data were then graphed in order to show the segments (see Appendix A2.1).

Table 3.5: Resultant values (RV) after adding the SD to the first and subsequent means, and the code (C) or state for which each species was allotted for character 36, following the procedure of segment coding for quantitative data.

| Taxa | Mean | RV | C | Taxa | Mean | RV | C |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Neodiolcogaster whitfieldi | 0.57 |  | 0 | Diolcogaster coenonymphae | 0.88 |  | 2 |
| Diolcogaster euterpus | 0.59 |  | 0 | Wilkinsonellus striatus | 0.88 |  | 2 |
| Diolcogaster nixoni | 0.64 |  | 0 | Diolcogaster rixosus | 0.88 |  | 2 |
| Buluka straeleni | 0.65 |  | 0 | Diolcogaster perniciosus | 0.88 |  | 2 |
| Parenion beelaronga | 0.67 |  | 0 | Diolcogaster robertsi | 0.88 |  | 2 |
| Diolcogaster alkingara | 0.67 |  | 0 | Diolcogaster scotica | 0.89 |  | 2 |
| Diolcogaster dangerfieldi | 0.68 |  | 0 | Diolcogaster tearae | 0.90 |  | 2 |
| Diolcogaster merata | 0.70 |  | 0 | Neodiolcogaster tegularis | 0.90 |  | 2 |
| Buluka achterbergi | 0.71 |  | 0 | Diolcogaster iqbali | 0.90 |  | 2 |
| Diolcogaster periander | 0.71 |  | 0 | Glyptapanteles alticola | 0.91 |  | 2 |
| Microplitis murrayi | 0.72 | 0.72 | 0 | Wilkinsonellus amplus | 0.92 |  | 2 |
| Diolcogaster harrisi | 0.73 |  | 1 | Dolichogenidea eucalypti | 0.93 |  | 2 |
| Prasmodon sp. | 0.75 |  | 1 | Fornicia ceylonica | 0.93 |  | 2 |
| Miropotes chookolis | 0.76 |  | 1 | Microplitis demolitor | 0.94 |  | 2 |
| Diolcogaster muzaffari | 0.78 |  | 1 | New genus | 0.95 |  | 2 |
| Cotesia glomerata | 0.79 |  | 1 | Diolcogaster yousufi | 0.95 |  | 2 |
| Cardiochiles fuscipennis | 0.80 |  | 1 | Protomicroplitis calliptera | 0.95 |  | 2 |
| Diolcogaster newguineaensis | 0.80 |  | 1 | Protapanteles popularis | 0.96 |  | 2 |
| Diolcogaster reales | 0.80 |  | 1 | Deuterixys carbonaria | 0.98 |  | 2 |
| Diolcogaster vulpinus | 0.81 |  | 1 | Deuterixys anica | 1.00 |  | 2 |
| Diolcogaster adiastola | 0.81 |  | 1 | Diolcogaster brevicaudus | 1.00 |  | 2 |
| Diolcogaster sons | 0.82 |  | 1 | Diolcogaster dichromus | 1.00 |  | 2 |
| Diolcogaster eclectes | 0.83 |  | 1 | Diolcogaster duris | 1.00 |  | 2 |
| Diolcogaster alvearius | 0.83 |  | 1 | Diolcogaster fasciipennis | 1.00 |  | 2 |
| Diolcogaster lucindae | 0.83 |  | 1 | Diolcogaster naumanni | 1.00 |  | 2 |
| Xenogaster insolens | 0.83 |  | 1 | Diolcogaster orontes | 1.00 |  | 2 |
| Diolcogaster ippis | 0.84 |  | 1 | Distatrix formosus | 1.00 |  | 2 |
| Diolcogaster hadrommatus | 0.85 |  | 1 | Fornicia muluensis | 1.00 |  | 2 |
| Diolcogaster masoni | 0.85 |  | 1 | Rasivalva stigmatica | 1.00 | 1.02 | 2 |
| Diolcogaster notopecktos | 0.86 |  | 1 | Glyptapanteles deliasa | 1.07 |  | 3 |
| Diolcogaster walkerae | 0.86 |  | 1 | Microgaster kuchingensis | 1.10 |  | 3 |
| Apanteles ippeus | 0.86 |  | 1 | Card. eremophilasturtiae | 1.11 | 1.17 | 3 |
| Diolcogaster ashmeadi | 0.87 | 0.87 | 1 | Diolcogaster abdominalis | 1.22 | 1.32 | 4 |
|  |  |  |  | Epsilogaster panama | 1.43 | 1.47 | 5 |

A balance was sought in choosing the segment size and selecting a multiple of the standard deviation that gave a reasonable number of segments across the eight quantitative characters. Too large a number of segments will drastically increase homoplasy, while the binary division of a character often does not properly represent the variability inherent in a quantitative character (Chappill 1989). An a priori decision was made that any quantitative
character should have no more than 10 segments and no less than three. Various multiples of the standard deviation were employed for each character to determine their affect on the number of segments obtained, viz. $0.5 \mathrm{xSD}, 1 \mathrm{xSD}, 2 \mathrm{xSD}$ and 3 xSD . For all characters (3643 ), 1 xSD proved to be the most suitable in that it produced 4 to 6 segments (states).

### 3.6.4 Discussion of theoretical phylogenetic methods

Klug and Farris (1969) advocate the use of parsimony criterion because it helps to generate the evolutionary pattern that is most consistent with a data set and, hence, able to detect any parallelism. Farris (1970) introduced the first methods for calculating Wagner trees and discussed its importance in regard to ease of programming and manipulation of a data set and the resultant trees and, importantly, its ability to optimise or provide the most parsimonious estimate of phylogenetic relatedness. Farris (1979) discussed the superiority of phylogenetic systematics over other approaches and these views are now widely reviewed in the general systematics literature (e.g. Wiley et al. 1991; Quicke 1993b). Critical to the phylogenetic approach of Farris (and others) is that it generates the most parsimonious solution to a data set, and this is the best estimate of relationships because 1) it has the highest information content, 2) on the basis of probability it is likely to represent the natural situation (or something close to it), and 3) it allows the robustness of the relationships among adjacent taxa to be tested. Trees are chosen on the basis of their shortest length to satisfy the parsimony criterion (i.e. trees with the minimum number of character reversals), and a single shortest tree gives the most powerful parsimonious result as there are no conflicting hypotheses. Anderberg and Tehler (1990) stressed that consensus trees are better than cladograms for interpreting classifications and, that if several equally parsimonious trees are generated from a data set (i.e. conflicting hypotheses - which is the norm for large data sets), then the strict consensus tree must always be included in the presentation of results. A strict consensus tree provides a compromise for assigning taxonomic status to clades because it takes into account all of the most parsimonious trees obtained. However, some authors have criticised the use of consensus information for erecting classifications. For example, Carpenter (1988) advocates the use of the successive reweighting method, instead of the consensus index (CI) or f-ratio, as a measure for selecting among equally most parsimonious cladograms. Alternatively, Miyamoto (1985) prefers parsimony (Wagner) procedures over
consensus procedures because they operate directly on the available information, uphold stability by corroborating evidence, resolve incongruence and ambiguity against the relative strength of support, and maximise efficiency as well as stability. Goloboff (1991) discussed the importance of the consistency index as the best statistical measure for comparing homoplasy evident in different and similar data sets. He also explained that lower values of the consistency index, retention index (RI), rescaled consistency index (RC) or a higher level of homoplasy does not mean that there is less information available for choosing among trees, because these indices do not directly vary with 'decisiveness' of a data set (i.e. the information allowing a choice or a decision between different classification). Decisiveness of a data set can be measured with another statistic which Goloboff (1991) calls "data decisiveness" (DD). The DD increases when the possible trees differ more in tree length, and it is zero when all the possible resolved trees have the same length. Page (1992) reviewed Mickevich and Platnick (1989) and pointed out that the information content of a tree can be judged with respect to the data (i.e. how well the tree describes the data) or as a topology (i.e. how many trees does the topology allow).

The controversy over how best to assess and compare multiple trees still continues. However, in this study the methods of Anderberg and Tehler (1990) are followed for presenting the results of cladistic analyses in the form of strict consensus tree(s), and using this tree to infer classification of the group in question, while the consistency index (after Goloboff 1991) is adopted as a best measure of homoplasy.

### 3.6.5 Methods of measuring information content of phylogenetic analyses

This section briefly reviews information on the indices and methods used to assess the results of phylogenetic analyses. One of the advantages of PAUP is that it can compute and display several indices that measure the 'fit' of characters to a particular tree that, in turn, can be used to interpret and/or explain the results of an analysis. The consistency index, mentioned above (Klug and Farris 1969) and the homoplasy index (HI) represent a direct measure of homoplasy in a tree. However, they are subject to variation with respect to the data set (Archie 1989). CI is the measure of how transformation series and entire data matrices fit particular tree topologies. Transformation series with little or no homoplasy will have higher CI values ( 1.0 being the highest possible), whereas those that show considerable
homoplasy will have low values (Wiley et al. 1991). 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 (Swafford and Begle 1993). HI is calculated as $1-\mathrm{CI}$, with a value of one representing maximum homoplasy. The retention index, proposed by Farris (1989) for a single character is $(g-s) /(g-$ $m$ ), where $g$ is the maximum possible amount of change that a character can acquire on any conceivable tree. He also proposed that the rescaled consistency index is the product of the CI and RI (i.e. RC = CI x RI; Swafford and Begle 1993).

PAUP can also reweight characters based on the CI, RI or RC, and this is referred to as successive reweighting. This procedure weights characters with high values for these indices moreso than those with lower values, and this process is continued until the same tree topology or character weights are found in two consecutive analyses. However, while using this method, tree lengths are not comparable.

The f-ratio, introduced as the f-value by Farris (1972), has been discussed by Brooks et al. (1986) in that it can be used to determine the best tree from those that have the same CI, as it is sensitive to the distribution of characters among taxa. The f-ratio has a value between one and zero, with the best tree having a value of zero.

As discussed above, consensus trees are used to summarise information when more than one most parsimonious tree is obtained from any data set (Anderberg and Tehler 1990). There are four types of consensus trees, i.e. strict consensus, semi-strict consensus, majority rule consensus and Adams consensus trees. The two types of consensus trees used here are strict and majority rule. The strict consensus tree contains only those monophyletic groups that are common to all competing trees, while nodes that disagree are collapsed to polytomies (inferring simultaneous divergence of multiple lineages). A majority rule tree operates on 'majority rule basis'. It shows nodes which are supported by the highest percentage of all most parsimonious trees, and they are given a percentage that indicates the proportion of trees in agreement with that node. When a large number of trees are obtained (i.e. $\geq 100$ ), an $50 \%$ majority rule will be taken as significant (e.g. when 50 or more of 100 trees agree with that node).

Rohlf's consensus index (Rohlf's CI) (Rohlf 1982) is a measure of the overall agreement of all trees included in the consensus tree. It is automatically calculated by PAUP
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

Analyses were conducted using PAUP 3.1.1 to obtain the most parsimonious solution to the data set generated in this study (Appendix A3). This computer-based phylogenetic program has many options and preliminary tests were undertaken on all of them to select those which were most appropriate. The specific features of the program are italicised here. As outlined in part in Section 5.4.1, analyses using the hypothetical ancestor as the out-group produced the shortest trees when PAUP was run on its factory default settings, compared with the other 3 out-group taxa. Also, the effect of including and excluding the quantitative characters was tested (see Section 5.4.3). Uninformative characters were retained in the final data matrix following the arguments of Yeates (1992) (see Section 5.4.4).

ACCTRAN or 'accelerated transformation' is a type of optimisation of trees that favours reversals over parallelisms when choosing among equally parsimonious trees. DELTRAN delays the transformation of a character on a tree and favours parallelisms over reversals. Delaying change will give two origins for a character, while accelerating change gives a single change followed by a reversal, and character change associated with a particular node will vary with the choice of optimisation method (Swafford and Begle 1993). This study adopted a single change of character rather than multiple changes, so that any changes were due to reversals, thus ACCTRAN was employed here.

PAUP has exact methods of search, namely 'Exhaustive' and 'Branch and Bound', as well as 'Heuristic' methods. Exhaustive search evaluates data for all possible trees. However, this method is not feasible for large data matrices because of the massive amount of calculation time required, i.e. 10 taxa create over 2 million strictly bifurcating trees (Swafford and Begle 1993). Branch-and-bound search can provide an exact solution for a larger number of taxa than exhaustive search, because the search procedure it uses has a provision for discarding trees without evaluating them, if they meet certain criteria (Wiley et al. 1991). However, this method is still a modified exhaustive search and it sometimes still
fails with large data matrices (such as in this study), again because of the large number of calculations required. The Heuristic search method in PAUP is the best method for large data sets. However, it has the disadvantage of searching for local optima in the data rather than a global optimum, and so it is never certain whether the optimum tree(s) is found, or not. Heuristic search adopts two strategies for calculations, i.e. 1) an initial tree is obtained by stepwise addition, and 2) this tree is subjected to rearrangements that attempts to find a shorter tree. This process is called branch swapping. Due to the size of the data matrix in this study ( 68 taxa by 43 characters), only the Heuristic search option could be used. The heuristic search option has four addition sequences, i.e. As is, Closest, Simple and Random, for the stepwise addition, and three branch swapping algorithms, i.e. NNI, SPR and TBR. These parameters and their effects on the data matrix in this study are discussed in detail in Section 5.4.2.

In all the analyses undertaken in this study multistate characters were interpreted as polymorphic. After investigating the effects of various PAUP parameters, the rooting options were investigated. When out-groups were defined, trees were rooted making the in-group monophyletic and, if more than one out-group taxon was defined, then these were made paraphyletic with respect to the in-group.

It was useful to let the maximum number of trees increase to maximum memory capability, otherwise a warning at 100 trees is shown in PAUP which slows down the analysis time. Also, increasing the RAM to the maximum allowable for a particular computer was necessary to save as many trees as possible for each analysis. Stepmatrix is a square matrix which is able to specify the distance from every character state to every other state, and this distance represents the 'cost' in tree length units. A stepmatrix may be used to define the models of character states that can not be expressed under any other method, i.e. 'partially unordered characters' where some states are allowed to follow a specific path while others can occur freely (Swafford and Begle 1993). This option was used here, when characters were ordered (see Section 5.3.2.4). The MULPARS and COLLAPSE options were always employed. MULPARS only saves minimal trees and COLLAPSE collapses zero length branches. Also, the successive reweighting option was used, although it did not produce conclusive results.

## Chapter 4

## Morphology of the Microgastrinae, particularly Diolcogaster Ashmead

4.1 Introduction
4.2 Adult morphology
4.2.1 Head
4.2.2 Mesosoma
4.2.3 Wings
4.2.4 Legs
4.2.5 Metasoma
4.2.6 Female genitalia
4.2.7 Male genitalia

### 4.3 General morphology of immature stages

Figures 4.1-4.10

### 4.1 Introduction

This chapter describes the general morphology of the Microgastrinae to support the selection of characters used in the phylogenetic analyses (Sections 5.3.2.2 and 5.3.2.3), and those used in the taxonomic revision of Australasian Diolcogaster (Chapter 6). The external morphology of the Microgastrinae and related subfamilies has been previously discussed by various authors, most recently by Mason (1981), Austin and Dangerfield (1992, 1993), and Dangerfield and Austin (1995), and more generally for the Braconidae by van Achterberg (1979, 1993). Abbreviations here are given in brackets (see Table 3.2), with those for specific terms in lower case (except for tergites and sternites), and those for measurements in upper case. The morphology of the adult stage is described in detail, while the morphology of larval and pupal stages is reviewed from the existing literature, as these stages are not wellknown for microgastrine genera and they have not been employed in the taxonomic revision and phylogenetic work on Diolcogaster. Further, information on male genitalia of Microgastrinae are also reviewed, and described and illustrated here for Diolcogaster. Male genitalic characters were not used in this study, partly because of their uniformity among microgastrine species and genera (Mason 1981), and because males of a significant number of Australasian Diolcogaster could not be associated. Many species are known (or identifiable) only on the female sex and, in this respect, ovipositor and related characters are important in distinguishing among species.

### 4.2 Adult morphology

### 4.2.1 Head

The head of Diolcogaster in dorsal view is similar to many microgastrines in that it is generally oval to subrectangular in shape (Figs 4.2, 6.5) with the occiput (op) (Fig. 6.24) being weakly concave. The vertex and occiput vary in sculpturing from smooth to rugulosepunctate, as does the frons (fr) (Fig. 4.2). Head width (HW) varies with respect to the head length (HL), and the ocelli (oc) form a low triangle, in that the tangent to the posterior margin of the median ocellus cuts through the anterior margin of the lateral ocelli (Figs 6.5, 6.24), or the triangle may be more equilateral, i.e. the tangent to the posterior margin of the median ocellus passes above the anterior margin of the lateral ocelli (Figs 6.6, 6.11, 6.15). The
distance between the inner margin of the lateral ocelli ( POL ) is almost always equal to the distance from the outer margin of the lateral ocellus to the edge of the eye (OOL) (Fig. 4.2).

In lateral view (Fig. 4.3), the width of the eye (EW) varies with respect to eye height (EH) and temple width (TW). In anterior view (Fig. 4.6), the antennal sockets (as) are positioned in the upper one-quarter of the head, the eyes are slightly emarginate at either side of the antennal sockets, and their pilosity varies from sparse to dense, but is never absent. The face (fa) is prominent anteriorly, often with a faint medial longitudinal carina (fc) in the dorsal half, and varies in width (FW) and height ( FH ). The maxillary palps (mp) have five segments, while the labial palps (lp) are three-segmented (Fig. 4.3). The labrum (lb) is separated from the clypeus (cl) and is either straight or concave at the apex. The clypeus varies in height (CH) and width (CW) and may be well-defined laterally or fused to the face. The anterior tentorial pits (ap) vary from being well-defined (Fig. 4.6) and deep to poorly defined and shallow.

The length of the antennae (AL) varies from longer than (Figs 4.1, 4.2) or shorter than the body (Figs 6.18, 6.19). The placodes (pl) (Fig. 5.2) are either missing on the ventrolateral surface of the medio-apical flagellomeres (fl) (Fig. 5.9) or are intact (Fig. 5.2). The arrangement of placodes on the flagellomeres varies from forming a regular double row on each flagellomere (Fig. 5.2), an overlapping double row on the basal flagellomeres, a single row on the apical flagellomeres (Fig. 5.3), to a single row on all flagellomeres (Fig. 5.4). The ventro-lateral surface of the antennae of female microgastrines bear various types of specialised sensilla, the fluted bent-tipped sensilla (bts) (Figs 5.6-5.8) being the most significant because of their possible involvement in host selection (see Section 5.3.2.2). These bts can be either absent or present and in an oblique row (Figs 5.6,5.7) or more scattered over the surface (Fig. 5.5).

### 4.2.2 Mesosoma

In dorsal view the mesosoma of microgastrines is usually moderately elongate, rounded anteriorly and square posteriorly (Fig. 4.2). The highest and most visible part of the mesosoma comprises the scutum (sc) and scutellum (scl), though the dorsal pronotum (pn1) is sometimes visible around the anterior margin of the scutum. The scutum often has the notauli (no) absent, or they can range from being faint (Fig. 5.16) to crenulate and deeply
grooved (Fig. 5.15). Sometimes a change in coloration or sculpturing indicates the position of notauli that otherwise are not indented. The surface of the scutum varies from being smooth to carinate-punctate or punctulate, and usually has a sparse covering of pilosity. The width of the scutum (SCW) varies with respect to head width. The scuto-scutellar sulcus (sss) varies in length (SSL) and width (SSW) and has a number of longitudinal carinae (Figs $4.2,6.38$ ). The dorsal scutellum (scl1) is triangular in shape, variable in length (SL) and width (SW), and is smooth or has weak to strong sculpturing. The apical margin of the scutellum sometimes has a transverse carina which separates the medial posterior band of the scutellum (scl4) from the dorsal scutellum: scl4 can be smooth (Fig. 4.2) or sculptured medially (Figs 6.1, 6.38). The lateral scutellum (scl2) is mostly crenulate (Fig. 6.38) but is sometimes smooth, and the lateral band of the scutellum (scl3) is almost always convex medially. The metanotum ( mt ) is composed medially of the dorsellum (ds), which is anteriorly excavated to form a cup-shaped structure, and is glabrous or strongly pilose medioposteriorly. The lateral band of the metanotum (lmt) is coarsely crenulate and can be withdrawn laterally so that the phragma of the scutellum (ph) is exposed (Fig. 5.10), or appressed to the posterior margin of the scutellum so that the phragma is completely hidden. The propodeum ( pp ) is always wider than long, broadest basally, and has the lateral spiracles (sp) positioned medially or slightly anterior to the lateral midline. The spiracles vary from circular to oval in shape. The sculpturing of the propodeum can be complex and vary from having a complete diamond-shaped areola (ar) (Figs 5.21 g , h) or an incomplete areola positioned either anteriorly (Fig. 5.21a) or posteriorly (Fig. 5.21i). When an areola is absent, the propodeum may be divided by a medial longitudinal carina (mlc) (Figs 4.2,5.21c) as in Diolcogaster. These structures may also occur together, i.e. anterior medial longitudinal carina and posterior areola (Fig. 5.21i), or posterior medial longitudinal carina and anterior areola (Fig. 5.21a), or the propodeum may be entirely smooth (Figs 5.14 k, l). The propodeum may have transverse lateral carinae (tc) and costulae (cs) present (Figs 5.21a, b, f-h), or only costulae (Figs $5.21 \mathrm{c}-\mathrm{e}$ ) which sometimes surround the spiracles. The sculpturing of the lateral fields of the propodeum (lf1) vary from being strongly carinate-punctate (Fig. 5.21e) to weakly punctulate (Figs $6.1,6.5,6.6$ ) or smooth (Fig. 5.21 k ). The posterior part of the medial longitudinal carina ends at a rounded or triangular carina called the nucha (nu) (Fig. 4.2).

The lateral mesosoma (Fig. 4.3) is composed of the lateral pronotum (pn2), propleuron (ppl), mesopleuron (msp) and metapleuron (mtp). The lateral pronotum has dorsal and ventral grooves present (Figs 4.3, 6.36) or only a ventral groove (lpg) (Fig. 5.13). The surface can be punctate to smooth medially with pilosity present only in the dorsal half. The ventral margin of the lateral pronotum varies from crenulate (Figs 4.3, 6.36) to smooth (Fig. 5.14). The propleuron sometimes has a weakly developed flange (pplf) (Figs 4.3, 6.39) which overlaps at least the base of the fore coxa. The mesopleuron varies from being weakly punctate antero-dorsally and ventrally but smooth posteriorly beside a carinate pleural suture (ps), to almost completely smooth throughout. The epicnemial furrow (ef) is deep and varies from being smooth to weakly carinate. The sternulus (st) is shallow and varies from being weakly punctate to smooth. The mesopleuron has an epistomal scrobe (es) dorsally. The metapleuron is composed of the metepimeron (mtm) and metepisternum (mts) and is rugose and dorsally pilose, except for a smooth glabrous antero-medial area.

### 4.2.3 Wings

Terms for wing venation are based on the modified Comstock-Needham system (see Eady 1974; van Achterberg 1979, 1993) and follow Austin and Dangerfield (1992) but with some modifications based on Wharton and Marsh (in press) (Figs 4.4, 4.5). Conventions used here for venation follow the above references: longitudinal veins are capitalised in their entirety, e.g. CU instead of Cu ; numbers indicate the major sections of the longitudinal veins, e.g. $2-\mathrm{M}$ and $\underline{3}-\mathrm{M}$ for the second and third abscissa of the median vein; when these major abscissae are intersected from the posterior side by cross-veins, such as cu-a and m-cu, lower case letters have been added to indicate the divisions of the major longitudinal abscissae, e.g. when $1 \mathrm{cu}-\mathrm{a}$ is postfurcal it divides $1-\mathrm{CU}$ into $1-\mathrm{CU} \underline{a}$ and $1-\mathrm{CU} \underline{\mathbf{b}}$; cross-veins have lower case letters, e.g. r-m; and terms for wing cells follow Austin and Dangerfield (1992) and van Achterberg (1979, 1993) (Figs 4.4, 4.5).

Fore wing (Fig. 4.4). The stigma (st) may be elongate or broad, measured as a ratio of stigmal length (STL) to stigmal width (STW). The cross-vein r arises from the middle or slightly posterior to the middle of the stigma and it may be straight (Fig. 6.20) or weakly oblique (Figs 4.4, 6.21, 6.28). The length of r is variable with respect to the width of the stigma. The second sub-marginal cell, called the areolet (art), varies from being broad and
four-sided (when 3-RS is present; Figs 6.21, 6.28), triangular (when 3-RS is absent; Fig. 6.20) smaller and triangular (when 2-RSb smaller than 2-RSa is present; Fig. 4.4), narrow and slit-like (when $2-\mathrm{RSb}$ longer than $2-\mathrm{RSa}$ is present; Fig. 6.30) to absent (Fig. 5.24). Length of vein $1-\mathrm{R} 1$ is also variable when compared to the stigmal length, or the distance from the stigma to the apical margin of 4-RS, and 1-CUa varies in length when compared to the length of $1-\mathrm{CUb}$. The first anal cross-vein 1a may be absent, and vein 1-1A straight or bent at this point, or 1a present as a spectral vein (Fig. 6.30). The fore wing of the Microgastrinae, like the Cardiochilinae and Miracinae, is notable for its reduced venation in the distal part of the wing. The intensity and pattern of infuscation of the fore wing is variable: it can be evenly infuscate and varying from light to dark; it can have dark spots on the apical margin and/or at the middle (Fig. 6.30); or it can be completely hyaline (Fig. 4.4).

The hind wing (Fig. 4.5) usually never shows any kind of infuscate pattern although sometimes it may be uniformly darkened. Veins $\mathrm{C}+\mathrm{SC}+\mathrm{R}, 1-\mathrm{SC}+\mathrm{R}, 2-\mathrm{SC}+\mathrm{R}, \mathrm{R} 1, \mathrm{M}+\mathrm{CU}, 1-$ $\mathrm{M}, 1 \mathrm{r}-\mathrm{m}, 1-1 \mathrm{~A}, \mathrm{cu}-\mathrm{a}$ and 2 A are always tubular, while veins $1-\mathrm{RS}, \mathrm{r}, 2-\mathrm{RS}, 2 \mathrm{r}-\mathrm{m}, 2-\mathrm{Ma}$ and $2-$ Mb are spectral. The vein $2 \mathrm{r}-\mathrm{m}$ can be present (Fig. 4.5) or absent (Fig. 5.23), while the first and second marginal cells ( $1 a$ and $l b$ ) vary from being the same width (Fig. 4.4) to 1a being broader than 1 b (Fig. 6.48). The angle between veins $1-1 \mathrm{~A}$ and $\mathrm{cu}-\mathrm{a}$ can differ as does the shape of the margin of the vannal lobe (va) beyond its widest part. It varies from being slightly convex to almost straight (Figs 4.4, 6.29) or weakly concave (Fig. 6.31). The pilosity along the margin of the vannal lobe also varies from the hairs being almost as long as the pilosity on the outer margin of the hind wing (Fig. 6.29), to having hairs shorter than this (Fig. 4.5), to having the margin almost glabrous (Fig. 6.31).

### 4.2.4 Legs

The legs are generally uniform across the subfamily but can vary from being slender to slightly more robust. The hind coxae (hx) are the most variable. They can be longer than the first metasomal tergite (T1) to much smaller than this. In dorso-lateral view (Fig. 6.2), the coxae are generally alveolate-punctate with sparse pilosity, but sometimes they have weak sparse punctation on the ventro-lateral surface which merges with the background micropunctation, or they can be completely smooth. The inner hind tibial spur (ihts) varies in
length from being longer than (Fig. 4.7) to almost as long as the outer hind tibial spur (ohts), but it is always shorter than the hind basitarsus (hb).

### 4.2.5 Metasoma

The metasoma of the Microgastrinae is typified by the partial fusion of the second and third tergites, and the tergites and pleurites being fused so that the pleurites are referred to as laterotergites (lt) (Fig. 4.2). In Diolcogaster the first metasomal tergite (T1) is longer than wide and varies in shape from broadening posteriorly to the apex (Figs 6.3, 6.5, 6.6), narrowing posteriorly (Figs 6.44, 6.49) to being almost parallel-sided (Figs 6.10, 6.12, 6.15). However, T 1 can also be medially constricted (Fig. 5.27) or bulging medially (Figs 4.2, 6.13). The sculpturing of T1 varies from the anterior half being smooth and glabrous and the posterior part areolate and sparsely pilose (Figs 6.3, 6.10), to being almost entirely smooth (Fig. 4.2). The medial longitudinal groove (mg) of T1 varies from being complete and ending at an apical bridge (ab) (Figs 6.8, 6.37), present only in the anterior half (Fig. 6.10), to being completely absent except for a small anterior excavation (Figs 6.44, 6.49).

The second metasomal tergite (T2) is shorter than T1, but can be shorter than (Fig. 6.6), as long as (Fig. 6.14) or much longer than the third metasomal tergite (T3) (Fig. 6.17). T2 varies from being as wide as or wider than long and broadening posteriorly (Fig. 6.14) to being almost parallel-sided (Figs 4.2, 6.12). The anterior and posterior margins of T 2 vary in that the anterior margin can be straight or slightly convex medially with a few coarse crenulae, the antero-medial node (an) slightly raised above the level of the anterior margin (Fig. 6.17), posterior margin broadly emarginate (Figs 6.4, 6.5), to the anterior and posterior margins being slightly concave to almost straight medially (Figs 6.12, 6.13). T2 sometimes has a median field (mf1) which can be bordered on either side by deep crenulate grooves (Figs 6.4, 6.9, 6.37), to present only as a raised area (Fig. 6.12). The sculpturing of the lateral fields of T2 (lf2) can vary from carinate to carinate-punctate, rugose (Figs 6.4, 6.5, 6.17) or smooth (Figs 4.2, 6.6, 6.14). The third metasomal tergite (T3) varies from being carinatepunctate, carinulate with a few scattered punctures (Figs 6.4, 6.5, 6.9, 6.23, 6.37), the anterior margin being medially convex and strongly crenulate, the posterior margin being rounded at the corners and smooth (Fig. 6.37), to the tergite being entirely smooth (Fig. 4.2). A median field on T3 (mf2) is usually absent (Fig. 4.2) but, if present, it can be diamond-shaped and
encircled by deep grooves (Fig. 6.37) or represented by a simple raised area (Fig. 6.25). T2 and T3 sometimes form a carapace (cp) covering all of the posterior metasomal segments (Fig. 5.12), or nearly so (Figs 6.5, 6.37). The suture between T 2 and T 3 varies from being absent when the tergites are fused (Figs 6.19, 6.41), sharp and well-defined (Fig. 4.2), or present in the form of a broad crenulate groove (Figs 6.4, 6.5, 6.9, 6.37). T4-T7 are virtually always smooth, and have a transverse row of sparse hairs medially or have hairs scattered sparsely over each tergite.

### 4.2.6 Female genitalia

The female genitalia (Figs $4.3,6.13$ ) are partly covered by sternite six ( S 6 ) which is referred to as the sub-genital plate or hypopygium (hy). The hypopygium varies from being medially desclerotised and expandable (Fig. 5.17) to fully sclerotised, and it can vary in length (HYL) when compared to the length of hind tibia (ht) (HTL). The ovipositor (ov) varies in length from elongate (about as long as the hind tibia) to very short and virtually hidden within the hypopygium. At rest the ovipositor is surrounded by the ovipositor sheaths (os) and the length of the latter (OSL) match that of the ovipositor. The ovipositor of microgastrines varies from being evenly tapering in the basal half and suddenly pointed and down-curved in the apical half, to evenly tapered throughout its length. The ovipositor sheaths are also variable and can be entirely pilose (Figs 5.18, 6.45), pilosity present in the apical half only (Figs $5.19,5.20$ ), to hairs being present only at the apex (Figs 6.35, 6.50). The apices of the ovipositor sheaths sometimes possess specialised sensilla (ss) (Figs 4.3, $5.19,6.27$ ), which were first recognised by Wilkinson (1929), and have been discussed and illustrated by subsequent workers (Nixon 1965; Mason 1981; Austin 1989).

### 4.2.7 Male genitalia

The genitalia of male microgastrines (Figs 4.8-4.10) are protected ventro-basally by sternite eight (S8) which forms a subgenital plate. The plate is variable in the shape of the postero-medial margin which differs from being almost straight (Fig. 4.8) to strongly concave (Fig. 4.9). Similarly, the shape of the postero-medial margin of sternite seven (S7) is also extremely variable and differs from being strongly concave (Fig. 4.9) to almost divided into two parts (Fig. 4.8). The genitalia are normally partly visible externally (Figs 4.8, 4.9) and
are rarely fully retracted within S8. The form of the male genitalia is generally rather uniform among genera and species of microgastrines although it does vary slightly among some taxa.

The internal male genitalia (Fig. 4.10) are contained within a roughly conical capsule formed from two well-sclerotised and large parameres (pa), which are surrounded basally by a sclerotised basal ring or gonocordo (gc). The parameres have long setae on the apical onethird. Projecting internally from the parameres are the volsellae (vo), which consist of a digitus (di) with stout apical spines, and a cusps (cup) which has apical nodules, and volsellar apodemes (va) which are of about the same length as the aedeagal apodemes (ada). The aedeagus (ad) is membranous and has apical nodules and two basal aedeagal apodemes, which are about as long as the aedeagus itself (Gauld and Bolton 1988).

### 4.3 General morphology of immature stages

Shaw and Huddleston (1991) state that the microgastrines generally have three larval instars, although some Microplitis apparently have four. The first instar larva is mandibulate and aggressive; it is caudate at first but soon develops an anal vesicle that persists until the third instar and which may have a respiratory function. The second instar has greatly reduced mandibles, while the final instar larva has more powerful and at least partly serrate mandibles, which help to scrap through the host integument. The open spiracles and a developed tracheal system are not present until the third instar.

The colour and shape of cocoons in microgastrines are highly variable within and between different genera. The cocoons of Microplitis are usually very tough, either strongly fluted or dark brown and parchment-like. However, during later stages cocoons are less fluted and of a lighter grey or striking green colour. The cocoons of some Diolcogaster are plain white to pinkish-brown, while those of Deuterixys are hammock-like in shape. The colour of Glyptapanteles cocoons vary from simple white to yellow, and those of Cotesia from white to various shades of yellow, pink or brown, while the shape differs from being simple to ovoid (Shaw and Huddleston 1991).

Due to the scarcity of immature stages available in collections and the fact that no Diolcogaster species were reared during the study, it was not possible to use characters from these stages in the taxonomic revision or phylogenetic analysis undertaken here.


Figs 4.1-4.2. Morphological structures and measurements (in upper case) used in taxonomic descriptions and phylogenetic analyses (see Table 3.2 for abbreviations). Diolcogaster masoni sp. nov. holotype $Q: 4.1$, antenna; 4.2 , dorsal view. Scale line $=0.7 \mathrm{~mm}$.


4.6


Figs 4.4-4.7. Morphological structures and measurements (in upper case) used in taxonomic descriptions and phylogenetic analyses (see Table 3.2 for abbreviations). 4.4, 4.5, Diolcogaster masoni sp. nov. holotype Q:4.4, fore wing; 4.5, hind wing; 4.6, Diolcogaster yousufi sp. nov. holotype $Q$, anterior view of head; 4.7, Diolcogaster perniciosus (Wilkinson) O, hind leg. Scale lines: $4.4,4.5$ and $4.7=1 \mathrm{~mm} ; 4.6=0.5 \mathrm{~mm}$.

Figs 4.8-4.10. Male genitalia of Diolcogaster spp. showing features of taxonomic importance (see Table 3.2 for abbreviations). 4.8, Diolcogaster euterpus (Nixon) $O^{7}$, external genitalia; 4.9, Diolcogaster alkingara sp. nov. $O^{\prime \prime}$, external genitalia; 4.10, Diolcogaster perniciosus (Wilkinson) $\mathrm{O}^{\prime \prime}$, genitalia drawn from a cleared, slide mounted preparation. Scale lines: $4.8=$ $200 \mu \mathrm{~m} ; 4.9=100 \mu \mathrm{~m}=4.10,250 \mu \mathrm{~m}$.


## Chapter 5

## Phylogenetics of Diolcogaster Ashmead

### 5.1 Introduction

### 5.2 Selection of taxa

5.2.1 The in-group taxa
5.2.2 The out-group taxa

### 5.3 Selection and treatment of characters

5.3.1 Selection of characters
5.3.2 Treatment of characters

### 5.3.2.1 Polarity of characters

5.3.2.2 Qualitative characters
5.3.2.3 Quantitative characters
5.3.2.4 Ordering and scoring of characters

### 5.4 Preliminary Analyses

5.4.1 Effect of out-groups
5.4.2 Swapping algorithm and addition sequence
5.4.3 Effect of inclusion and exclusion of quantitative characters
5.4.4 Effect of autapomorphies
5.5 Analyses to determine the relationships among Diolcogaster species
5.5.1 Analysis with the unpolarised data (Analysis A): comparing the strict consensus and $50 \%$ majority rule trees
5.5.2 Analysis with the polarised and ordered data (Analysis B)
5.5.3 Comparison of Analysis A and B
5.5.4 Level of homoplasy

### 5.6 Classification of Diolcogaster

5.6.1 Limitations of Analyses
5.6.2 The genus Diolcogaster

Figures 5.1-5.33

### 5.1 Introduction

This chapter examines the relationships among species of Diolcogaster and other exemplar microgastrines. It discusses the selection of taxa, characters and their states, as well as the polarity and order of these characters. A data matrix of 68 taxa and 43 characters is then used to undertake cladistic analyses with the help of the maximum parsimony-based computer program PAUP 3.1.1 (Swofford 1991). Finally these data are employed to investigate the monophyly or otherwise of Diolcogaster and to develop a preliminary classification for the group.

### 5.2 Selection of taxa

### 5.2.1 The in-group taxa

Nixon (1965) divided Protomicroplitis into 21 species-groups, 16 of which were transferred to Diolcogaster by Mason (1981) and the remaining five being accommodated in Protomicroplitis s.str. Of these 16 species groups of Diolcogaster, representatives of all of them were used in this study, along with the 28 species recognised to comprise the Australasian fauna. Several species groups were represented only by new species (recognised here - see Chapter 6), while described species were used as exemplars for non-Australasian species-groups. In addition, the type species of the genus Diolcogaster brevicaudus (Provancher) was included in the in-group, along with Choeras tegularis (Szépligeti) because it had previously been associated with Diolcogaster (Austin and Dangerfield 1992), as well as another 25 taxa from 19 other micorgastrine genera, comprising representatives of the Cotesia-complex of genera and non-cotesiine genera (Table. 5.1).

### 5.2.2 The out-group taxa

As outlined in section 2.1, the relationships for subfamilies most recently proposed by Whitfield and Mason (1994) are adopted here for the selection of out-groups, viz. Mendesellinae $+($ Cardiochilinae $+($ Microgastrinae $+($ Miracinae + Khoikhoiinae $))$. Given that the Miracinae and Khoikhoiinae are small and highly derived groups, the Cardiochilinae and Mendesellinae were used as out-groups to the microgastrines. Two species of Cardiochilinae, Cardiochiles fuscipennis Szépligeti and C. eremophilasturtiae Dangerfield and Austin were selected, the former having a medially desclerotised hypopygium and the
latter an evenly sclerotised hypopygium, along with Epsilogaster panama Whitfield and
Mason as a member of the Mendesellinae.

Table: 5.1 List of in-group and out-group taxa used in analyses (abbreviations: A=Austin; $A l=$ Allen; $D=$ Dangerfield; $M=$ Mason; $W=$ Whitfield

## Out-groups taxa

Epsilogaster panama W \& M Cardiochiles fuscipennis Szépligeti
Cardiochiles eremophilasturtiae D \& A

## In-group taxa

Apanteles ippeus Nixon
Buluka achterbergi Austin
Buluka straeleni De Saeger
Cotesia glomerata (L.)
Deuterixys carbonaria (Wesmael)
Deuterixys quericola Whitfield
Diolcogaster abdominalis (Nees)
Diolcogaster adiastola sp. nov.
Diolcogaster alkingara sp. nov.
Diolcogaster alvearius (F)
Diolcogaster ashmeadi sp. nov. Diolcogaster brevicaudus (Provancher)
Diolcogaster coenonymphae (Watanabe)
Diolcogaster dangerfieldi sp. nov.
Diolcogaster dichromus sp. nov.
Diolcogaster duris (Nixon)
Diolcogaster eclectes (Nixon)
Diolcogaster euterpus (Nixon)
Diolcogaster fasciipennis (Gahan)
Diolcogaster hadrommatus sp. nov.
Diolcogaster harrisi sp. nov.
Diolcogaster ippis (Nixon)
Diolcogaster iqbali sp. nov.
Diolcogaster lucindae sp. nov.
Diolcogaster masoni sp. nov.
Diolcogaster merata sp. nov.
Diolcogaster muzaffari sp. nov.
Diolcogaster naumanni sp. nov.
Diolcogaster newguineaensis sp. nov.

Diolcogaster nixoni sp. nov.
Diolcogaster notopecktos sp. nov.
Diolcogaster orontes (Nixon)
Diolcogaster pariander (Nixon)
Diolcogaster perniciosus (Wilkinson)
Diolcogaster reales (Nixon)
Diolcogaster rixosus (Wilkinson)
Diolcogaster robertsi sp. nov.
Diolcogaster scotica (Marshall)
Diolcogaster sons (Wilkinson)
Diolcogaster tearae (Wilkinson)
Diolcogaster vulpinus (Wilkinson)
Diolcogaster walkerae sp. nov.
Diolcogaster yousufi sp. nov.
Distatrix formosus (Marshall)
Dolichogenidea eucalypti A \& Al
Fornicia ceylonica Wilkinson
Fornicia muluensis Austin
Glyptapanteles alticola (Ashmead)
Glyptapanteles deliasa A \& D
Microgaster kuchingensis (Wilkinson)
Microplitis murrayi A \& D
Microplitis demolitor Wilkinson
Miropotes chookolis Austin
Neodiolcogaster tegularis (Szépligeti)
Neodiolcogaster whitfieldi sp. nov.
New genus (Brazil)
Parenion beelaronga A \& D
Prasmodon sp.
Protapanteles popularis (Haliday)
Protomicroplitis calliptera (Say)
Rasivalva stigmatica (Muesebeck)
Wilkinsonellus amplus A \& D
Wilkinsonellus striatus A \& D
Xenogaster insolens (Wilkinson)

### 5.3 Selection and treatment of characters

### 5.3.1 Selection of characters

Although a list of 85 characters of phylogenetic potential was initially considered, only
43 of these were eventually. The other 42 characters were found to be too variable, or difficult to assign discrete states. The inclusion of taxa other than Diolcogaster (Table 5.1) in analyses aggravated this problem. Of the 43 characters employed, 35 were qualitative characters and eight were quantitative. The quantitative characters were treated by using the
segment coding method of Chappill (1989), as discussed in Chapter 3 (see appendices A1 and A2.1-A2.8 for states of quantitative characters).

### 5.3.2 Treatment of characters

### 5.3.2.1 Polarity of characters

The out-group species from the Cardiochilinae and Mendesellinae were found not to have constant states for all the morphological characters. Therefore, a multiple out-group comparative approach was adopted to polarise characters for phylogenetic analyses. If a character varied between the two species of Cardiochiles, then it was polarised against $E$. panama. Only two characters were left unpolarised: character 22 - hind wing vein $2 \mathrm{r}-\mathrm{m}$, and character 23 - hind wing vein 2-1A (character 23). This was because these veins are absent in the out-group species and, according to Pimentel and Riggins (1987), the absence of a character cannot be coded as plesiomorphic.

### 5.3.2.2 Qualitative characters

1. Arrangement of placodes on flagellomeres. Placodes are longitudinal plate-like sensory structures present on flagellar segments and they differ among microgastrine genera in their arrangement. Mason (1981) discussed this character and polarised it as follows: placodes irregularly distributed on all flagellomeres as plesiomorphic (e.g. Protomicroplitis calliptera (Say)), then an apomorphic series from placodes regularly arranged in double-row on a few medial flagellomeres to many flagellomeres, apical flagellomeres shortened and with only one row of placodes, to all flagellomeres short and with a single row of placodes. Walker et al. (1990) in their reinterpreted character matrix for the Microgastrinae retained Mason's scheme and coded the plesiomorphic state for the Cardiochilinae, Khoikhoiinae and Miracinae, and placodes regularly arranged in double-rows as apomorphic in all microgastrine taxa. However, strictly this is not the case, as the plesiomorphic state is also present in some microgastrine genera, i.e. Protomicroplitis calliptera (Mason 1981) and Xanthapanteles (Whitfield 1995b). Given that Protomicroplitis plus Larissimus form a genus group which may be the sister-group to Diolcogaster (Walker et al. 1990), the character is clearly variable within the Microgastrinae.

Out-group comparison indicates that the polarity and order of this character used by Mason (1981) and Walker et al. (1990) should be accepted. The cardiochiline out-group species indicate that placodes irregularly distributed on all flagellomeres is the plesiomorphic state (state 3). Other states are better treated as derived and unordered as follows, given that the various states do not form a clear transition series: placodes in a double-row on basal and medial flagellomeres, and then overlapping to become a single row on apical flagellomeres (Fig. 5.3) (0); placodes regularly distributed in a double row on all flagellomeres (so that the medial constriction of flagellomeres is clear on most or all flagellomeres) (Fig. 5.2) (1); placodes present in a single row on all flagellomeres (Fig. 5.4) (2); placodes irregularly distributed on all flagellomeres (Fig. 5.1) (3).
2. Distribution of placodes on flagellomeres. Placodes are either intact on all sides of a flagellomere or missing from the ventro-lateral surface of medio-apical flagellomeres in females. Mason (1981) discussed this character separately from the presence of a patch of basiconic sensilla in the same position as follows: placodes present on all sides of flagellomere as plesiomorphic; placodes absent on the ventral surface of medio-apical flagellomeres as apomorphic. However, he combined the two characters (absence of placodes and the presence of a patch of basiconic sensilla) as a single character on his phylogenetic tree. Walker et al. (1990) followed Mason's (1981) polarity of this character and coded the medio-apical flagellomeres of females with a ventral patch of basiconic sensilla to the exclusion of the placodes as apomorphic, and the absence of such a patch (no mention was made about presence/absence of placodes) as plesiomorphic. The presence or absence of placodes from the ventro-lateral surface of flagellomeres is treated here independently of the presence/absence of any type of sensilla because, while the presence of sensilla is accompanied by the exclusion of placodes in many genera (e.g. Buluka, Fornicia, Diolcogaster basimacula-group), sometimes the sensilla occur in the presence of placodes (e.g. Parenion, Protapanteles), or the placodes are widely spaced and no sensilla are present.

The polarity and order for this character used by Mason (1981) and Walker et al. (1990) is rejected here for the previous reasons. This character is the same in all the outgroups used. Therefore, the state found in the Cardiochilinae, placodes intact on all sides of medio-apical flagellomeres, is considered to be the plesiomorphic state (state 1 ) and the other state apomorphic. The states adopted for this character are therefore: placodes missing on
ventro-lateral surface of medio-apical flagellomeres (Fig. 5.9) (0); placodes intact on all sides of medio-apical flagellomeres (Figs 5.2, 5.4) (1).
3. Fluted bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres (female only). Norton and Vinson (1974) studied the antennal sensilla of three species (Cardiochiles nigriceps Viereck, Microplitis croceipes (Cresson) and Campoletis sonorensis (Cameron)), and found the following six types to be present: (1) trichoid sensilla, the most common sensilla found in all three species; (2) fluted basiconic sensilla, found on all three species; (3) placoid sensilla, common sensilla present on all three species; (4) smooth basiconic sensilla, common in all three species; (5) curved non-fluted sensilla, unique to Cardiochiles nigriceps, but present in both sexes, and (6) fluted bent-tipped sensilla, found only on the ventro-lateral surface of flagellomeres of female Cardiochiles nigriceps. These workers suggested that these sensilla function in detecting chemicals emitted by the host, Heliothis vivescens (F.). Fluted bent-tipped sensilla are also found in some microgastrine genera (e.g. Buluka, and the some Diolcogaster ).

Walker et al. (1990) combined the presence/absence of these sensilla with the inclusion/exclusion of placodes, and stated that the absence of them is the plesiomorphic state, and their presence is apomorphic. However, this character is treated here independently, as discussed above. Fluted bent-tipped sensilla are not found in all the outgroup taxa, therefore the absence of these sensilla (state 2) is considered here to be the plesiomorphic state with all other states as apomorphic and unordered. The states for this character are: fluted bent-tipped sensilla present in scattered form on ventro-lateral surface of medio-apical flagellomeres of female (Fig. 5.5) (0); fluted bent-tipped sensilla developed and in an oblique-row on ventro-lateral surface of medio-apical flagellomeres of female (Figs 5.65.8) (1); fluted bent-tipped sensilla absent (2).
4. Presence of grooves on lateral pronotum. The lateral pronotum has one or two grooves or sometime only a depression. Mason (1981) discussed this character and described its polarity and order as follows: presence of both ventral (lower) and dorsal (upper) grooves, plesiomorphic; only the lower groove present, (no pronotal groove) or lower margin excavated, apomorphic. Walker et al. (1990) apparently ignored this character. The character is variable in the in-group and the conditions found are: a weak ventral depression which is not defined by a ventral carina (e.g. Parenion beelaronga); ventral groove, defined
by a ventral carina, narrow or sometimes so broad that its position is shifted upwards to the median area of lateral pronotum (Microplitis, Fornicia); and both ventral and dorsal grooves present (Diolcogaster sons, D. ippis, Protapanteles, Glyptapanteles). However, when the dorsal groove is present together with the ventral groove it varies from narrow and complete to broad and short, or as a depression indicating only its origin. This groove was considered to be present even if it was indicated only by a short depression.

Out-group comparison shows that the polarity and order of this character used by Mason (1981) should be rejected. All out-group taxa have an excavated area rather than grooves, and so this state is considered plesiomorphic with other states treated as derived and unordered. The following character states for this character were therefore adopted: groove missing, an excavated area or a depression present (Fig. 5.14) (0); only ventral groove present (Fig. 5.13) (1); both ventral and dorsal grooves present (Figs 4.3, 6.36) (2).
5. Sculpturing of ventral area of lateral pronotum. The sculpturing of the ventral area of the lateral pronotum is variable; it can be strong, weak, or absent. This character has not been used by previous workers. It appears to be dependent on the presence/absence of the lateral pronotal grooves, discussed above. Usually the area is smooth when the grooves are absent (Parenion); weakly sculptured when the groove(s) are weak and narrow (Glyptapanteles); and strongly crenulate when the grooves are broad (Wilkinsonellus). This character is variable in the cardiochiline out-group species, therefore a smooth pronotal groove found in the mendeselline is here considered to be plesiomorphic and a sculptured groove as apomorphic. The states adopted for this character are: ventral area of lateral pronotum smooth (Fig. 5.13)(0); ventral area of lateral pronotum crenulate to carinate (crenulation or carination strong to weak but always easily recognisable) (Figs 4.3, 6.36) (1).
6. Propleural flange. The lower outer corner of the propleuron has a projecting lobe that overlaps the lower pronotal margin (e.g. Fornicia). Mason (1981) discussed this character as follows: flange absent as plesiomorphic; flange present as apomorphic. Walker et al. (1990) did not use this character. Quicke and van Achterberg (1990) reversed the polarity used by Mason (1981) by citing van Achterberg (1988). However, this was criticised by Wharton et al. (1992) as follows: "van Achterberg (1988) stated that a propleural flange was present in Histeromerinae, Ichneutinae and Neoneurinae, while Quicke and van Achterberg (1990) coded the character in these taxa as present, polymorphic, and
polymorphic respectively, but without giving any reason of this discrepancy". Wharton et al. (1992) cited Wahl (1991) and stated that a flange is absent in most ichneumonids, but present in Anomaloninae, Cremastinae and Campopleginae. However, van Achterberg and Quicke (1992) explained that the flange mentioned by Wahl (1991) was different to 'their' propleural flange. Whitfield (1992) used this character but without assigning any polarity, because of the equivocal results of his out-group analysis.

All out-groups used here have the flange absent, thus the polarity used by Mason (1981) should be accepted. The states adopted for this character therefore are: propleuron simple and flange absent (i.e. the base of fore coax visible) (Fig. 6.26) (0); propleuron with a poorly developed flange (covering only the base of fore coax) (Figs 4.3, 6.39) (1); propleuron with a well-developed flange (extending up to lower margin of lateral pronotum) (Fig. 5.11) (2).
7. Epicnemial carina. The epicnemial carina is a ridge that more-or-less parallels the anterior margin of the mesepisternum, and it has been widely discussed in the literature (Mason 1981, 1983; Quicke and van Achterberg 1990; Walker et al. 1990; van Achterberg and Quicke 1992; Wharton et al. 1992; Whitfield 1992). The epicnemial carina is either incomplete and present only ventrally, or complete and extending laterally. However, it is considered here to be present even if only on the ventral part. Out-group comparison shows that the polarity and order of this character adopted by Mason (1981) should be rejected. The epicnemial carina is not developed in the out-group taxa, and so the absence of this carina is considered to be plesiomorphic and its development as apomorphic. The states for this character therefore are: epicnemial carina absent (Fig. 4.3) (0); epicnemial carina developed (1).
8. Presence of notauli. In many adult Hymenoptera notauli are present as a pair of posteriorly converging lines or grooves on the scutum (Gauld and Bolton 1988). Mason (1981) discussed this character as follows: complete notauli as plesiomorphic, then the reduction of notauli through different stages to their absence as apomorphic. However, this character was not included in his list of apomorphies and it has not been discussed by subsequent authors.

This character is variable within the Microgastrinae as follows: notauli well-defined and crenulate (Snellenius); well-defined and smooth (Prasmodon); grooves weak and present only in the form of an impression (Microplitis demolitor); notauli absent (Xenogaster
(Mason), Microgaster, Diolcogaster). Out-group comparison shows that the polarity adopted by Mason (1981) should be accepted. The character is variable in the cardiochiline species, therefore, the state found in the E. panama, i.e. scutum with well-defined grooved and crenulate notauli (state 0 ) is accepted as plesiomorphic with the other states being treated as apomorphic and unordered, as follows: scutum with well-defined grooved and crenulate notauli (Fig. 5.15) (0); scutum with well-defined but smooth grooves (Fig. 5.16) (1); scutum with an impression of grooves only (2); scutum without any indication of notauli (Figs 4.2, 6.5) (3).
9. Shape of scutellum. The scutellum of Philoplitis is such that it is posteriorly extended over the metanotum. This appears to be an autapomorphic character for this genus, but was coded here to determine whether it appeared in any other genus in a less obvious form. This character was included in the initial analyses, but the exclusion of Philoplitis from later analyses rendered this character constant. However, the character was not excluded from (see Section 5.4.4). Out-group comparison shows that a normal (not extended) scutellum is the plesiomorphic state and an extended scutellum is apomorphic. The states recognised therefore are: scutellum of normal shape and not extended over metanotum (Fig. 4.2) (0); scutellum extended backwards over metanotum (1).
10. Carina on posterior margin of scutellum. The sculpturing or smoothness of the scutellum is either continuous with the medial posterior band of scutellum, or it is separated by a well-defined transverse carina. This carina, when present, is variable across the Microgastrinae, e.g. weakly to well-developed (some Diolcogaster spp., Fornicia muluensis), extended posteriorly in a broad flap-like structure (Fornicia ceylonica). This is a new character which is absent in all out-group species. The states adopted for this character therefore are: posterior margin of scutellum without carina (Fig. 4.2) (0); posterior margin with weak or strongly developed carina (Figs $6.1,6.5,6.7$ ) (1); posterior margin with a broad flap-like structure (2).
11. Sculpturing of medial posterior band of scutellum. The medial posterior band of the scutellum is either entirely smooth or has some type of sculpturing, but the specific pattern is variable. The sculpturing can be punctate, carinate or rugose, and each type varies from weak to strong. Some microgastrine genera (Prasmodon, Xenogaster, Microgaster, Deuterixys) have a smooth medial posterior band, while others (Fornicia, Buluka and most Diolcogaster)
have a sculptured medial posterior band. However, this character is sometimes variable within a genus, such as among some species of Diolcogaster. This is a new character which has not been previously discussed in the literature. Out-group comparison shows that the character is variable in the cardiochilines, and so the character state found in E. panama, i.e. medial posterior band of scutellum smooth (state 0 ) is considered as plesiomorphic: medial posterior band of the scutellum smooth (Fig. 4.2) (0); medial posterior band of the scutellum interrupted by weak or strong sculpturing (Figs 6.1, 6.5, 6.38) (1).
12. Phragma of scutellum. The anterior margin of the metanotum is either straight and closely appressed to the apical margin of the posterior scutellum, or this margin is withdrawn laterally exposing the phragma of the scutellum. Mason (1981) discussed this character as follows: closely appressed scutellum to the anterior margin of the metanotum, plesiomorphic; separation of these plates and lateral exposure of the scutellar phragma and anterior margin of the metanotum with sharply projected lateral lobes bearing a tuft of hairs, apomorphic. It seems likely that Mason included two independent characters here. Walker et al. (1990) separated these characters but largely discussed the presence or absence of marginal and sub-marginal lobes on the metanotum, rather than the phragma of the scutellum. Out-group comparison shows that the polarity used by Mason (1981) should be accepted, but here the lateral lobes with hair tufts are excluded. The out-group species here have the anterior margin of the metanotum closely appressed to the scutellum and the phragma of the scutellum hidden, so this state is considered to be plesiomorphic (state 0 ). The states adopted for this character therefore are: anterior margin of metanotum closely appressed to scutellum and phragma of scutellum not exposed even in part (Figs 4.2, 6.1, 6.17, 6.38) (0); anterior margin of metanotum sloping away from scutellum and phragma of scutellum exposed at least in part (Fig. 5.10) (1).
13. Median spine on metanotum. Fornicia and some Microplitis spp., (not used in this study) have a median spine on the metanotum which is an extension of the dorsellum. This is a new character and has not been used before in the analysis of relationships among microgastrine genera. Out-group comparison shows that a metanotal spine is absent in all out-group species, and therefore the absence of this spine is considered to be plesiomorphic (state 0): metanotum medially without a spine (Figs 4.2, 6.1, 6.5, 6.6) (0); metanotum medially with a spine (Fig. 5.11) (1).
14. Shape of propodeum. This character can be divided into two distinct states, i.e. anterior part of the propodeum discretely angled with the posterior part of the propodeum, and the anterior part of the propodeum not discretely angled (flat or round) with the posterior part of the propodeum. Both cardiochiline out-groups show the anterior part of propodeum discretely angled with posterior part (state 0 ), and this is considered here to be the plesiomorphic state: anterior part of propodeum discretely angled with posterior part of propodeum (0); anterior part of propodeum not discretely angled relative to posterior part of propodeum (Figs 4.2, 6.1, 6.5, 6.6, 6.10) (1).

Propodeal carination. The carination of the propodeum is probably one of the most complex and confusing characters in microgastrine systematics. Mason (1981) discussed this character in detail and showed that there are a number of independent reductional pathways leading from the complete areolated plesiomorphic form to a smooth unsculptured propodeum, which is the most apomorphic condition. Walker et al. (1990) reinterpreted Mason's (1981) character states and divided it into two characters, describing a number of character states for each as follows: character 1 - propodeal sculpturing without distinct transverse carinae (states - anterior and posterior diagonal carinae of areola meeting apex of costula at a point, and transverse carinae distinct) character 2 - propodeal sculpturing comprising a complete diamond-shaped areola with a distinct angle between the anterior diagonal and transverse carinae (states - angle between anterior diagonal and longitudinal carinae obtuse, latter carina short; longitudinal carina continued posteriorly through the areola, anterior diagonal and transverse carinae colinear; longitudinal carina long, angle between anterior diagonal and longitudinal carinae approximately $90^{\circ}$; posterior diagonal carinae lost, areola open posteriorly; anterior diagonal carinae basally disjunct from longitudinal carina; all carinae absent). However, Walker et al. (1990) stated that their treatment of this character was a gross oversimplification. Whitfield and Mason (1994) described the fully areolate structure with transverse carinae as the plesiomorphic state and introduced a new apomorphic state, i.e. propodeum with four more or less parallel longitudinal carinae, found only in the Mendesellinae.

It seems highly likely that the carination of the propodeum should be treated as multiple characters, each with multiple states. However, the major aim of the current work is to
resolve the relationships around and within Diolcogaster, not the microgastrines as a whole. For this reason, the number of characters and states have been kept to a minimum by simplifying those that are only associated with taxa outside of the cotesiine-complex. Based on the examination of in-group and out-group taxa, propodeal carination was divided into three independent characters (characters $15,16,17$ ) as follows.
15. Medial longitudinal carina of propodeum. This character deals only with the medial longitudinal element of the propodeum. A closer examination of the in-group and outgroup taxa shows that the propodeum in many microgastrine genera has a medial longitudinal carina, but it varies from being complete to present only anteriorly or posteriorly. A medial longitudinal carina is not developed in any of the out-group species, and so this is considered to be the plesiomorphic state, with other states being treated as apomorphic and unordered. The character states adopted for this character are: medial longitudinal carina present and complete (Figs 4.2, 5.21b-f; 6.1, 6.4, 6.7) (0); medial longitudinal carina present only anteriorly (Fig. 5.21i) (1); medial longitudinal carina present only posteriorly (Fig. 5.21a) (2); medial longitudinal carina absent (Figs $5.21 \mathrm{~g}, \mathrm{~h}, \mathrm{j}-1$ ) (3).
16. Areola of propodeum. This character deals only with the areolated form of the propodeum. Examination of the in-group shows that some microgastrines have an areola which is closed anteriorly and posteriorly, but sometimes the areola is incomplete and is broadly open anteriorly (Fornicia) or absent. Out-group comparison indicates that the presence of a complete median areola is the plesiomorphic state for this character. The other states are treated as apomorphic and unordered. The character states adopted for this character are: propodeal areola present and complete (Figs $5.21 \mathrm{~g}, \mathrm{~h}, \mathrm{i}, \mathrm{j}$ ) (0); propodeal areola incomplete (broadly open anteriorly) (Fig. 5.21a) (1); propodeal areola absent (Figs 5.21b-f, k, l) (2).
17. Lateral carinae of propodeum. This character deals only with the lateral transverse elements of the propodeum, i.e. the transverse carinae and costulae. Examination of the ingroup taxa reveal the following conditions: transverse carinae joining the costulae with the medial longitudinal carina or median areola; transverse carinae missing and only costulae present which are complete; transverse carinae as well as costulae absent (the costulae are considered here absent when they are not complete e.g. Diolcogaster masoni sp. nov.). Outgroup comparison shows that a complete transverse carinae and costulae is the plesiomorphic
state with other states being treated apomorphic and unordered. The character states adopted for this character therefore are: transverse carinae as well as costulae present and complete (Figs $5.21 \mathrm{a}, \mathrm{b}, \mathrm{f}, \mathrm{g}-\mathrm{j})(\mathbf{0})$; transverse carinae missing but costulae present and complete (Figs $5.21 \mathrm{c}-\mathrm{f}$ ) (1); transverse carinae and costulae both absent (Figs $5.21 \mathrm{k}, \mathrm{l}$ ) (2).
18. Anal cross vein offore wing (1a). Mason (1981) discussed this character as follows: vein 1a (=2A in Mason 1981) in fore wing present and anal vein 1-1A (=1A in Mason 1981) bent from where the 1 a originates, plesiomorphic ; and vein 1 a absent and vein $1-1 \mathrm{~A}$ bent from where the 1a originates, and 1a absent but 1-1A not bent, as separate apomorphic states. However, he did not include this character in his phylogenetic tree, nor did Walker et al. (1990) in their analysis.

Out-group comparison shows that the polarity used by Mason (1981) should be accepted. The character states found in the cardiochiline out-groups are variable, while the mendeselline has anal cross vein 1a present in fore wing but spectral (state 0 ) which is considered as the plesiomorphic state, with other states treated as derived and unordered. The character states adopted for this character are: anal cross vein of fore wing 1a present but often spectral (Figs 6.28, 6.30) (0); anal cross vein of fore wing 1a absent but 1-1A bent (Fig. 6.47 ) (1); anal cross vein of fore wing 1 a absent, and $1-1 \mathrm{~A}$ not bent (Fig. 4.4) (2).
19. 4th Radius Sector (4-RS) of fore wing. Vein 4-RS (=3Rs in Mason 1981) of fore wing is either basally convex anteriorly, or the vein forms a continuous straight to slightly curved line. Mason (1981) discussed this character as follows: vein 4-RS sharply bent in its last abscissa and giving rise to an anteriorly directed 3 r (as in some cardiochilines), plesiomorphic; 4-RS basally convex anteriorly; 4-RS missing in the middle and the separated distal section directed so that, if prolonged, it passes far in front of the proximal section (Miracinae); and 4-RS forming a continuous straight or slightly curved line (Microgastrinae), all as separate apomorphic states. However, he did not include this character in his phylogenetic tree. Quicke and van Achterberg (1990) mentioned this character but only coded it as the vein being bent or not.

Examination here of in-group taxa show that all microgastrine species have 4-RS forming a continuous straight or slightly curved line. The Cardiochilinae and Mendesellinae have 4-RS basely convex anteriorly. Thus, the polarity used by Mason (1981) should be rejected. The state found in the cardiochilines, 4-RS basely convex anteriorly, is considered
to be plesiomorphic, and 4-RS forming a continuous straight or slightly curved line as apomorphic. The states adopted for this character therefore are: 4-RS basely convex anteriorly (Fig. 5.22) (0); 4-RS forming a continuous straight or slightly curved line (Figs 6.20-23) (1).
20. Fore wing areolet. The presence or absence of the vein $\mathrm{r}-\mathrm{m}$ in the fore wing results in the second sub-marginal cell (areolet) being open or closed. When this cell is closed the size of the areolet can differ markedly. Mason (1981) described the presence of a large quadrangular areolet as the plesiomorphic state, and identified two separate reductional pathways leading to an open areolet as the most apomorphic form. Walker et al. (1990) examined this character in detail and gave it a quantitative form by comparing the length of r m to 2 -RS (now 3-RS (Fig. 5.22). They pointed out that the character was not as simple as described by Mason and sometimes r-m disappears by retreating towards the angle formed by 2-RS and 2-M. However, this sequence was not observed in any of the species examined by them and was consequently not coded.

The character is divided here into the following conditions: areolet quadrangular and large when vein $3-\mathrm{RS}$ is present and much longer than vein $2-\mathrm{RS}$; areolet quadrangular and small when vein 3-RS is present but shorter than vein 2-RS; areolet triangular, when vein 3RS is absent and vein $r-m$ arises from the base of vein $r$; areolet triangular and small, when vein r-m is intersecting vein $2-\mathrm{RS}$ from the middle or in the apical half; areolet slit-like, when vein $r-m$ is intersecting vein $2-R S$ in the basal half; and areolet open, when vein $r-m$ is absent. The polarity used by Mason (1981) and Walker et al. (1990) was accepted here after out-group comparison. The out-group species have a large quadrangular areolet and this is considered to be the plesiomorphic state, with other states treated as apomorphic and unordered. The states adopted for this character are: areolet quadrangular and large (i.e. 3RS longer than 2-RS) (Fig. 5.22) (0); areolet quadrangular and small (i.e. 3-RS shorter than 2-RS) (Figs 6.21, 6.28) (1); areolet triangular (i.e. r-m intersecting 2-RS where r meets 2-RS) (Fig. 6.20) (2); areolet as a small triangle (i.e. r-m intersecting 2-RS from middle or in distal half) (Fig. 4.4) (3); areolet slit-like (i.e. r-m intersecting 2-RS in basal half) (Fig. 6.30) (4); areolet open (Fig. 5.10) (5).
21. Vein 2-RS of hind wing. This is a new character and the following two discrete states are evident for this character with the in-group: vein 2 -RS of hind wing approximately
straight, in line with $1-R S$ and first and second marginal cells, i.e. cell 1 a and 1 b about equal in width; vein 2-RS of hind wing concave towards anterior margin, so that cell 1 a is wider than cell lb . Out-group comparison shows that this character is variable between the two cardiochiline species, therefore the state found in E. panama, vein 2-RS straight and cells 1a and 1 b the same width, is considered to be plesiomorphic. The states adopted for this character therefore are: vein 2-RS of hind wing straight, in line with 1 -RS, cells 1 a and 1 b about same width (Fig. 4.5) (0); vein 2-RS of hind wing concave towards anterior margin and not in line with 1-RS, so that cell 1a wider than cell 1b (Fig. 6.48) (1).
22. Vein 2r-m of hind wing. Mason (1981) discussed this character and stated that the presence of vein $2 \mathrm{r}-\mathrm{m}$ is plesiomorphic and its absence is apomorphic. Walker et al. (1990) reversed this polarity decision by applying out-group criteria. Out-group comparison here shows that $2 \mathrm{r}-\mathrm{m}$ is missing and this should be the plesiomorphic state. However, the absence of a character can only be an apomorphic state, not plesiomorphic (Pimentel and Riggins 1987), therefore this character was left unpolarised and was coded 'missing (?)' in the hypothetical ancestor. The states for this character are: hind wing vein $2 \mathrm{r}-\mathrm{m}$ absent (Fig. 5.23 ) (0); hind wing vein $2 \mathrm{r}-\mathrm{m}$ present (Fig. 4.5) (1).
23. Vein 2-1A of hind wing. Mason (1981) discussed this character as follows: the presence of a sclerotised vein, plesiomorphic; vein reduced to a stump or completely absent as apomorphic. However, he did not use this character in his phylogenetic tree. Out-group comparison here shows that the polarity discussed by Mason (1981) should be rejected. All three out-group species lack this vein, so the absence of this vein should be considered to be plesiomorphic. However, as for character 22, the absence of a character can only be treated as apomorphic, not plesiomorphic (Pimentel and Riggins 1987), therefore it was left unpolarised and was coded 'missing (?)' in hypothetical ancestor. The states adopted for this character are: 2-1A vein of hind wing absent (Figs 5.23, 5.25, 6.29, 6.31) (0); 2-1A vein of hind wing present in form of a stump (Fig. 4.5) (1).
24. Vein cu-a of hind wing. Mason (1981) discussed this character and stated that a sinuate vein is the plesiomorphic state, while a straight or slightly curved vein represented increasing stages of apomorphy. The plesiomorphic state described by Mason apparently occur only in Fornicia, while all other in-group taxa have the vein straight, oblique, or convex posteriorly. Out-group comparison shows that the polarity used by Mason (1981)
should be rejected. The two cardiochiline species differ in this character so, the state found in E. panama, i.e. vein cu-a roundly convex posteriorly, is considered to be plesiomorphic, with other states treated as apomorphic and unordered as follows: vein cu-a of hind wing straight, meeting vein 1 A at almost a right angle (Fig. 6.31)(0); vein cu-a of hind wing oblique, meeting vein 1 A at a very wide angle (Fig. 6.29) (1); vein cu-a roundly convex posteriorly (Fig. 5.25) (2); vein cu-a of hind wing sinuate (Fig. 5.26) (3).
25. Shape of hind wing vannal lobe margin. Mason (1981) discussed this character together with the pilosity of the margin of the hind wing vannal lobe. But the two characters can be logically separated into the shape of the margin of the vannal lobe, and the pilosity of its margin (see character 26). It is difficult to distinguish sometimes between a weakly convex and almost straight vannal lobe, therefore only two states are recognised here, i.e. vein weakly convex to straight, and vein concave. Out-group comparison shows that the polarity used by Mason (1981) should be accepted. All the out-group taxa have the hind wing vannal lobe margin beyond its widest part convex to almost straight, so this is considered to be the plesiomorphic state. The states adopted for this character are: hind wing vannal lobe margin beyond its widest part weakly convex to almost straight (Figs 4.5, 6.29, 6.48) (0); hind wing vannal lobe margin beyond its widest part concave (Fig. 6.31) (1).
26. Pilosity of hind wing vannal lobe margin. The pilosity of the hind wing vannal lobe margin beyond its widest part differs in that the hairs can be long and dense, to small and sparse, or absent. The hairs are here considered long when they are almost equal to or longer than the length of the hairs on the posterior margin of the hind wing, and shorter when they are conspicuously shorter than the latter. Out-group comparison shows that the polarity used by Mason (1981) should be accepted. The out-group species have long hairs on the margin of the hind wing vannal lobe, and so this is considered the plesiomorphic state, with other states being treated as apomorphic and unordered. The states adopted for this character are: hairs on margin of hind wing vannal lobe beyond its widest part long and thick (Figs 6.29, 6.48) (0); hairs on margin of hind wing vannal lobe beyond its widest part short and sparse (Fig. 4.5) (1); margin of hind wing vannal lobe beyond its widest part glabrous (Fig. 6.31) (2).
27. Shape of first metasomal tergite (T1). In this study the shape and size of the first metasomal tergite are treated as two independent characters with the former being treated qualitatively and the latter quantitatively, i.e. character 43 (maximum length of the tergite was
compared to its maximum width). The shape of T1 can be broad or narrow posteriorly, parallel-sided, constricted or bulging medially. Mason (1981) discussed this character together with the presence of a medial longitudinal groove on T 1 , but he did not include it in his analysis. Here the shape of T1 is treated separately from the medial longitudinal groove (character 28) as follows: T1 regularly widening apically with the widest point on the apical margin; T1 constricted medially; T1 regularly narrowing apically with the narrowest point across the apex; T 1 almost parallel-sided throughout its length, sometime slightly rounded and narrow on apical one-third; T1 bulging medially with narrow basal and apical margins. Out-group comparison shows that T1 being broadest at the posterior margin in both cardiochilines is plesiomorphic, while other states are treated apomorphic and unordered. The states adopted for this character therefore are: T1 regularly widening apically with the widest point on apical margin (Figs 6.3, 6.5, 6.6, 6.8, 6.14, 6.17) (0); T1 long, slightly widened at base, narrowed medially and then widened in apical one-third (Fig. 5.27) (1); T1 regularly narrowing with the narrowest point on apical margin (Figs 6.44, 6.49) (2); T1 parallel-sided almost in its entire length (Figs 6.10, 6.12, 6.15) (3); T1 narrow at base, widened medially and then narrow apically (Figs 4.2,6.13) (4).
28. Medial groove of T1. The first metasomal tergite has a medial longitudinal groove which can be deep and present along its entire length, present in the anterior half only, or absent and the anterior part of the tergite broadly depressed (e.g. Neodiolcogaster tegularis). Mason (1981) discussed the presence of a medial longitudinal groove on T1 in different forms and positions as apomorphic and its absence as plesiomorphic. Later, Mason (1983) described the presence of a medial groove as the apomorphic state but did not divide the character further. Walker et al. (1990), following Mason (1981), used the absence of a groove on T 1 as the plesiomorphic state. In this study, a groove was coded as complete when an 'apical bridge' (see Section 4.2.5) was present and the groove extended posteriorly beyond the middle of the tergite.

Out-group comparison shows that the polarity used by Mason (1981) should be accepted. All out-group taxa lack a groove on T1, and so this is considered as the plesiomorphic state with other states treated as apomorphic and unordered, as follows: T1 without a medial longitudinal groove, but with a basal depression or excavated area (Figs $6.44,6.49)(0)$; T 1 with a complete medial longitudinal groove, i.e. groove present on more
than half of tergite (Figs 4.2, 6.3, 6.37) (1); T1 with medial longitudinal groove present in anterior half only (Fig. 6.10) (2).
29. Suture between $T 2$ and T3. The suture between the second and third metasomal tergites varies among microgastrines as follows: suture distinct and tergites clearly differentiated from each other; suture indistinct and tergites not distinguishable from each other; the two tergites fused but a deep and strongly crenulate groove present. Mason (1981) discussed this character and defined the presence of a fine transverse suture as the plesiomorphic state, while increasing stages of the apomorphy were suture being stronger and deeper; or weak, incomplete, or absent. Walker et al. (1990) apparently ignored this character. Out-group comparison shows that the polarity used by Mason (1981) should be accepted. Both cardiochiline species have a distinct suture between T 2 and T 3 , and this state is therefore considered to be plesiomorphic, with other states being treated as apomorphic and unordered as follows: suture between T 2 and T 3 distinct, the two tergites easily distinguishable (Figs $4.2,6.6,6.12,6.14$ )(0); suture between T 2 and T 3 indistinct, the two tergites indistinguishable (Figs 6.19, 6.41) (1); T2 and T3 fused, but divided by a deep sculptured groove (Figs 6.4, 6.5, 6.9, 6.25, 6.37) (2).
30. Median field of T2. Mason (1981) discussed this character together with the sculpturing of the tergite. He defined a slightly raised median area widening posteriorly as plesiomorphic, and the following states as apomorphic - median area marked by grooves; median area triangular, rectangular, or as an inverted triangle; median area widening to form a pentagonal or rectangular shape. Walker et al. (1990) apparently ignored this character.

The median field of T 2 is treated here independent of the sculpturing of the tergite. Out-group comparison shows that a median field on T2 is not developed in the two cardiochiline species, and this is considered to be plesiomorphic (state 3), with other states treated apomorphic and unordered. The states adopted for this character are: median field of T2 defined by strongly crenulate grooves (Figs 6.4, 6.5, 6.9, 6.25, 6.37) (0); median field of T 2 present as only a raised area (Figs $6.6,6.12$ ) (1); median field of T 2 defined by smooth to weakly carinate grooves (Figs 6.14, 6.34, 6.44) (2); median field of T2 not developed (Figs $4.2,6.13,6.19)(3)$.
31. Median field of T3. This is a new character which closely parallels character 30. The median field of T3 varies from being defined by strong crenulate lateral grooves, as a
weak raised area, to not developed. Out-group comparison shows that a median field on T3 is absent in all out-group species and this is considered to be the plesiomorphic state (state 2), with other states being treated as apomorphic and unordered. The states adopted for this character are: median field of T3 defined by strongly crenulate grooves (Fig. 6.37) (0); median field of T3 present only as a raised area (Figs 6.4, 6.9) (1); median field of T3 not developed (Figs 4.2, 6.6, 6.8, 6.12-6.14) (2).
32. Carapace. When the second and third metasomal tergites are fused together to form a 'shell-like' structure, this is called carapace. It occurs in different forms in the Microgastrinae and some other braconids (van Achterberg 1984). This character varies from T2-T3 being fused to form a carapace which covers all of the remaining metasomal tergites (e.g. Buluka, Fornicia); T2-T3 fused to form a carapace covering most of the metasomal tergites but with some posterior tergites visible (e.g. Deuterixys, Diolcogaster basimaculagroup); to T2-T3 not being fused (as in most microgastrine genera). Mason (1981) discussed this character and treated it simply as a binary character, i.e. carapace present or absent, and not recognise an intermediate state. None of the out-group species have a carapace, and so this is considered to be plesiomorphic, with other states being treated as apomorphic and unordered. The states adopted for this character therefore are: T2-T3 never fused and not forming a carapace (Figs 4.2, 6.6, 6.12-6.15) (0); T2-T3 fused to form a partial carapace, leaving T4-T6 visible posteriorly (Figs 6.5, 6.37) (1); T2-T3 fused to form a complete carapace covering the posterior tergites (Fig. 5.12) (2).
33. Sclerotisation of hypopygium. The variability in sclerotisation of the hypopygium is considerable among braconid subfamilies. It can be completely sclerotised and nonexpandable; medially desclerotised and expandable; or medially desclerotised with an apical sclerotised bridge (Austin 1990; Dangerfield and Austin 1995). Mason (1981) discussed this character together with the length of the hypopygium. However, these are independent characters and better treated separately (see character 41). A uniformly desclerotised (membranous) hypopygium was proposed by Mason to be the plesiomorphic state, while a medio-basally weakly sclerotised to completely sclerotised hypopygium were treated as increasing stages of apomorphy. Austin (1990) reversed Mason's polarity, based on outgroup comparison and his treatment was followed by Walker et al. (1990).

Out-group comparison here indicates that the polarity proposed by Austin (1990) should be accepted. The character states are variable between the two cardiochilines and so the uniformly sclerotised non-expandable hypopygium of E. panama is considered to be plesiomorphic. Because members of the Cotesia-complex, including Diolcogaster, only possess the plesiomorphic state, this is treated as a binary character as follows: hypopygium evenly sclerotised and inflexible (Figs 4.3, 6.16, 6.35) (0); hypopygium with ventro-medial part membranous, folded and expandable (Fig. 5.17) (1).
34. Pilosity of ovipositor sheaths. The ovipositor sheaths can be entirely pilose, have the pilosity concentrated in the apical half, or have reduced pilosity with hairs concentrated only at the apex. Mason (1981) discussed this character and proposed that uniformly hairy ovipositor sheaths is the plesiomorphic state, and that hairs present only apically to almost absent, are increasing stages of apomorphy. Austin (1990) surveyed this character across a range of braconid subfamilies and microgastrine genera, but eventually left the character unpolarised. After out-group comparison, the polarity used by Mason (1981) is accepted here. The two cardiochiline out-groups have the ovipositor sheaths uniformly hairy along their length and this is considered to be the plesiomorphic state, with other states treated as apomorphic and unordered, as follows: ovipositor sheaths uniformly hairy along their length (Figs $5.18,6.45$ )(0); ovipositor sheaths with hairs present in apical half only (Figs 6.35, 6.50 )(1); ovipositor sheaths with hairs present at the apex only (Figs 6.35, 6.50) (2).
35. Specialised sensilla on ovipositor sheaths. The ovipositor sheaths sometimes posses specialised sensilla. Mason (1981) discussed this character and stated that the absence of "obconical sensilla" is the plesiomorphic state, while their presence is apomorphic. Austin ( 1989,1990 ) reported the development of flattened sensilla on the tip of the ovipositor sheaths in Buluka and Diolcogaster, while Walker et al. (1990) apparently omitted this character from their analysis. The polarity proposed by Mason (1981) is accepted here after out-group comparison. All the out-groups lack such specialised sensilla and this is adopted as the plesiomorphic state. The states adopted for this character therefore are: specialised sensilla on ovipositor sheaths absent (Fig. 5.20) (0); specialised sensilla on ovipositor sheaths present (Figs 5.19, 6.27) (1).
36. Length of $M+C U$ vs length of $1-M$ of hind wing. The length of the vein $\mathrm{M}+\mathrm{CU}$ in hind wing varies with respect to the length of 1-M (Fig. 4.5). The states found in the two outgroup species are different, therefore that in the E. panama, i.e. hind wing vein M+CU 1.331.47 x as long as vein $1-\mathrm{M}$ (state 5), is considered to be plesiomorphic, with other states being treated as apomorphic and unordered. Whitfield (1992) discussed this character and used it qualitatively. The character is treated here quantitatively and the codes assigned to different character states are: hind wing vein $\mathrm{M}+\mathrm{CU} 0.57-0.72 \mathrm{x}$ as long as vein $1-\mathrm{M}(0)$; hind wing vein $\mathrm{M}+\mathrm{CU} 0.73-0.87 \mathrm{x}$ as long as vein $1-\mathrm{M}(1)$; hind wing vein $\mathrm{M}+\mathrm{CU} 0.88-1.02 \mathrm{x}$ as long as vein 1-M (2); hind wing vein $\mathrm{M}+\mathrm{CU} 1.03-1.17 \mathrm{x}$ as long as vein $1-\mathrm{M}(3)$; hind wing vein $\mathrm{M}+\mathrm{CU} 1.18-1.32 \mathrm{x}$ as long as vein $1-\mathrm{M}(4)$; hind wing vein $\mathrm{M}+\mathrm{CU} 1.33-1.47 \mathrm{x}$ as long as vein 1-M (5).
37. Length of plical cell (vannal lobe) vs length of sub-basal cell of hind wing. The length of the plical cell (vannal lobe) varies with respect to the length of the sub-basal cell of the hind wing (Fig. 4.5). Mason (1981) discussed this character and compared the length of the vannal lobe with the length of the submediellan cell. He described its polarity and order as follows: vannal lobe longer than submediellan cell, plesiomorphic; vannal lobe shorter than submediellan cell, apomorphic. The polarity used by Mason (1981) is rejected here after out-group comparison and application of segment coding. The two cardiochiline species fall into the same segment, i.e. hind wing plical cell 1.37-1.64 x as long as sub-basal cell (state 2 ), and this is considered to be plesiomorphic, with other states treated as apomorphic and unordered as follows: hind wing plical cell $0.8-1.08 \mathrm{x}$ as long as sub-basal cell (0); hind wing plical cell 1.09-1.36 x as long as sub-basal cell (1); hind wing plical cell 1.37-1.64 x as long as sub-basal cell (2); hind wing plical cell 1.65-1.92 x as long as sub-basal cell (3); hind wing plical cell 1.93-2.20 x as long as sub-basal cell (4); hind wing plical cell 2.21-2.48 x as long as sub-basal cell (5).
38. Size of hind coxa. The length of the hind coxa varies from small to very large when compared with the length of T1 (Fig. 4.7). Mason (1981) combined this character with the sculpturing of the hind coxa, but the latter is a separate character, is highly variable and more useful at species level. He described the polarity and order of this character as follows: moderately short coxa, plesiomorphic; larger coxa, apomorphic. Walker et al. (1990) listed
only two states for this character; coxa normal (plesiomorphic) or strongly enlarged (apomorphic). Quicke and van Achterberg (1990) described a medium-sized coxa as plesiomorphic and longer coxa as apomorphic. However, these descriptions are all very subjective and confusing, and the variation in this character can only be assessed if treated quantitatively. After out-group comparison the polarity assigned by Mason (1981) and subsequent workers is accepted but divided into five states after segment coding. The two cardiochiline species fall into different segment and therefore the state found in E. panama, i.e. hind coxa $0.86-1.22 \mathrm{x}$ as long as T 1 (state 0 ), is considered here to be plesiomorphic, with other states treated as apomorphic and unordered as follows: hind coxa $0.86-1.22 \mathrm{x}$ as long as $\mathrm{T} 1(\mathbf{0})$; hind coxa 1.23-1.58 x as long as T 1 (1); hind coxa 1.59-1.94 x as long as T 1 (2); hind coxa 1.95-2.30 x as long as T1 (3); hind coxa 2.31-2.66 x as long as T1 (4); hind coxa 2.67-3.02 x as long as T1 (5).
39. Length of hind tibial spurs. The length of the hind tibial spurs is variable with respect to each other (Fig. 4.7). This is a new character used here for the first time. The two cardiochiline species fall into different segments and therefore the state found in E. panama, i.e. inner hind tibial spur $1.00-1.25 \mathrm{x}$ as long as outer hind tibial spur (state 0 ), is considered here to be plesiomorphic, with other states treated as apomorphic and unordered as follows: inner hind tibial spur 1.00-1.25 x as long as outer hind tibial spur (0); inner hind tibial spur $1.26-1.50 \mathrm{x}$ as long as outer hind tibial spur (1); inner hind tibial spur $1.51-1.75 \mathrm{x}$ as long as outer hind tibial spur (2); inner hind tibial spur 1.76-2.00 x as long as outer hind tibial spur (3).
40. Length of inner hind tibial spur vs length of hind basitarsus. The length of the inner hind tibial spur varies with respect to the length of the hind basitarsus (Fig. 4.7). This is a new character. The two cardiochiline species fall into different segments and so the state found in E. panama, i.e. inner hind tibial spur 0.43-0.58 x as long as hind basitarsus (state 1), is considered here to be plesiomorphic, with other states being treated as apomorphic and unordered as follows: inner hind tibial spur $0.26-0.42 \mathrm{x}$ as long as hind basitarsus ( $\mathbf{0}$ ); inner hind tibial spur 0.43-0.58 x as long as hind basitarsus (1); inner hind tibial spur 0.59-0.74 x as long as hind basitarsus (2); inner hind tibial spur 0.75-0.90 x as long as hind basitarsus (3); inner hind tibial spur 0.91-1.06 x as long as hind basitarsus (4).
41. Length of hypopygium. The length of the hypopygium varies compared to the length of the hind tibia (Fig. 4.3). This character has been discussed by various authors (e.g. Mason 1981; Austin 1990) and generally a longer hypopygium has been considered to be plesiomorphic, and a shorter hypopygium apomorphic. Mason (1981) combined this character with the sclerotisation of the hypopygium, but these characters are treated separately in this study. The size of hypopygium is best examined quantitatively with the medio-ventral length of the hypopygium being measured and compared to the length of hind tibia. The two cardiochiline species fall into the same segment, i.e. medio-ventral hypopygium $0.48-0.61 \mathrm{x}$ as long as hind tibia (state 2 ), and so this is considered to be plesiomorphic, with other states treated as apomorphic and unordered as follows: medioventral hypopygium $0.19-0.33 \mathrm{x}$ as long as hind tibia ( 0 ); medio-ventral hypopygium 0.340.47 x as long as hind tibia (1); medio-ventral hypopygium $0.48-0.61 \mathrm{x}$ as long as hind tibia (2); medio-ventral hypopygium $0.62-0.75 \mathrm{x}$ as long as hind tibia (3); medio-ventral hypopygium $0.76-0.89 \mathrm{x}$ as long as hind tibia (4).
42. Length of ovipositor sheaths. The length of the ovipositor sheaths (Fig. 4.3) closely parallels the length of the ovipositor and, given that the ovipositor is often hidden within the sheaths, only the latter character is considered here. Mason (1981) discussed this character as part of the "Macrolepidoptera suite" of characters and described long ovipositor sheaths as plesiomorphic, and short ovipositor sheaths as apomorphic. He compared the length of the sheaths to the length of the metasoma. Walker et al. (1990) followed Mason's polarity for this character without modification. The length of sheaths may be compared more accurately to the length of the hind tibia as metasomal length may vary because of the compression of metasomal segments particularly when specimens are drying. In this study the character is treated quantitatively and the length of the ovipositor sheaths was measured against the length of the hind tibia. The polarity adopted by Mason (1981) and Walker et al. (1990) is rejected here after out-group comparison. Both cardiochiline have the ovipositor sheaths $0.63-0.81 \mathrm{x}$ as long as hind tibia (state 3), and this is considered to be plesiomorphic, with other states treated as apomorphic and unordered as follows: ovipositor sheaths $0.05-0.24 \mathrm{x}$ as long as hind tibia (0); ovipositor sheaths $0.25-0.43 \mathrm{x}$ as long as hind tibia (1); ovipositor sheaths $0.44-0.62 \mathrm{x}$ as long as hind tibia (2); ovipositor sheaths $0.63-0.81 \mathrm{x}$ as long as hind tibia (3); ovipositor sheaths $0.82-1.00 \mathrm{x}$ as long as hind tibia (4).
43. Size of $T 1$ (Maximum length of $T 1$ vs maximum width of $T 1$ ). The shape and size of T1 varies considerably among microgastrine genera. While the shape of this tergite can be treated qualitatively (character 27), its size (Fig. 4.2) may be best treated quantitatively. This is a new character and is assessed by comparing the maximum length of T1 against the maximum width of the tergite. Out-group comparison shows that the two cardiochiline species fall into the same segment, i.e. T1 0.62-1.48 x as long as maximum width (state 0 ), and so this is considered here to be plesiomorphic, with other states treated as apomorphic and unordered as follows: T1 0.62-1.48 x as long as maximum width (0); T1 1.49-2.34 x as long as maximum width (1); T1 2.35-3.20 x as long as maximum width (2); T1 3.21-4.06 x as long as maximum width (3); T1 4.07-4.92 x as long as maximum width (4); T1 4.93-5.78 x as long as maximum width (5).

### 5.3.2.4 Ordering and scoring of characters

Where possible characters were ordered as linear transformations or as step matrices. A stepmatrix is a square matrix specifying the distance from every character state to every other state, where this distance represents the 'cost' in tree length units of the corresponding transformations. Characters 4, 6, 34 and 36-43 were ordered by linear transformation between states, which restricted the path of these states, while stepmatrices were defined for characters $8,10,18,20,26,27,30,31$ and 32 (Table 5.2)

Characters were coded for the 67 species listed in Table 5.1 and a data matrix was prepared (Appendix A3). Ancestral states were determined by the method discussed above (Section 5.3.2.1) (Table 5.2), and a hypothetical ancestor was created from the three outgroup species using the plesiomorphic states for each character. A detailed account of the out-group format is given in Chapter 3.

Table: 5.2 Summary of the polarity (ancestral states), ordering and transformations adopted for characters used in phylogenetic analyses (l=linear transformations; o=ordered; $s=$ stepmatrices; $u=$ unordered.

|  | 1 |  |  |  |  | 2 | 3 | 4 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Character | 1234567890123456789012345678901234567890123 |  |  |  |  |  |  |  |

### 5.4 Preliminary Analyses

The data matrix was used to conduct a number of analyses using the options available in PAUP 3.1.1. These analyses were undertaken to determine which out-group (if any) generated a shorter trees(s), the effect of the swapping algorithms and addition sequence, the effect of inclusion and exclusion of quantitative characters, and the effect of inclusion or exclusion of autapomorphies.

### 5.4.1 Effect of out-groups

A series of analyses were conducted with the data set unpolarised to determine which, if any, of the three out-group species or hypothetical ancestor yielded a shorter tree(s) and which had the highest consistency index. Tree length is the number of evolutionary transformations needed to explain the data, given a particular tree topology, while consistency index shows how the data matrix fits a particular tree topology and it is inversely proportional to homoplasy, i.e. the higher is homoplasy the lower is the consistency index. A summary of the results for these analyses is given in Table 5.3.

Table: 5.3 Summary of analyses using unpolarised data to compare different out-groups and combinations of out-groups, showing number of most parsimonious trees generated ( $T$ ), length of shortest trees (TL) and the consistency index (CI).

| Out-group | T | TL | CI |
| :--- | ---: | ---: | :---: |
| E. panama+ C. eremophilasturtiae+ C. fuscipennis | 563 | 467 | 0.212 |
| E. panama+ C. fuscipennis | 9600 | 460 | 0.215 |
| E. panama + C. eremophilasturtiae | 53 | 460 | 0.215 |
| C. eremophilasturtiae+ C. fuscipennis | 161 | 461 | 0.213 |
| E. panama |  |  |  |
| C. eremophilasturtiae | 311 | 450 | 0.216 |
| C. fuscipennis | 176 | 450 | 0.216 |
| Hypothetical ancestor | 4523 | 450 | 0.218 |

They show that of the four possible single out-groups, the hypothetical ancestor yields the shortest trees which are one step shorter (449) than the other three out-groups (450). The hypothetical ancestor also yields the highest consistency index ( 0.220 ). When the cardiochiline and mendeselline species were used as out-groups in pairs, E. panama $+C$. fuscipennis and E. panama + C. eremophilasturtiae, gave equally shortest trees with the same
consistency index. The hypothetical ancestor was obviously not used in tandem with any of the other three species as its coding has been generated from these three out-groups.

From these results the hypothetical ancestor was selected as the most suitable out-group taxon to be used in further analyses.

### 5.4.2 Swapping algorithm and addition sequence

PAUP 3.1.1 uses three branch-swapping algorithms, NNI, SPR and TBR (Swofford and Begle, 1993). In NNI, 'nearest neighbour interchange', each internal branch of the tree defines a local region of four subtrees connected by the internal branch. Interchanging a subtree on one side of the branch with one from the other constitutes an NNI. Two such rearrangements are possible for each internal branch. In SPR, 'subtree pruning and regrafting', a subtree is pruned from the tree and is then regrafted to a different location on the tree. All possible subtree removals and reattachment points are evaluated. In TBR 'treebisection and reconnection', the tree is bisected along a branch yielding two disjointed subtrees. The subtrees are then reconnected by joining a pair of branches, one from each subtree. All possible bisections and pairwise reconnections are evaluated. None of these three methods is perfect but use of TBR was found to be more efficient than the other two. Therefore this branch-swapping algorithm was used in further analyses.

PAUP 3.1.1 also uses stepwise addition to connect taxa in that the first three taxa are chosen for the initial tree and then one taxon is connected at a time to the developing tree, until all taxa have been placed. To determine which three taxa will be joined initially and which one of the unplaced taxa will be connected to the tree at each step, PAUP uses four addition sequences. These sequences are 1) simple, where the addition sequence is determined prior to beginning the stepwise addition process. First, the distance between each taxon and a reference taxon is calculated. The taxa are then added in order of increasing advancement, i.e. the reference taxon and the two taxa closest to it form the initial three-taxon tree, and the remaining taxa are added in the order given by their rank in the array of advancement indices. 2) asis, where taxa are simply added in the same order in which they are presented in the data matrix, starting with the first three and sequentially adding the rest. 3) closest, where initially the lengths of all possible three-taxon trees, formed by joining a triplet of terminal taxa to a single internal node, are evaluated. The three taxa yielding the
shortest tree compose the starting tree. At each successive step, all remaining unplaced taxa are considered for connection to every branch of the tree, and the taxon-branch combination that requires the smallest increase in tree length is chosen. 4) random, where a pseudorandom number generator is used to obtain a permutation of the taxa to be used as the addition sequence.

Three of these four addition sequence options were tested with the branch-swapping algorithm TBR. The random option could not be tested because of the enormous time it takes to analyse large data sets using this option. The results from these analyses are compared in Table 5.4 and, again, the criteria used to select the best option was that which generated the shortest tree(s) and had the highest consistency index.

Table: 5.4 Summary of analyses with the hypothetical ancestor nominated as the out-group, comparing different options of addition sequence and showing the number of most parsimonious trees generated (T), length of shortest trees (TL) and the consistency index (CI).

| Options | T | TL | CI |
| :--- | ---: | :---: | :---: |
| TBR-asis | 3327 | 450 | 0.220 |
| TBR-closest | 9600 | 449 | 0.220 |
| TBR-simple | 454 | 449 | 0.220 |

Results from these analyses show that the closest and simple options yield the shortest trees (449) and that the consistency index is the same in each case. However, the analysis with the TBR-closest option produced a 'tree-buffer overflow' due to lack of RAM and this probably reduced the effectiveness of the search. Therefore, the TBR-simple option was preferred over the other two and was adopted in all following analyses.

### 5.4.3 Effect of inclusion and exclusion of quantitative characters

The effect of quantitative characters was examined by conducting analyses with and without these characters included. Analysis using only the 35 qualitative characters generated 8,525 shortest trees of 268 steps and had a consistency index of 0.239 (Table 5.5). When compared with the analysis with all characters included (i.e. 454 trees of 449 steps; consistency index 0.220 ), the shorter tree length in the first analysis is obviously due to there being few characters. Although the statistics for these analyses are not comparable because they are based on different data sets, they do recover several identical clades (i.e. nodes 69 ,

70, 78 and 85 in Fig. 5.28). However, the analysis with the quantitative characters removed has a higher consistency index ( 0.239 versus 0.220 ), indicating that the morphometric characters are responsible for a high level of homoplasy in the data. When the quantitative characters only were used, this restricted data set generated 4,600 shortest trees of 121 steps (Table 5.5).

Table: 5.5 Summary of analyses using the hypothetical ancestor as the out-group, comparing results for the inclusion and exclusion of quantitative characters, showing the number of most parsimonious trees generated $(T)$, length of shortest trees ( $T L$ ), and the consistency index (CI).

| Options | T | TL | CI |
| :--- | ---: | :---: | :---: |
| Quantitative characters only | 4600 | 121 | - |
| Qualitative characters only | 8525 | 268 | 0.239 |
| Excluding characters 39, 40 and 43 | 9600 | 377 | 0.231 |
| Qualitative plus quantitative characters | 454 | 449 | 0.220 |

Because the quantitative characters were responsible for a high level of homoplasy in the data, an attempt was made to reduce this, but still maintain the structure of the trees, by including only those quantitative characters that had been treated as qualitative by previous workers (Mason 1981; Walker et al. 1990; Whitfield 1992). Using this criterion, only three quantitative characters were excluded: character 39 (length of the inner hind tibial spur versus the length of the outer spur), character 40 (length of the inner hind tibial spur versus the length of the hind basitarsus), and character 43 (maximum length of T1 versus maximum width of T1). Analysis of the data set with these three characters removed generated 9500 shortest trees of 377 steps and had a consistency index 0.231 (Table 5.5). However, this analysis produced a 'tree-buffer overflow', that may have reduced the effectiveness of the PAUP analysis. The shorter length of the trees in this case is again due to there being few characters. Although the consistency index is slightly improved, suggesting that the morphometric characters are responsible for substantial homoplasy, the removal of characters 39,40 and 43 caused nodes $78,82,85$ and 89 (Fig. 5.28) partly to collapse, indicating that these three characters are important to the structure of the resultant trees and, therefore the morphometric characters should not be excluded.

### 5.4.4 Effect of autapomorphies

Autapomorphies are characters unique to a particular monophyletic group. This is only when the group in question is compared to another group, however, they become synapomorphies when the relationships within the group are examined (Hennig 1966). It has been suggested by different workers that autapomorphies should be removed from a data set and phylogenetic analysis based only on 'informative characters'. For instance, Colless (1981) states that autapomorphies make phenograms different from cladograms for the same data set. Brooks et al. (1986) argue that the consistency index is increased by the inclusion of autapomorphies and claim that the "true consistency of a data matrix is one calculated with informative characters only, and one calculated with all characters is artificially high". Carpenter (1988) suggests that autapomorphies and constant characters should be excluded from data matrices because they are not relevant to the cladistic problem. However, Yeats (1992) argues that autapomorphies do not cause any affect to the relationships among ingroup taxa, and their inclusion does not reduce the resolution if they are retained in a data matrix. Further, he points out that the removal of autapomorphies may in fact cause a loss of some important information, therefore, they should be clearly described and retained so that future workers can use them to assess the evidential support for the monophyly of the ingroup taxa. In the data matrix under discussion here, characters 14,19 and 22 , are autapomorphic and character 9 is constant across all taxa. A comparison of analyses with these four characters included and removed was conducted using the hypothetical ancestor as an out-group. Although these analyses yield trees of different lengths as expected, they generated the same number of trees (454) and identical consistency indices (0.220). More importantly, the inclusion of these four characters had no effect on the internal structure of the strict or $50 \%$ majority rule trees. Therefore, following the arguments of Yeates (1992), these four characters were retained in the data matrix for all subsequent analyses.

### 5.5 Analyses to determine the relationships among Diolcogaster species

To determine the relationships among Diolcogaster species and other included microgastrines, the following two analyses were conducted and the results compared.

1. Analysis A: with the hypothetical ancestor used as the out-group and all characters unpolarised (Fig. 5.28).
2. Analysis B : with the hypothetical ancestor used as the out-group, the data polarisecd and some characters ordered (as discussed above in Section 5.3.2.4) (Fio.5.30).

A summary of the statistics of these two analyses is presented in Table Thase statistics can only be used to compare the differences between trees that have been generated from the same data set (Wiley et al. 1991), i.e. between the strict consensus and $50 \%$ majority-rule trees for analysis A, not between Analysis A and B. For Analysis A the 50\% majority rule tree was used for comparison because there was little difference between the strict and $80 \%$ majority rule trees.

Table: 5.6 Summary of analyses using the hypothetical ancestor as the out-group, for Analyses A and B (Figs 5.28-5.30) showing the number of most parsimonious trees generated
( $T$ ), length of the shortest trees (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), f-ratio and Rohlf's consensus index (Rohlf's CI)
(strict $=$ strict consensus tree; $50 \%=50 \%$ majority rule tree )

| Analysis | T | TL | CI | RI | RC | f-ratio | Rohlf's CI |
| :--- | ---: | :---: | :---: | :---: | :---: | :---: | ---: |
| A | 454 | 449 | 0.220 | 0.563 | 0.124 |  | - |
| A strict | - | 589 | 0.168 | 0.387 | 0.065 | 0.6010 | 0.147 |
| A 50\% | - | 458 | 0.216 | 0.551 | 0.119 | 0.7180 | 0.745 |
| B | 1 | 549 | 0.181 | 0.525 | 0.095 | 1.1144 | - |

5.5.1 Analysis with the unpolarised data (Analysis A): comparing the strict consensus and 50\% majority rule trees

The strict consensus tree for Analysis A, based on 454 shortest trees, differentiates several clades but leaves many taxa unresolved as part of a large basal polytomy at node 95 (Fig. 5.28). This is not surprising given that close examination of the data matrix shows that there are few unequivocal synapomorphies for any clades. However, the strict consensus tree does reveal a number of important groups. The genera, other than Diolcogaster and Glyptapanteles, included in the analysis for which two species were included (i.e. Buluka, Deuterixys, Fornicia, Microplitis and Wilkinsonellus) are all resolved as monophyletic at nodes 66, 81, 91, 93 and 94 in Figure 5.28, respectively (these correspond to nodes 66, 109, 116, 92 and 84 in Fig. 5.29). Also, the exemplar species of Apanteles, Miropotes and Dolichogenidea (belonging to the Apantelini sensu Mason) fall outside of the clade that contains all the Cotesia-group genera (i.e. node 95 in Fig. 5.28 and 118 in Fig. 5.29).

However, the Cotesia-group of genera are not resolved as monophyletic in either the strict or $50 \%$ majority rule trees, because of the inclusion of Microgaster, Prasmodon and Xenogaster.

When the representatives of Diolcogaster used in the analysis are assessed (indicated by dots on Fig. 5.28), it is clear that the genus is not resolved as monophyletic in either the strict or $50 \%$ majority rule trees. For instance, Parenion falls within the euterpus-group of Diolcogaster (node 87), Protomicroplitis s. str. falls within the connexus-group (node 78), Buluka falls within the basimacula-group (node 89), while many Diolcogaster species form part of the polytomy above node 95 in the strict consensus tree. The most well-resolved clade is that at node 80 (in both Figs 5.28 and 5.29) which includes all of the basimacula- and connexus-group species, D. yousufi, D. merata, D. fasciipennis (a monotypic group), D. ashmeadi (representative of the xanthaspis-group), as well as the Buluka spp. and Protomicroplitis calliptera. Other groups of Diolcogaster species resolved in this analysis are the scotica- and abdominalis- groups (represented each by single species; node 82 in Fig. 5.28 and 81 in Fig. 5.29), the spretus-group (node 85 in Fig. 5.28 and 114 in Fig. 5.29), the hadrommatus-group (node 89 in Fig. 5.28 and 102 in Fig. 5.29), and the euterpus-group but with Parenion beelaronga included (node 87 in Fig. 5.28 and 90 in Fig. 5.29). Also, the species tegularis, previously included in Protomicroplitis s.l. (Nixon 1965) and whitfieldi, are resolved together (node 90 in Fig. 5.28 and 106 in Fig. 5.29) and are described as a new genus (see Chapter 6).

The $50 \%$ majority rule tree (Fig. 5.29) is almost fully resolved and reveals a number of other relationships not evident in the strict consensus tree. The species of Dolichogenidea and Miropotes form the sister-group to Apanteles and all other microgastrines (nodes 119 and 120); Fornicia spp. are the sister-group to Distatrix formosus (node 117), and these species with Cotesia glomerata are the sister-group to the remaining microgastrines (node 118); the spretus-group is placed basally to the clade containing all other Diolcogaster (node 114); a number of Diolcogaster species (D. alvearius, D. masoni, D. tearae, D. pariander, D. vulpinus, $D$. rixosus) fall out in a group that also contains the hadrommatus-group, Prasmodon sp. and Xenogaster insolens (node 103); while D. scotica, D. brevicaudus, and D. orontes come out with Microgaster and Wilkinsonellus (node 87). However, it should be pointed out that the $50 \%$ majority rule tree, although not an estimate of true confidence in the
data, is a relatively poor estimator of 'true relationships', compared with the strict consensus tree.

### 5.5.2 Analysis with the polarised and ordered data (Analysis B)

This analysis was based on polarised and partly ordered data with linear transformation and stepmatrices included (as in Table 5.2), but with characters 22 and 23 left unpolarised (as discussed in Section 5.3.2.1) and characters 1-3, 5, 7, 9, 11-17, 19, 21-25, 28, 29, 33 and 35 left unordered (see Section 5.3.2.4).

Table: 5.7 Summary of analyses using the hypothetical ancestor as the out-group, comparing results from polarised-ordered and unpolarised data, showing the number of most parsimonious trees generated ( $T$ ), length of the shortest tree(s) (TL) and consistency index (CI).

| Options | T | TL | CI |
| :--- | :---: | :---: | :---: |
| Polarised and ordered (Analysis B) <br> Unpolarised (Analysis A) | 1 | 549 | 0.181 |

Hauser and Presch (1991) discuss the effect of ordering characters on resultant phylogenies and state that it has often been perceived that ordered characters are more informative, produce more resolution, and fewer equally parsimonious trees than do unordered characters. However, they concluded that if we accept that the most reliable criterion for determining the evolution of a character is the cladogram itself (which presumably means consistency with other independent characters), then hypotheses of order are unnecessary. For the data set in this study when characters were polarised and ordered as above (Analysis B), the results (Fig. 5.30) generated a tree which is very different in structure rather than showing an 'improved topology' over that generated from Analysis A using unpolarised data (Fig. 5.28) (as discussed below). Although Analysis B produced only one tree, it was 100 steps longer than the tree generated with the unpolarised data set, and it had a lower consistency index ( 0.181 versus 0.220 ; Table 5.7).

### 5.5.3 Comparison of Analysis $A$ and $B$

In both Analysis A and B, the species of Apanteles, Miropotes and Dolichogenidea fall out below the remaining microgastrines (node 128 in Fig. 5.30) and the Cotesia-complex
(sensu Mason 1981; Walker et al. 1990) is not resolved. Likewise, the genera Buluka, Deuterixys, Fornicia, Microplitis and Wilkinsonellus are resolved as monophyletic in Analysis B (nodes 68, 86, 87, 107 and 119 in Fig. 5.30) but, in addition, so is Glyptapanteles (node 92 in Fig. 5.30).

In both Analysis A and B, only one clade is supported by unequivocal synapomorphies, i.e. the two species of Fornicia, on the presence of a well-developed propleural flange (character 6), the development of an epicnemial carina (character 7), the presence of a medial spine on the metanotum (character 13), the presence of only the posterior part of the medial longitudinal carina on the propodeum (character 15), the presence of an incomplete propodeal areola (character 16), and a sinuate cu-a vein in the hind wing (character 24). All of these characters have previously been recognised for the genus (Austin 1987).

Analysis A and B also resolve several clades in common for Diolcogaster species: D. hadrommatus + D. walkerae (node 78 in Fig. 5.30), the basimacula-group (node 72), the nodes 73 and 76, and the euterpus-group including Parenion beelaronga (node 115). Both analyses also show a sister-group relationship between species of the new genus, Neodiolcogaster (node 117). Other than these similarities, the relationships among Diolcogaster species between the two analyses are dramatically different (compare Figs 5.28 and 5.30). Further, a comparison of the statistics for Analysis A and B (Table 5.7) shows that the former is the most parsimonious solution to the data set ( 449 versus 549 steps) and has a higher consistency, retention and rescaled consistency indices.

### 5.5.4 Level of homoplasy

The data matrix shows a very high level of homoplasy, as indicated by the fact that the only unequivocal synapomorphies define a minor terminal clade, viz. Fornicia ceylonica $+F$. muluensis (see above). To show the extent and pattern of homoplasy in the data, three characters are used as examples, viz. characters 2,3 and 39 , and their distribution is plotted onto the strict consensus tree for Analysis A (Figs 5.31-5.33).

Character 2 (Fig. 5.31) - placodes on antennal flagellomeres. This is a binary character in that placodes are either present or absent on the ventral surface of the medioapical flagellomeres. The apomorphic state (absences of placodes) appears independently on 12 branches ( $2,21,42,45,48,52,53,60,64,65,69$ and 91 ).

Character 3 (Fig. 5.32). - fluted bent-tipped sensilla on ventral surface of medio-apical flagellomeres of females. This character has three states: sensilla present in a scattered form (0), present in an oblique-row (1), and missing (2). The two apomorphic states ( 0 and 1 ) have clearly arisen multiple times; on branch $2,5,8,15,23,35,44,45,48,53,64,86$ and 91 for state 0 and branches $39,41,47$ and 71 for state 1 .

Character 39 (Fig. 5.33). - comparison of length of the inner hind tibial spur to the length of the outer hind tibial spur. This is a quantitative character and consists of four states determined by segment coding: inner hind tibial spur 1.00-1.25 as long as outer hind tibial spur (0); inner hind tibial spur 1.26-1.50 as long as outer hind tibial spur (1); inner hind tibial spur 1.51-1.75 as long as outer hind tibial spur (2); and inner hind tibial spur 1.76-2.00 as long as outer hind tibial spur (3). The plesiomorphic is state 0 and there are numerous reversals to this state, viz. on branches $2,21,25,26,31,32,42,52,53,59,60,63-65,84,93$ and 96 , while the apomorphic states appear in parallel on branches $4,6,7,9,11,12,14,19$, $20,41,43,44,58,69,82$ and 91 for state 1 , on branches $3,8,10,13,15,28,30,33,34,49$, 54,57 and 62 for state 2 , and on 24,89 and 61 for state 3 .

### 5.6 Classification of Diolcogaster

### 5.6.1 Limitations of Analyses

Clear from the above results of analyses with polarised and unpolarised data is that the structure of the trees obtained is not particularly stable, and the large degree of homoplasy in the data set must be partly responsible for this. Further, the results may be limited by the selection of taxa in that non-Diolcogaster genera were represented only by a single or at most two species. This meant that characters scored for exemplar species may not be representative of the whole genus, and this may have resulted in some bias in the data. However, this is thought not to have been a major problem, given that virtually all genera represented by two species, with the exception of Diolcogaster and Glyptapanteles, were resolved as monophyletic. More difficult to explain is the inclusion of Protomicroplitis calliptera and Parenion beelaronga within connexus-and euterpus-groups, respectively (nodes 78 and 87 in Fig. 5.28). Both these genera have numerous described species (Mason 1981; Austin and Dangerfield 1992) but were represented by single species in the analysis. Until more detailed analyses can be undertaken of these genera and species-groups, the latter
groups must be considered to be paraphyletic. However, the primary task here was to determine the status of Diolcogaster as a genus and the relationships among its speciesgroups. For this reason, the in-group was overloaded with members of Diolcogaster, and other genera were included only in a token way to test its monophyly. Ultimately, the total number of species included was limited to 67 so that the time to run PAUP analyses on the computers available was not too long, and this restricted the number of non-Diolcogaster species that could be accommodated.

### 5.6.2 The Genus Diolcogaster

In no analyses undertaken do the currently recognised members of Diolcogaster form a monophyletic group, rather the genus is demonstrably polyphyletic. However, because the results obtained with polarised versus unpolarised data varied substantially in tree topology, the more conservative results and the one with superior statistics (i.e. the strict consensus tree for the unpolarised data matrix) was used to infer a classification for Diolcogaster species.

The results obtained here are somewhat unsatisfactory in that Diolcogaster is obviously polyphyletic, but they are not robust or extensive enough to show how best the genus can be broken up into stable monophyletic units. As an interim measure, it is proposed to maintain Diolcogaster as a separate taxonomic unit, given that its members are easily recognisable (see Chapter 6), and until its relationships can be better determined by more detailed studies, possibly including DNA sequence comparisons (see Chapter 7).

The analyses do resolve a number of groups and several of these correspond to previously recognised species-groups of Nixon (1965). These are the basimacula-group (node 89 in Fig. 28), the connexus-group (node 78), the spretus-group (node 85), and the euterpus-group (node 87). In addition, one new species-group, the hadrommatus-group, is recognised here. Further, the relationships of some other species are resolved: D. merata, $D$, fasciipennis, Buluka spp. and D. ashmeadi (xanthaspis-group) are the sequential sister taxa to the basimacula-group (nodes 70, 71, 72 and 73, respectively), the connexus-group is the sister-group to this large clade (node 79), to which D. yousufi is placed basally (node 80 ). The two monobasic groups recognised by Nixon (1965) for D. abdominalis and D. scotica are resolved as sister species (node 82) and this can be logically combined into the one group, while the two sister species, tegularis and whitfieldi (node 90), are recognised as a new genus,

Neodiolcogaster (see Chapter 6). The relationships of the species D. brevicaudus, D. masoni, D. orontes, D. pariander, D. rixosus, D. tearae and D. vulpinus (marked with black dots in Fig. 5.28) are unresolved and they are provisionally given the rank of monotypic speciesgroups, as are D. merata, D. fasciipennis and $D$. yousufi, although the relationships of the latter three species are better resolved. D. alvearius, D. ashmeadi and D. duris were the sole representative of the alvearius-, xanthaspis-, and lelaps-groups included in the analysis, respectively.

The characters defining the above species-groups, and the description, recognition and distribution of the species of Diolcogaster in Australasia is the subject of Chapter 6.

Figs 5.1-5.4. Arrangement of placodes on antennal flagellomeres. 5.1, Cardiochiles fuscipennis Szépligeti Q, scattered placodes; 5.2, Diolcogaster alkingara sp. nov. holotype $Q$, double row of placodes; 5.3, Diolcogaster harrisi sp. nov. holotype $Q$, overlapping placodes; 5.4, Epsilogaster panama Whitfield and Mason $Q$, single row of placodes. Scale lines: $5.1=100 \mu \mathrm{~m} ; 5.2=40 \mu \mathrm{~m} ; 5.3,5.4=50 \mu \mathrm{~m}$.


Figs 5.5-5.8. Arrangement of fluted bent-tipped sensilla. 5.5, Diolcogaster harrisi sp. nov. holotype $Q$, scattered sensilla; 5.6, Buluka achterbergi Austin $Q$, oblique row of sensilla; 5.7, 5.8, Diolcogaster sons (Wilkinson) $\odot: 5.7$, oblique row of sensilla; 5.8 , oblique row of sensilla at higher magnification. Scale lines: $5.5,5.6=20 \mu \mathrm{~m} ; 5.7=40 \mu \mathrm{~m} ; 5.8=4 \mu \mathrm{~m}$.


Figs 5.9-5.12. 5.9, Diolcogaster eclectes (Nixon) $\bigcirc$, placodes missing on part of apical flagellomere; 5.10, Apanteles ippeus Nixon $Q$, phragma of scutellum exposed; 5.11, Fornicia muluensis Austin $\bigcirc$, showing metanotal spine and propleural flange; 5.12, Buluka achterbergi Austin $\mathrm{O}^{\prime \prime}$, complete metasomal carapace. Scale lines: $5.9=40 \mu \mathrm{~m} ; 5.10,5.11=200 \mu \mathrm{~m} ; 5.12=100 \mu \mathrm{~m}$.


Figs 5.13-5.16. 5.13, Diolcogaster nixoni sp. nov. holotype $Q$, showing ventral groove on lateral pronotum; 5.14, Cardiochiles eremophilasturtiae Dangerfield and Austin $Q$, showing absence of lateral pronotal groove; 5.15, Cardiochiles fuscipennis Szépligeti $Q$, showing crenulate notauli; 5.16, Prasmodon sp., showing smooth indented notauli. Scale lines: $5.13=100 \mu \mathrm{~m} ; 5.14=200 \mu \mathrm{~m} ; 5.15,5.16=500 \mu \mathrm{~m}$.


Figs 5.17-5.20. 5.17, Miropotes chookolis Austin $Q$, showing medially desclerotised hypopygium; 5.18, Epsilogaster panama Whitfield and Mason $\bigcirc$, showing pilosity on entire length of ovipositor sheaths; 5.19, Diolcogaster sons (Wilkinson) $Q$, ovipositor sheaths with specialised sensilla; 5.20, Diolcogaster perniciosus (Wilkinson) $Q$, ovipositor sheaths without specialised sensilla. Scale lines: 5.17, 5.18 $=100 \mu \mathrm{~m} ; 5.19,5.20=40 \mu \mathrm{~m}$.




### 5.21

Figs 5.21 (a-l). Propodeal carination in different microgastrine and out-group genera: (a) Fornicia ceylonica Wilkinson; (b) Prasmodon sp.; (c) Wilkinsonellus amplus Austin and Dangerfield; (d) Cotesia rubecula (L.); (e) Buluka achterbergi Austin; (f) Xenogaster insolens (Wilkinson); (g) Cardiochiles fuscipennis Szépligeti; (h) Epsilogaster panama Whitfield and Mason; (i) Miropotes chookolis Asutin; (j) Dolichogenidea eucalypti Austin and Allen; (k) Distatrix formosus (Marshall); (l) Apanteles ippeus Nixon. Scale line $=0.5 \mathrm{~mm}$. ar $=$ areolet; $\mathrm{tc}=$ transverse lateral carinae; mlc $=$ medial longitudinal carina; cs = costulae.

$\qquad$
5.23


Figs 5.22-5.27. 5.22, 5.23, Cardiochiles fuscipennis Szépligeti $Q: 5.22$, fore wing showing large quadrangular areolet; 5.23 , hind wing showing absence of $2 \mathrm{r}-\mathrm{m} ; 5.24$, Cotesia rubecula (L.) Q, showing fore wing areolet absent; 5.25, Protapanteles popularis (Haliday) Ọ, showing hind wing cu-a roundedly convex; 5.26, Fornicia chalcoscelidis Wilkinson $\uparrow$, showing hind wing cu-a sinuate; 5.27 , Protomicroplitis calliptera (Say) $Q$, showing medially
constricted T1. Scale lines: $5.22-5.25$ constricted T1. Scale lines: $5.22-5.25=1 \mathrm{~mm} ; 5.26$, not to scale; $5.27=0.5 \mathrm{~mm}$.


Fig. 5.28. Strict consensus tree of 454 trees of length 449 produced from Analysis A (see Section 5.5), which used the hypothetical ancestor as the defined out-group. All characters were treated unpolarised. Species groups of Diolcogaster are marked with black circles and those discussed in the text (Section 5.5.1) are numbered.


Fig. 5.29. 50\% Majority-rule tree of 454 trees of length 449 produced from Analysis A (see Section 5.5), which used hypothetical ancestor as the defined out-group. All characters were treated unpolarised. Nodes discussed in the text (Section 5.5.1) are numbered.


Fig. 5.30. The single shortest tree of length 549 produced from Analysis B (see Section 5.5), which used hypothetical ancestor as the defined out-group. The data are polarised and characters $4,6,34$ and $36-43$ were ordered. Nodes discussed in the text (Section 5.5.2, 5.5.4) are numbered.


Fig. 5.31. Amount of homoplasy shown in character 2 ( 2 states): The distribution of placodes on ventro-lateral surface of flagellomeres ( $\square=$ placodes missing; $\boldsymbol{\square}=$ placodes intact; $\mathbb{\|}=$ equivocal).


Fig. 5.32. Amount of homoplasy shown in character 3 ( 3 states): Fluted bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres ( $\square=$ sensilla scattered; $\bullet=$ sensilla in an oblique row; $=$ sensilla missing; $[\mid=$ equivocal).


Fig. 5.33. Amount of homoplasy shown in character 39 ( 4 states); The comparison of length between inner hind tibial spur and outer hind tibial spur ( $\square=$ ihts $1.00-1.25 \mathrm{x}$ as long as ohts; $\bullet=$ ihts $1.26-1.50 \mathrm{x}$ as long as ohts; $\Delta=$ ihts $1.51-1.75 \mathrm{x}$ as long as ohts; $\mathrm{o}=$ ihts $1.76-2.00 \mathrm{x}$ as long as ohts; $\mathbb{\|}=$ equivocal).

## Chapter 6

## Taxonomic treatment of Diolcogaster Ashmead

### 6.1 Introduction

### 6.2 The genus Diolcogaster Ashmead

6.3 Species-groups of Diolcogaster
6.3.1 alvearius-group
6.3.2 basimacula-group
6.3.3 connexus-group
6.3.4 euterpus-group
6.3.5 hadrommatus-group
6.3.6 lelaps-group
6.3.7 scotica-group
6.3.8 spretus-group
6.3.9 xanthaspis-group
6.4 Key to Australasian species of Diolcogaster
6.5 Treatment of Diolcogaster species
6.5.1-6.5.26 Description of species
6.6 The genus Neodiolcogaster gen. nov.
6.7 Key to species of Neodiolcogaster gen. nov.
6.8 Treatment of Neodiolcogaster species
6.8.1-6.8.2 Description of species

### 6.9 New genus

Figures 6.1-6.60

### 6.1 Introduction

This chapter presents a taxonomic revision of the genus Diolcogaster for the Australasian region. Following the results of the phylogenetic analysis presented in Chapter 5, the genus is treated as a single taxonomic entity, even though it is clear from the analysis that it is not monophyletic. The Australasian species are divided into numerous speciesgroups and these are discussed in relation to the previous species-group classification of Nixon (1965) and the results of the phylogenetic analysis. The defining characters of the genus are documented and discussed, and a key to the species of Australasian Diolcogaster is presented. Each species is described in detail and information on its distribution, general comments and host information (where possible) are provided. A new genus, Neodiolcogaster, is recognised, described, and its relationships discussed following the results presented in Chapter 5. Further, a second generic taxon which appears to represent a new genus is discussed, but is not formally described here because of a lack of appropriate material. Note that the authorship of species in the text for this chapter are given in Tables 2.8, 2.9 and 5.1.

### 6.2 The genus Diolcogaster Ashmead

Diolcogaster Ashmead, 1900a: [Type species, by monotypy, Microgaster brevicaudus Provancher 1886]. Mason, 1981: 113; Tobias, 1986: 650. Austin and Dangerfield, 1992: 25; Whitfield, 1995a: 250.

## Diagnosis

Scutum smooth to reticulate-punctate, notauli absent; scutellum smooth to weakly punctate; medial posterior band of scutellum smooth or sculptured; metanotum with phragma of scutellum hidden (except the alvearius-group where it is slightly exposed); propodeum smooth to rugose-punctate, always with complete medial longitudinal carina, with or without costulae but lateral carinae never present; fore wing areolet present, variable in shape from small and quadrangular to slit-like; hind wing vannal lobe mostly weakly convex to straight, rarely concave (basimacula-group only), margin with row of long thick hairs, or hair sparse or absent; vein 1-RS of hind wing straight, in line with vein 2-RS so that first marginal cell (1a) and second marginal cell (1b) of about same width; hind coxa large, up to
twice as along as T 1 ; hind tibial spurs unequal in length, with inner spur always longer than outer spur, its length varying from half to almost as long as hind basitarsus; first metasomal tergite (T1) broad posteriorly to parallel-sided but never narrowing posteriorly; medial groove of T1 always present at in anterior half, usually for almost entire length of tergite; T2 variable but mostly rectangular and wider than long, as long as or shorter than T 3 (except in D. merata, where T3 is much shorter than T2); T2 usually with well-defined median field, T3 sometimes with median field; hypopygium short, not more than half length of hind tibia, evenly sclerotised; ovipositor short, mostly hidden within hypopygium, exposed part much less than half length of hind tibia; pilosity on ovipositor sheaths variable from present on entire length to a few hairs concentrated at apex.

## Comments

As discussed in Chapter 5, Diolcogaster is undoubtedly not a monophyletic group. However, given that it has also not been possible to break up the genus into stable monophyletic units, it seems most sensible to maintain Diolcogaster as a 'holding' genus for the time being. This concept can then be used to place existing and newly described species, without further confusing the classification of the subfamily. More importantly, this approach can be used to explore the relationships among the Cotesia-complex of genera, in the hope of more precisely resolving a stable classification for the species currently accommodated in Diolcogaster. Although, this arrangement is far from satisfactory, the recognition of Diolcogaster species remains a relatively easy task, in that all members of the genus possess the following characters: propodeum with medial longitudinal carina; hind coxae large; areolet present in fore wing; first and second marginal cells of hind wing of equal width; T 1 with medial longitudinal groove at least in part; hypopygium short and evenly sclerotised; ovipositor very short. In addition, virtually all species possess a median field on T 2 .

The relationships among the various elements comprising Diolcogaster are unclear, primarily due to the inordinate amount of homoplasy in the data set. Clear from the analysis in Chapter 5 is that some species-groups of Diolcogaster align more closely with other microgastrine genera than with each other. However, the placement of only one previously described species, tegularis, has been seriously questioned by previous authors as to its
placement in Diolcogaster. This species was originally described in Microgaster (Szépligeti 1905), then hesitantly placed in Protomicroplitis (Nixon 1965). Most recently, Austin and Dangerfield (1992) transferred this species to Choeras. However, until this study the species was only known from the male. Discovery of female specimens during this study clearly shows that tegularis does not belong to Choeras (see under Neodiolcogaster, below). Further, its inclusion in Diolcogaster would substantially broaden the limits of this genus to the point where it would not be readily identifiable, i.e. it lacks medial longitudinal carina on the propodeum and medial groove on T1, and the first marginal cell of the hind wing (1a) is broader than the second (1b). For this reason, tegularis is here placed in a new genus, Neodiolcogaster, along with a newly described species.

In total 26 species of Diolcogaster are recognised from Australasia, however, during the study at least a further three species represented by males only were identified as different (but not described). This figure is approximately half the 70 species of Diolcogaster estimated for the region by Austin and Dangerfield (1992).

## Distribution

Diolcogaster has an almost world-wide distribution, but the genus is often not commonly encountered compared with other microgastrine genera. The Australasian region is relatively rich in Diolcogaster species and the genus is well-distributed across the region. The genus is found in mainland Australia, Tasmania, New Guinea, New Caledonia, and is here recorded from New Zealand for the first time. Most species have restricted distributions, often associated with particular habitats or climate zones. D. merata, D. muzaffari, D. euterpus and D. newguineaensis are apparently endemic to New Guinea (Figs 6.52, 6.54, $6.57,6.60$ ). D. perniciosus is widely distributed across eastern and south-western Australia and is the only species recorded from New Zealand (Fig. 6.53). D. sons is also widely distributed in Australia and is the only species known from New Caledonia (Fig. 6.52). D. iqbali is distributed across most of mainland Australia (Fig. 6.56), including both the arid interior and coastal tropical and subtropical locations. D. vulpinus is restricted to the arid interior and south-west (Fig. 6.58), while D. naumanni is so far known only from Augustus Island, north-western Australia (Fig. 6.59). Virtually all other species have restricted eastern coastal distributions, sometimes including Tasmania.

## Biology

Members of Diolcogaster are all endoparasitoids of lepidopteran larvae and have been recorded from more than a dozen families of Lepidoptera (see Sections 2.4 and 2.5). Very little is known about the biology of the Australasian species and only three of the 26 species have been reared from known hosts, $D$. perniciosus has been bred from larvae of Ardices glatignyi, Nyctemera amica and N. annulata (Arctiidae), D. rixosus has been reared from Doratifera oxleyi (Limacodidae), and D. tearae from Epicoma tristis (Thaumetopoeidae).

### 6.3 Species-groups of Diolcogaster

Of the Diolcogaster species included in the phylogenetic analysis undertaken in Chapter 5, five species-groups were recognised that included two or more species. In addition a further four multi-species groups, (viz. alvearius-, lelaps-, scotica- and xanthaspis-groups, Nixon 1965) were represented by a single taxon in the Analysis. Of these nine groups, six are found in Australasia, while three are extra-limital to the region. This section discusses the characters that define these groups, their relationships and distribution. The relationships of a further 10 species were not resolved and, accordingly, they represent monotypic speciesgroups. These latter groups are not treated separately here, but the six found in Australasia are discussed under the relevant species' descriptions, viz. the masoni-, merata-, rixosus-, tearae-, vulpinus- and yousufi- groups.

### 6.3.1 alvearius-group

This species-group is not found in Australasia and comprises species only from Europe. It was first described by Nixon (1965) and differs from all other Diolcogaster in having the phragma of scutellum partly exposed and T1 without a medial longitudinal groove. The group contains only two species: D. alvearius and D. minuta.

### 6.3.2 basimacula-group

This species-group was first described by Nixon (1965). It can be easily separated from other Diolcogaster groups by the following combination of characters, in particular the partial carapace of the metasoma: ventral area of lateral pronotum crenulate, with dorsal as well as
ventral grooves; propleural flange not well-developed; areolet slit-like; hind wing vannal lobe concave and glabrous; metasomal tergites forming a partial carapace; T 2 and T 3 with well-defined median field; suture between T2 and T3 deep, wide and crenulate; hind coxa about 1.6 x as long as T 1 or longer.

The group consists of 11 described species, five of which are Australasian, the remainder being African or Oriental in distribution. From the latter two regions a further five or six new species are known in collections (AEIC, BMNH, CNCI, WARI). The Australasian species are $D$. sons, $D$. eclectes, $D$. alkingara sp. nov., $D$. dangerfieldi sp. nov. and $D$. newguineaensis sp. nov.

### 6.3.3 connexus-group

Nixon (1965) placed two species in the connexus-group, D. perniciosus, from Australia and $D$. connexus (Nees) from Europe. However, the cladistic analysis undertaken here resolved a monophyletic group containing four described species, D. perniciosus, D. ippis, D. reales, and Protomicroplitis calliptera and three new species of Diolcogaster. D. ippis from Brazil and D. reales from South Africa were classified by Nixon (1965) as separate monotypic species-groups. Based on results of the analysis, these species, with the exception of $P$. calliptera, are included in an expanded connexus-group. All the members of this group share the following characters: ventral area of lateral pronotum crenulate; propleural flange less developed; placodes missing on ventro-lateral surface of medio-apical flagellomeres; medial groove of T1 present only in anterior half; hind coxa about 1.25-1.6 x as long as T 1 .
P. calliptera is one of several species that Mason (1981) retained in his more narrowly defined concept of Protomicroplitis, after most species were transferred to Diolcogaster. For the time being this species is retained in that genus, but it having been placed cladistically within the connexus-group serves to highlight the problem of recognising monophyletic genera within the Cotesia-complex. There are four Australasian species in this group, viz. D. perniciosus, $D$. harrisi sp. nov., D. robertsi sp. nov. and $D$. muzaffari sp. nov.

### 6.3.4 euterpus-group

This species-group, which was originally described by Nixon (1965) as monotypic, is endemic to Australasia and is here expanded to include a new species. In the present study
this group is resolved as paraphyletic with respect to Parenion beelaronga and is defined by the following characters: flagellomeres with a regular double row of placodes; costulae and lateral carinae of propodeum absent; fore wing vein la absent; hind wing vein $\mathrm{M}+\mathrm{CU}$ very short ( $0.57-0.72 \mathrm{x}$ as long as $1-\mathrm{M}$ ); and inner hind tibial spur very long (1.95-2.3 x as long as outer hind tibial spur). Parenion contains about eight species, three of which are described and it is apparently restricted to tropical Australasia. The genus was postulated to be closely related to Diolcogaster by Austin and Dangerfield (1992) and this is borne out in the present study. However, as with the connexus-group, for pragmatic reason, the limits to Parenion are unchanged here, primarily because of its very distinctive morphology (viz. smooth body and pectinate tarsal claws). Species included in this group are D. euterpus and D. nixoni sp. nov.

### 6.3.5 hadrommatus-group

This is a new group which consists of three new Australasian species. Members of hadrommatus-group share the following combination of characters which separate them from all other species of Diolcogaster: placodes arranged in a regular double row on all flagellomeres but missing on ventro-lateral surface of medio-apical flagellomeres; lateral pronotum crenulate ventrally, with dorsal and ventral grooves; propodeum without costulae and lateral carinae; medial posterior band of scutellum sculptured; and ovipositor sheaths pilose only in apical half. The species comprising this group are D. hadrommatus, sp. nov. D. walkerae sp. nov. and D. iqbali sp. nov.

### 6.3.6 lelaps-group

This species-group was described by Nixon (1965) to accommodate two species from Nearctic region, D. lelaps and D. duris, and it has since not been recorded from Australasia. It can be separated from other Diolcogaster by the following characters: lateral pronotum ventrally crenulate; propleural flange less developed; hind wing vannal lobe weakly convex to almost straight, with short sparse pilose margin; placodes intact on ventro-lateral surface of medio-apical flagellomeres; suture between T2 and T3 distinct; ovipositor sheaths pilose over entire length; inner hind tibial spur 0.75-0.90 x as long as hind basitarsus.

### 6.3.7 scotica-group

Nixon (1965) placed five North American and European species in this group. In the analysis here it is resolved as the sister-group to the monotypic European group which contains $D$. abdominalis. This clade is defined as follows: antennae with a regular double row of placodes on all flagellomeres; lateral pronotum ventrally crenulate, with a ventral groove only; propleural flange less developed; medial posterior band of scutellum sculptured; T1 with complete medial longitudinal groove; suture between T 2 and T 3 wide and crenulate; fore wing areolet triangular; propodeum with costulae present but lateral carinae absent; and ovipositor sheaths pilose in apical half only. However, these two groups can be separated by loss of fore wing vein 1a and median field of T2 laterally encircled by smooth grooves in the scotica-group, and development of the apical carina of scutellum and raised median field of T 2 and T 3 in the abdominalis-group. Because the abdominalis-group is monotypic, it is here combined with the scotica-group, as defined by the above characters. No species of this group are known from Australasia.

## 6.3 .8 spretus-group

Nixon (1965) included three species in this group, one each from the Oriental, Ethiopian and Palearctic regions. The phylogenetic analysis undertaken here shows that a further five new species from the Australasian region, as well as the monotypic coenonymphae-group of Nixon (1965) from Japan, form a monophyletic assemblage and they are here accommodated in this group. The spretus-group s.l. is defined as follows: flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres in a scattered form; lateral pronotum crenulate ventrally; costulae present but lateral carinae absent on propodeum; and vein 1 a of fore wing absent.
D. coenonymphae has a median field on T3 in the form of a raised area, and medial longitudinal groove present only in the anterior part of T1 and, although distinctive, it is better accommodated in this larger group, rather than be treated as monobasic. The following members of the group are known from the Australasian region: Diolcogaster adiastola sp. nov., D. naumanni sp. nov., D. dichromus sp. nov., D. notopecktos sp. nov., and D. lucindae sp. nov.

### 6.3.9 xanthaspis-group

Nixon (1965) based this group of Apanteles xanthaspis from the West Indies, and he included a further five species in the group, all described as new species from the Oriental region (Philippines and Borneo). The group is defined by the head, scutum and scutellum being rugose-punctate; the posterior band of the scutellum being sculptured medially; 1CUa and 1-CUb being equal in length; T1 virtually parallel-sided; and T2 with a distinct median field. The group is recorded from Australasia for the first time by D. ashmeadi sp. nov.

### 6.4 Key to Australasian species of Diolcogaster based on females

1. Ventral area of lateral pronotum smooth (Fig. 5. 13) ................................................ 2

Ventral area of lateral pronotum sculptured (Fig. 6.36) ........................................... 5
2(1). Medial posterior band of scutellum smooth (as in Figs 4.2, 6.15) (euterpus-group)

Medial posterior band of scutellum sculptured (Figs 6.1, 6.5) 4

3(2). T1 $1.1 \times$ as long as maximum width, regularly widening posteriorly with widest point at apex (Fig. 6.14); T2 divided into three longitudinal fields with median field defined by smooth lateral grooves (Fig. 6.14); suture between T2 and T3 distinct (Fig. 6.14); lateral pronotum ventrally with an excavated area (Fig. 5.14); flute bent-tipped sensilla present in scattered form on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.5); inner hind tibial spur 0.75-0.90 x as long as hind basitarsus $\qquad$ D. euterpus (Nixon)

T1 2.5 x as long as maximum width, parallel-sided (Fig. 6.41); T2 not divided into three fields, median field present as a raised area (Fig. 6.41); suture between T2 and T3 indistinct (Fig. 6.41); lateral pronotum with ventral groove (5.13); flute bent-tipped sensilla absent on ventro-lateral surface of medio-apical flagellomeres; inner hind tibial spur 0.43-0.74 x as long as hind basitarsus $\qquad$
D. nixoni sp. nov.

4(2). T2 with well-defined median field (as in Fig. 6.14); apex of T2 strongly concave medially (as in Fig. 6.14); propodeum with strong medial longitudinal carina; areolet triangular (Fig. 6.20); lateral pronotum with ventral groove only (as in Fig.
5.13); inner hind tibial spur $0.26-0.42 \mathrm{x}$ as long as hind basitarsus; hypopygium $0.48-0.61 \mathrm{x}$ as long as hind tibia D. tearae (Wilkinson)

T2 with weakly defined median field (Fig. 6.42); apex of T2 straight to weakly concave medially (Fig. 6.42); propodeum with weak medial longitudinal carina; areolet as a small triangle (as in Fig. 4.4); lateral pronotum with ventral and dorsal groove (Fig. 6.36); inner hind tibial spur 0.59-0.74 x as long as hind basitarsus; hypopygium 0.34-0.47 x as long as hind tibia ................... D. vulpinus (Wilkinson)
5(1). Hind wing vein 2-1A present in form of a stump (Fig. 4.5); hypopygium 0.62-0.75 x as long as hind tibia (Fig. 6. 35)
D. masoni sp. nov.

Hind wing vein $2-1 \mathrm{~A}$ absent (Fig. 6.29); hypopygium less than 0.62 x as long as hind tibia6
6(5). Propleural flange absent (Fig. 6.26) ..... 7
Propleural flange present (Fig. 6.39) ..... 15
7(6). Antenna shorter than body length (Figs 6.18, 6.19); vein 1a of fore wing absent,vein 1-1A not bent at this position (as in Fig. 4.4) (spretus-group)8

Antenna as long as or longer than body length (as in Figs 4.1, 4.2); vein 1a of fore wing present (Fig. 6.30), if absent, then 1-1A bent at this position (as in Fig. 6.47)

8(7). Medial posterior band of scutellum sculptured (Fig. 6.6); fore wing areolet triangular (Fig. 6.22); ovipositor sheaths uniformly pilose (as in Fig. 6.45)
D. naumanni sp. nov.

Medial posterior band of scutellum smooth (Fig. 6.15); fore wing areolet quadrangular and small (i.e. 3-RS present but smaller than 2-RS) (as in Fig. 6.21); ovipositor sheaths pilose in apical half only (as in Figs 5.19, 5.20) ...................... 9
9(8). Placodes of flagellomeres in a single row (as in Fig. 5.4); lateral pronotum with ventral and dorsal grooves (as in Fig. 6.36); T1 parallel-sided (6.15); inner hind tibial spur 0.91-1.06 x as long as hind basitarsus .................... D. lucindae sp. nov.

Placodes in double row on basal and medial flagellomeres then overlapping to form a single row in medio-apical flagellomeres (as in Fig. 5.3); lateral pronotum with ventral groove only (as in Fig. 5.13); T1 widest apically (Fig. 6.3); inner hind tibial spur 0.43-0.58 x as long as hind basitarsus

10(9). Median field of T 2 defined by smooth lateral grooves (as in Fig. 6.14); hind wing vannal lobe with dense long pilosity (as in Fig. 6.29); placodes missing on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.9); vein cu-a of hind wing meeting vein 1 A at a wide angle (as in Fig. 6.29) $\qquad$
D. adiastola sp. nov.

Median field of T2 absent (Figs 6.13, 6.19); hind wing vannal lobe glabrous (as in Fig. 6.31); placodes intact on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.2); vein cu-a of hind wing straight meeting vein 1 A at almost right angle (as in Fig. 6.31)

11(10). Suture between T2 and T3 distinct (Fig. 6.13); T1 bulging medially (Fig. 6.13); 1CUa as long as $1-\mathrm{CUb}$; ovipositor sheaths pilose in apical half (as in Fig. 5.19); T1 2.35-3.2 x as long as wide (Fig. 6.13); head, scutum and scutellum orangeyellow, metanotum, propodeum and mesosoma black
D. dichromus sp. nov. Suture between T2 and T3 indistinct (Fig. 6.19); T1 widening posteriorly with widest point at apex (Fig. 6.19); 1-CUa shorter than 1-CUb; ovipositor sheaths with a few hairs only at apex (Fig. 6.50); T1 $0.62-1.48 \mathrm{x}$ as long as wide (Fig. 6.19); body entirely light brown
D. notopecktos sp. nov.

12(7). Placodes intact on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.2); ovipositor sheaths $0.25-0.43 \mathrm{x}$ as long as hind tibia, with few hairs at apex (as in Fig. 6.50)
D. rixosus (Wilkinson)

Placodes missing on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.9); ovipositor sheaths $0.05-0.24 \mathrm{x}$ as long as hind tibia, with pilosity in apical half only (Fig. 6.27) (hadrommatus-group)

13(12). Ovipositor sheaths without specialised sensilla (as in Fig. 5.20); fore wing vein $\mathrm{M}+\mathrm{CU} 0.88-1.02 \mathrm{x}$ as long as $1-\mathrm{M}$; inner hind tibial spur $0.75-0.90 \mathrm{x}$ as long as hind basitarsus; T1 0.62-1.48 x as long as wide (Fig. 6.12) ....... D. iqbali sp. nov. Ovipositor sheaths with specialised sensilla (Fig. 6.27); fore wing vein $\mathrm{M}+\mathrm{CU} 0.73$ 0.87 x as long as $1-\mathrm{M}$; inner hind tibial spur $0.59-0.74 \mathrm{x}$ as long as hind basitarsus; T1 1.49-2.34 x as long as wide

14(13). In lateral view medial temples 0.1-0.2 x as wide as width of eye; dorsal head 1.1-1.2 x as wide as scutum; distance between inner margins of lateral ocelli $2.5-5.0 \mathrm{x}$
distance between outer margin of lateral ocellus to edge of eye; face as high as wide; medio-apical flagellomeres with flute bent-tipped sensilla in scattered form (as in Fig. 5.5); fore wing areolet small and quadrangular (i.e. 3-RS present but smaller than 2-RS) (as in Fig. 6.21); hind coxa 1.59-1.94 x as long as T 1 ; hypopygium $0.34-0.47 \mathrm{x}$ as long as hind tibia
$\qquad$ D. hadrommatus sp. nov.

In lateral view medial temples $0.4-0.5 \mathrm{x}$ as wide as width of eye; dorsal head equal in width to scutum; distance between inner margins of lateral ocelli 1.7-2.0 x distance between outer margin of lateral ocellus to edge of eye; face 1.4 x as high as wide; medio-apical flagellomeres with flute bent-tipped sensilla in oblique row (as in Fig. 5.6-5.8); fore wing areolet triangular (as in Fig. 5.20); hind coxa $1.23-1.58 \mathrm{x}$ as long as T 1 ; hypopygium $0.19-0.33 \mathrm{x}$ as long as hind tibia
$\qquad$
15(6) T1 and T2 strongly sculptured (Figs 6.5, 6.17); areolet slit-like (Fig. 6.30); hind wing vannal lobe concave and glabrous (Fig. 6.31); 16

T1 and T2 not sculptured (Fig. 6.43); areolet more open, not slit-like (Fig. 6.21); hind wing vannal lobe weakly convex to almost straight, marginal pilosity variable (Fig. 6.29) 21

16(15) T2 sculptured, T3 smooth, these tergites not forming a partial carapace (Fig. 6.17); T3 without median field (Fig. 6.17); T3 less than half medial length of T2 (Fig. 6.17); suture between T2 and T3 distinct (Fig. 6.17); hind coxa 1.95-2.3 x as long as T 1 ; inner hind tibial spur $1.59-1.94 \mathrm{x}$ as long as outer hind tibial spur D. merata sp. nov.

T2 and T3 similarly sculptured and fused to form partial carapace (Fig. 6.5); T3 with a well-defined median field (Fig. 6.5); medial length of T3 almost equal to or slightly longer than medial length of T 2 (Fig. 6.5); suture between T 2 and T 3 deep, wide and crenulate (Fig. 6.5); hind coxa 1.59-1.94 x as long as T 1 ; inner hind tibial spur $1.23-1.58 \mathrm{x}$ as long as outer hind tibial spur (basimacula-gp.)
$17(16) \quad \mathrm{M}+\mathrm{CU} 0.57-0.72 \mathrm{x}$ as long as $1-\mathrm{M}$; plical cell of hind wing $1.93-2.2 \mathrm{x}$ as long as sub-basal cell; inner hind tibial spur 0.75-0.90 x as long as hind basitarsus ....... 18
$\mathrm{M}+\mathrm{CU} 0.73-0.87 \mathrm{x}$ as long as $1-\mathrm{M}$; plical cell of hind wing $1.65-1.92 \mathrm{x}$ as long as sub-basal cell; inner hind tibial spur $0.59-0.74 \mathrm{x}$ as long as hind basitarsus 19

18(17) T2 with postero-lateral yellow spots, median field carinate and defined by crenulate lateral grooves (Fig. 6.4); dorsal scutellum weakly punctate (Fig. 6. 1); placodes intact on ventro-lateral surface of medio-apical flagellomeres (Fig. 5. 2); flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres in scattered form (as in Fig. 5. 5); T1 0.62-1.48 x as long as wide (Fig. 6.3); ovipositor sheaths pilose in apical half only .......................... D. alkingara sp. nov. T2 entirely black, median field smooth and defined by smooth lateral grooves (Fig. 6.5); dorsal scutellum strongly areolate-punctate (Fig. 6.5); placodes missing on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.9); flute benttipped sensilla on ventro-lateral surface of medio-apical flagellomeres in an oblique row (as in Figs 5.6-5.8); T1 1.49-2.34 x as long as wide (Fig. 6.5); ovipositor sheaths evenly pilose (as in Figs 5.18 , 6.45) $\qquad$
D. dangerfieldi sp. nov.

19(17) Median field of T3 encircled by crenulate grooves (Fig. 6.37); vein 1a of fore wing present (Fig. 6.30); vein cu-a of hind wing straight meeting vein 1A at almost right angle (Fig. 6.31)
D. sons (Wilkinson)

Median field of T3 present as a raised area (Fig. 6.9); vein 1a of fore wing absent (as in Fig. 4.5); vein cu-a of hind wing meeting vein 1 A at an angle wider than $90^{\circ}$ (as in Fig. 6.29) 20

20(19) Specialised sensilla on ovipositor sheaths present (as in Fig. 5.19); placodes missing on ventro-lateral surface of medio-apical flagellomeres (Fig. 5.9); flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres in an oblique row (as in Figs 5.6-5.8); T1 0.62-1.48 x as long as wide (Fig. 6.8)
D. eclectes (Nixon)

Specialised sensilla on ovipositor sheaths absent (as in Fig. 5.20); placodes intact on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.2); flute benttipped sensilla on ventro-lateral surface of medio-apical flagellomeres scattered (as in Fig. 5.5); T1 2.35-3.2 x as long as wide $\qquad$ D. newguineaensis sp. nov.

21(15) Flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres in an oblique row (as in Figs 5.6-5.8)
D. ashmeadi sp. nov.

Flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres missing or present in scattered form (as in Fig. 5.5) ............................................... 22

22(21) Medial groove of T1 present in more than half of the length of tergite (Fig. 6.43); hind coxa $1.59-1.94 \mathrm{x}$ as long as T 1 D. yousufi sp. nov.

Medial groove of T1 present in less than half of the length of tergite (Fig. 10); hind coxa 1.23-1.58 x as long as T 1 (connexus-group)

23(22) Fore wing vein 1a present (Fig. 6.28); fore wing areolet small and quadrangular (Fig. 6.28)
D. perniciosus (Wilkinson)

Fore wing vein 1a absent (as in Fig. 4.4); fore wing areolet triangular (Fig. 6.20) 24

24(23) Median field of T2 encircled by smooth grooves (Fig. 6.34); apical carina of scutellum present (as in Fig. 6.1); propodeum without costulae or lateral carinae (Fig. 6.34); placodes regularly distributed in double row on all flagellomeres (as in Fig. 5.2); flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres present in a scattered form (as in Fig. 5.5) $\qquad$
D. muzaffari sp. nov.

Median field of T2 present as a raised area (Fig. 6.33); apical carina of scutellum absent (as in Fig. 6.15); propodeum with costulae present but lateral carinae absent (Fig. 6.33); placodes in a double row on basal and medial flagellomeres then overlapping to form a single row on apical flagellomeres (Fig. 5.3); flute bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres absent 25

25(24). Antennal flagellomeres 5-8 white, the rest dark brown; suture between T2 and T3 distinct (Fig. 6.33); T1 1.49-2.34 x as long as wide (Fig. 6.33); $\mathrm{M}+\mathrm{CU}$ of hind wing $0.88-1.02 \mathrm{x}$ as long as $1-\mathrm{M}$; plical cell of hind wing $1.37-1.64 \mathrm{x}$ as long as sub-basal cell; hind coxa 1.59-1.94 x as long as T 1 ................ D. robertsi sp. nov. All antennal segments dark brown; suture between T2 and T3 indistinct (as in Fig. 6.19); T1 2.35-3.2 x as long as wide; $\mathrm{M}+\mathrm{CU}$ of hind wing $0.73-0.87 \mathrm{x}$ as long as $1-\mathrm{M}$; plical cell of hind wing 1.93-2.2 x as long as sub-basal cell; hind coxa

### 6.5 Treatment of Diolcogaster species

6.5.1 Diolcogaster adiastola, sp. nov. (Fig. 6.59)

## Material Examined

Holotype. $\uparrow$, Australian Capital Territory, ‘Black Mtn., xi.1982, I. Naumann \& J. C. Cardale' (ANCI).

Paratypes. Australian Capital Territory: 1 Q, Black Mountain, ix.1982, I.D. Naumann \& J.C. Cardale (ANIC); 7 O, Black Mountain, 27.xi-14.xii.1979, D.H. Colless (ANCI); $1 O^{\prime}$, Piccadilly Circus, ix.1984, J. Lawrence, T. Weir \& M.L. Johnson (ANIC). New South Wales: $1 O^{\prime}$, Royal National Park, ii.1983, I. Gauld (BMNH). Queensland: 5 O', Stanthorpe., 6.v-13.vii, no collector (AEIC). Tasmania: 1 O, Barrow Ck, 8 km NE of Nunamara, 11.i.1983, I.D. Naumann \& J.C. Cardale (ANIC); $1 \bigcirc, 10 \mathrm{~km}$ ENE of Nunamara, 12.i-6.ii.1983, I.D. Naumann \& J.C. Cardale (ANIC); 1 Q, Mt. Field N.P., 8-14.i.1984, L. Masner (CNCI); $1 O^{\text {T, Mt. Barrow }} 1000 \mathrm{~m}$, ii.1983, I. Gauld (BMNH).

## Female

Length. 2.7-3.8 mm.
Colour. Body mostly black, T3-T7 dark brown; basal half of antennae light brown, apical half dark brown; mouth parts light to dark brown; fore and mid leg dark brown; hind leg dark brown except basal half of hind coxa and hind femur which are black, hind tibial spurs yellow; stigma and fore wing venation dark brown, fore wing transparent with brown spots medially as well as apically.

Head. In dorsal view 1.0-1.1 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth; face at widest $1.6-1.8 \mathrm{x}$ as wide as high, weakly punctate with short faint medial longitudinal carina in dorsal half; temples smooth; in lateral view medial temples $1.0-1.2 \mathrm{x}$ as wide as width of eye; eyes $0.5-0.6 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus touching anterior margin of lateral ocelli; distance between lateral ocelli 1.5-1.8 x distance from lateral ocellus to edge of eye; antenna $0.5-0.8 \mathrm{x}$ as long as body, last flagellomere 0.7 x as long as first.

Mesosoma. Scutum 1.3-1.7 x as wide as long, sparsely punctate with white pilosity; notauli absent; scutellar sulcus with 5-7 longitudinal carinae; dorsal scutellum 1.0-1.1 x as wide as long, smooth with sparse pilosity; lateral scutellum carinate; medial posterior band of scutellum smooth; metanotum coarsely carinate; propodeum 1.6-1.7 x as wide as long,
smooth in anterior one-third, areolate-rugose in posterior two-third; medial longitudinal carina complete; propodeal spiracle oval, positioned medially or slightly anterior to midline, surrounded with costulae; lateral pronotum sparsely punctate glabrous medially, only ventral crenulate groove present; propleuron weakly punctate with weak dorsal ridge; mesopleuron carinulate-punctate to punctulate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove weakly strigulate, shallow; metapleuron areolate-carinate and dorsally pilose, except for smooth glabrous antero-median area; hind coxa $0.5-0.9 \mathrm{x}$ as wide as long, 1.4-1.7 x as long as T 1 , punctate, pilose on outer surface; inner hind tibial spur 1.2-1.3 x as long as outer spur, $0.4-0.5 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing glabrous to sparsely pilose on basal and sub-basal cells, rest with evenly dense pilosity; 1 -RS $0.4-0.5 \mathrm{x}$ as long as $1-\mathrm{RS}+\mathrm{M}, 0.4-0.5 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M}$ 1.0 x as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 0.9-1.3 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma $1.9-2.3 \mathrm{x}$ as long as wide; 1-R1 0.6-0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.5-0.7 \mathrm{x}$ as long as width of stigma, straight, forming an obtuse angle with 2-RS; areolet small quadrangular, i.e. 3-RS present but smaller than 2-RS; r-m and apex of 2-RS+M spectral; 1-CUa 0.4-0.5 x as long as 1-CUb; hind wing vannal lobe weakly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.0-1.1 x as long as maximum width, broadening posteriorly, rugulosepunctate and glabrous, medial longitudinal groove complete except at apex; T2 smooth to rugulose, weakly broadened posteriorly, in midline 0.7-1.0 x as long as $\mathrm{T} 1,0.7-1.1 \mathrm{x}$ as long as T3, medial length $0.5-0.6 \mathrm{x}$ as long as maximum width; median field 0.2 x as wide as tergite, parallel-sided to weakly broadening anteriorly, demarcated by smooth lateral grooves; suture between T 2 and T 3 distinct; T 3 in midine $0.4-0.6 \mathrm{x}$ as long as maximum width, smooth, sparsely pilose at apex; T4-T7 smooth, with sparse pilosity apically; hypopygium sparsely pilose, medio-ventral length $0.6-0.7 \mathrm{x}$ as long as hind basitarsus; ovipositor sheaths 0.1-0.3 x as long as hind basitarsus, with few hairs on apical half, specialised sensilla absent.

## Male

As for females except antenna 1.2 x as long as body.

Unknown.

## Comments

This species is similar to some other spretus-group species in that the antennae are shorter than the body. However, D. adiastola differs from these and other Diolcogaster species in having a short inner hind tibial spur and a well-defined median field on T 2 . Because of its apparent similarity with numerous other Diolcogaster, this species is here named after the Greek adiastolos meaning confused. This species is known from southeastern Australia and Tasmania (Fig. 6.59).
6.5.2 Diolcogaster alkingara sp. nov. (Figs 4.9, 5.2, 6.1-6.4, 6.54)

## Material Examined

Holotype. O, New Guinea, 'New Guinea, Wabo, Gulf Province Papua, 12-18.xi.1975, J.R. Pippet' (CNCI).

Paratypes. New Guinea: $30^{n}$, same data as holotype (CNCI); $20^{7}$, Jimmy Valley, 650 m, 7.ii-2.iii.1979, J. Sedlacek, (AEIC); $1 O^{\prime}$, Madang, vi.1969, B. Heinrich, (AEIC). Queensland: $10^{7}$, Kuranda, 300 m , i-ii.1984, J. Sedlacek, (CNCI); $10^{\prime \prime}$, Kuranda, 1.5 km SE, 16-17.v.1980, I.D. Naumann \& J.C. Cardale (ANIC).

## Female

Length. 3.7 mm .
Colour. Body generally black; scape and pedicle yellow, flagellum brown; basal two segments of labial and maxillary palps brown, rest creamy-white; fore leg with coxa black, fore trochantellus and femur dark brown, tibia and tarsus yellow, mid coxa and trochantellus yellow, mid femur and tibia brown, tarsus yellow, hind leg black except for apex of hind coxa, hind trochantellus and basal half of tibia which are yellow; stigma dark brown; fore wing with dark brown spot on apex; T1 yellow with dark brown apical margin, T2 dark brown to black with postero-lateral yellow spot on lateral fields; T4-T7 and hypopygium dark brown.

Head. In dorsal view as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons rugulose; face at widest as wide as high, acinoserugulose with faint medial longitudinal carina in dorsal half; temples striolate; in lateral view
medial temples 0.6 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between inner margin of lateral ocelli as much as distance from outer margin of lateral ocellus to edge of eye; antenna 1.1 x as long as body, first flagellomere 3.7 x as long as wide.

Mesosoma. Scutum 1.6 x as wide as long, areolate with fine granulate background and sparse white pilosity; scutellar sulcus with 7 longitudinal carinae; dorsal scutellum 1.4 x as wide as long with scattered weak punctation anteriorly, smooth posteriorly, sparsely pilose; lateral scutellum generally coarsely carinate except for smooth median area, lateral band of scutellum smooth, with posterior margin carinate; medial posterior band of scutellum with an excavated area interrupted by short longitudinal carina; metanotum coarsely crenulate; dorsellum about as long as anteriorly wide, smooth anteriorly, with white pilosity in posterior half; propodeum smooth, 2.0 x as wide as long, medial longitudinal carina with radiating short carinae on either side; propodeal spiracle positioned medially, surrounded by costulae which is joined with posterior margin of propodeum by a longitudinal carina; lateral pronotum smooth, glabrous medially, punctate and pilose in dorsal half; propleuron carinulate, with dorsal ridge; mesopleuron areolate-punctate antero-dorsally, smooth posteriorly beside carinate pleural suture, epicnemial furrow deep, precoxal groove shallow, strigate; metapleuron areolate-punctate with strong pilosity, except for smooth, glabrous antero-median area; hind coxa 0.6 x as wide as long, 1.9 x as long as T 1 , punctate with micro-punctation in background, dorsally pilose.

Wings. Fore wing sparsely pilose in basal half, evenly dense in apical half; stigma 2.5 x as long as wide; 1-R1 0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r}$ as long as width of stigma, forming an obtuse angle with RS; areolet slit-like, r-m and apex of 2-RS+M unsclerotised; 1-CUa 0.6 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe weakly concave without hairs beyond its widest part; 2-SC+R 0.4 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 $1.2 \times$ as long as apical width, broadening posteriorly, anterior half smooth, glabrous, posterior half carinate with sparse pilosity, medial longitudinal groove shallow in anterior half, deeper in posterior half, posterior margin of tergite with few coarse crenulae; T 2 in midline 0.6 x as long as $\mathrm{T} 1,0.8 \mathrm{x}$ as long as T 3 , medial length 0.7 x as long as anterior width, slightly broadening posteriorly, anterior margin straight medially with few coarse crenulae, antero-median node absent, posterior margin broadly emarginate, lateral
fields carinate; median field 0.4 x as wide as T 2 at anterior margin, carinate, bordered on either side by deep crenulate groove; T 3 in midline 0.8 x as long as wide across anterior margin, carinate, anterior margin medially convex and strongly crenulate, posterior margin rounded at corners, smooth; median field 0.5 x as long as medial length and 0.5 x as wide as anterior width of T3, carinate, widest anteriorly; suture between T2 and T3 deep and sculptured; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, 0.5 x as long as medial length of T3; ovipositor sheaths rounded apically, with few scattered hairs in apical half, specialised sensilla present, obliquely truncate at apex.

## Male

As for females except as follows: Fore leg with femur and tibia light brown, mid tibia yellow; head in dorsal view $0.9-1.0 \mathrm{x}$ as wide as scutum; vertex pilose or glabrous; face at widest 1.1-1.2 x as wide as high; antenna 1.1-1.2 x as long as body, robust, first flagellomere 2.6-2.8 x as long as wide; scutum $1.5-1.6 \mathrm{x}$ as wide as long; propodeum 1.9-2.1 x as wide as long; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long. 1.8-2.0 x as long as T 1 ; inner hind tibial spur 1.31.5 x as long as outer, $0.7-0.9 \mathrm{x}$ as long as hind basitarsus; stigma 2.3-2.5 x as long as wide; $\mathrm{r} 1.0-1.1 \mathrm{x}$ as long as width of stigma; 1-CUa $0.5-0.7 \mathrm{x}$ as long as $1-\mathrm{CUb} ; 2-\mathrm{SC}+\mathrm{R} 0.3-0.4 \mathrm{x}$ as long as $1 \mathrm{r}-\mathrm{m}$; $\mathrm{T} 11.0-1.2 \mathrm{x}$ as long as apical width; T 2 in midline $0.6-0.8 \mathrm{x}$ as long as T 1 , $0.8-1.0 \mathrm{x}$ as long as T3, medial length $0.6-0.7 \mathrm{x}$ as long as anterior width, tergite parallelsided or slightly broadening posteriorly; median field $0.3-0.4 \mathrm{x}$ as wide as tergite at anterior margin; T3 in midline $0.7-0.8 \mathrm{x}$ as long as wide across anterior margin with median field 0.5 0.6 x as long as medial length, $0.5-0.6 \mathrm{x}$ as wide as anterior width of T3.

## Host

Unknown.

## Comments

D. alkingara can be distinguished from other Australasian basimacula-group species by the presence of an anteriorly widened and carinate median field on T2. This species is here named after an aboriginal word alkingar meaning eye, due to the characteristic coloured 'eye-
spot's on the postero-lateral corners of the second metasomal tergite. This species has been recorded from New Guinea and north Queensland (Fig. 6.54).
6.5.3 Diolcogaster ashmeadi, sp. nov. (Fig. 6.60)

## Material Examined

Holotype. ©, Tasmania, '9 km E Scottsdale, 12.i.1983, I.D. Naumann \& J.C. Cardale' (ANIC).

Paratypes. New South Wales: 1 Q, Monga State Forest, 1.ii.1984, L. Masner (CNCI); $1 Q$, Barrington Tops, 8-9.i.no year, no collector (AEIC); $2 \bigcirc^{\circ}$, Nerriga, 19.i-4.ii.1984, L. Masner (CNCI); $1 \mathrm{O}^{\text {T, }}$, Royal National Park., 20 km S. of Sydney, 5-14.vi.1978, S. \& J. Peck
 21.xii.1974, G. Daniels (UQBA). Queensland: 1 Q, Brisbane, i-vi.1971, J. Sedlacek (CNCI); $1 \bigcirc^{7}$, Mt. Glorious, 17.xi.no year, no collector, (AEIC); $1 O^{7}$, Mt. Tambourine, x.1977, I.D. Galloway (BMNH); $1 O^{\prime \prime}$, Mt. Glorious, 10-31.i.1982, no collector (QDPI). Tasmania: $1 O^{\prime \prime}$, data as holotype. Victoria: $2 O^{\prime \prime}$, Wilson Prom National Park, 1116.v.1978, S. \& J. Peck (CNCI); 1 O', Frankston, 12.iii.1966, Neboiss (MVMA); $1 O^{*}$, Warburton Acheron, 7.v.1978, S. \& J. Peck (CNCI).

## Female

Length. 3.0-3.7 mm.
Colour. Body generally black; metasoma dark brown to black except for lateral membranous area of T1 and entire T2-T3 which are white-yellow to light brown; labial and maxillary palps light to dark brown; antenna dark brown; fore leg light to dark brown; mid and hind leg dark brown to black; hind tibial spurs yellow; stigma and fore wing venation dark brown, fore wing transparent and without any brown spots or with brown spots on apices of marginal, submarginal, discal and sub-basal cells, sub-discal cell entirely brown.

Head. In dorsal view 1.0-1.1 x as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons strongly punctate; face at widest $1.2-1.3 \mathrm{x}$ as wide as high, strongly punctate with faint medial longitudinal carina in dorsal half; temples punctate; in lateral view medial temples $0.6-0.7 \mathrm{x}$ as wide as width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus touching anterior margin of lateral ocelli; distance between lateral ocelli 1.0-1.3 x distance from lateral ocellus to edge of eye; antenna 1.0-1.2 x as long as body, last flagellomere 0.6 x as long as first, pre-apical antennal segment 2.2-2.6 x as long as wide.

Mesosoma. Scutum 1.3-1.7 x as wide as long, strongly punctate, with white pilosity; scutellar sulcus with 3-6 longitudinal carinae; dorsal scutellum 1.0 x as wide as long,
strongly punctate with sparse white pilosity; lateral scutellum carinate; medial posterior band of scutellum interrupted by strong to weak rugosity; metanotum rugose-carinate, posterior margin medially smooth to interrupted by strong rugosity; propodeum 1.3 x as wide as long, strongly rugose-punctate, medial longitudinal carina strong; propodeal spiracle oval, positioned medially or slightly anterior to midline, without costulae; lateral pronotum strongly rugose, weakly pilose to glabrous; propleuron punctate, with weak dorsal ridge; mesopleuron strongly rugose-punctate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, strongly punctate; metapleuron punctate and dorsally pilose, except for smooth glabrous anteromedial area; hind coxa $0.6-0.7 \mathrm{x}$ as wide as long, $1.7-1.8 \mathrm{x}$ as long as T , strongly punctate and pilose on outer surface; inner hind tibial spur 1.3-1.5 x as long as outer spur, 0.6-0.7 x as long as hind basitarsus.

Wings. Fore wing sparsely pilose on basal and sub-basal cells, rest with evenly dense pilosity; 1-RS 0.2 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.3 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.2-1.3 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 0.7-0.9 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma $2.5-2.6 \mathrm{x}$ as long as wide; 1-R1 0.6-0.8 x distance from stigma to 4-RS; r 0.4-0.6 x as long as width of stigma, forming an obtuse angle with 2-RS; 3-RS present; areolet small quadrangular; r-m and apex of $2-\mathrm{RS}+\mathrm{M}$ spectral; 1CUa $0.4-0.6 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to weakly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.6-3.3 x as long as apical width, parallel-sided to weakly narrowed at apex, smooth to strigate-punctate, weakly pilose to glabrous, medial longitudinal groove deep in anterior half weak in posterior half; T 2 smooth, in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.6-0.8$ x as long as T3, medial length 0.6 x as long as maximum width; median field narrow, indicated by yellow raised area; suture between T 2 and T 3 indistinct; T 3 in midline 0.5 x as long as maximum width, smooth, sparsely pilose to glabrous; T4-T7 smooth, pilose; hypopygium pilose, medio-ventrally $0.4-0.7 \mathrm{x}$ as long as hind basitarsus; ovipositor sheaths $0.2-0.4 \mathrm{x}$ as long as hind basitarsus, pilose in apical half, specialised sensilla absent.

Male
As for female.

Unknown.

## Comments

D. ashmeadi is the only known Australasian representative of the xanthaspis-group. It is not closely related to any other species, but is similar to D. harrisi from which it differs in having a large fore wing areolet. This species is here named after W. H. Ashmead, the famous American Hymenopterist who worked around the turn of the century. It is restricted to coastal south-eastern Australia and Tasmania (Fig. 6.60).

### 6.5.4 Diolcogaster dangerfieldi, sp. nov. (Figs 6.5, 6.52)

## Material Examined

Holotype. ©, Queensland, 'Leo Creek Road, ca. 500 m , Mcllwraith Range, 30km NE of Coen, 29.vi-4.vii.1976, G.B. \& S.R. Monteith' (ANIC);

Paratypes. Queensland: $1 O^{\prime \prime}, 143.17 \mathrm{E}, 9 \mathrm{~km}$ ENE Mt Tozer, 5-10.vii.1986, J.C. Cardale (ANIC). New Guinea: $1 \bigcirc, 1 O^{\prime}$, Bulolo, 13.ii-13.iii.1979, 800 m , J. Sedlacek (AEIC).

## Female

Length. 2.9-4.6 mm.
Colour. Body generally black; scape and pedicle light brown, flagellum dark brown; basal two segments of labial and maxillary palps brown, rest yellow; fore leg light brown, mid coxa black to dark brown, mid trochantellus tibia and tarsus light brown, mid femur dark brown, hind leg black except for trochantellus, basal half of tibia and tibial spurs which are yellow; stigma dark brown, fore wing with brown spot on apex; metasoma dark brown to black with T1 yellow.

Head. In dorsal view 0.8-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; lateral frons rugulose; face at widest $1.2-1.4 \mathrm{x}$ as wide as high, acinose, with faint medial longitudinal carina in dorsal half; temples striolate to striolate-punctate; in lateral view medial temples 0.5 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between inner margin of lateral ocelli 1.0-1.1 x distance from lateral ocellus to edge of eye; antenna 1.0-1.2 x as long as body, first flagellomere $3.5-3.8 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.5-1.6 x as wide as long, areolate-punctate with fine granulate background microsculpture and sparse white pilosity; notauli indicated by dark weaklyimpressed areolate-punctate depressions; scutellar sulcus with 5-6 longitudinal carinae; dorsal scutellum 1.4 x as wide as long, areolate-punctate with fine granulate background microsculpture, sparsely pilose; lateral scutellum generally coarsely carinate but smooth medially, lateral band of scutellum smooth, with posterior margin carinate; medial posterior band of scutellum interrupted by longitudinal carinae or punctation; metanotum coarsely crenulate except for smooth sub-margin, dorsellum about as long as anteriorly wide; propodeum 1.9-2.1 x as wide as long, medial longitudinal carina with radiating short carinae on either side, rest of propodeum generally smooth; propodeal spiracle oval, positioned medially or slightly anterior to midline, surrounded by costula which is joined to posterior margin of propodeum by a longitudinal carina; lateral pronotum smooth medially with weak strigations and pilosity in dorsal half; propleuron with dorsal ridge; mesopleuron strigate, smooth posteriorly beside carinate pleural suture, epicnemial furrow deep, precoxal groove shallow, strigate; metapleuron areolate-carinate and pilose, except for smooth, glabrous antero-median area; hind coxa $0.6-0.7 \mathrm{x}$ as wide as long, $1.6-1.7 \mathrm{x}$ as long as T 1 , punctate mixed with micro-punctation in background, sparsely pilose, ventrally areolate; inner hind tibial spur 1.5 x as long as outer spur, 0.8 x as long as hind basitarsus.

Wings. Fore wing with scattered pilosity in basal half evenly dense in apical half; stigma 2.8-3.0 x as long as wide; 1-R1 0.7 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.9-1.1 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with $2-R S$; areolet slit-like; r-m and apex of 2-RS+M unsclerotised; 1-CUa 0.7-0.8 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to slightly concave, glabrous beyond its widest part; 2-SC+R 0.5 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 0.9-1.0 x as long as apical width, broadening posteriorly, anterior half smooth and glabrous, posterior half weakly punctate and with sparse pilosity, medial longitudinal groove shallow in anterior half, deeper in posterior half; T 2 in midline 0.6-0.7 x as long as $\mathrm{T} 1,0.8 \mathrm{x}$ as long as T 3 , medial length $0.6-0.7 \mathrm{x}$ as long as anterior width, slightly broadening posteriorly, anterior margin straight with few weak crenulae, antero-median node slightly raised above level of anterior margin, posterior margin weakly emarginate, lateral fields weakly punctate to carinate-punctate, with sparse white pilosity; median field 0.3-0.4 x as wide as tergite at anterior margin, entirely smooth to anteriorly smooth, posteriorly
carinate, bordered on either side by shallow, smooth to weakly crenulate groove; T3 in midline $0.7-0.8 \mathrm{x}$ as long as wide across anterior margin, strigate to carinulate-punctate with sparse pilosity, anterior margin medially convex and crenulate, posterior margin rounded at corners, smooth, median field of T3 $0.6-0.7 \mathrm{x}$ as long as medial length, $0.5-0.7 \mathrm{x}$ as wide as anterior width of tergite, weakly carinate, widest anteriorly; suture between T2 and T3 deep and crenulate; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, $0.3-0.6 \mathrm{x}$ as long as medial length of T 3 ; ovipositor sheaths rounded apically, with hairs on their entirety, specialised sensilla present, truncate at apex.

## Male

As for females except as follows: Fore and mid leg light brown except dark brown coxae; in lateral view medial temples 0.6 x width of eye; antennae more robust, first flagellomere 2.7-3.1 x as long as wide; hind coxa 1.7-2.0 x as long as T 1 ; stigma 2.5-2.7 x as long as wide; 1-CUa 0.6 x as long as $1-\mathrm{CUb} ; 2-\mathrm{SC}+\mathrm{R} 0.3-0.4 \mathrm{x}$ as long as $1 \mathrm{r}-\mathrm{m}$.

Host
Unknown.

## Comments

D. dangerfieldi is close to $D$. alkingara within the basimacula-group but can be distinguished from it and other species by the presence of strigate sculpturing on the mesopleuron, and the median field on T2 being smooth to very weakly carinate. This species is named after Dr. Paul C. Dangerfield in Crop Protection at Adelaide University. It is apparently restricted in distribution to north Queensland and New Guinea (Fig. 6.52).
6.5.5 Diolcogaster dichromus, sp. nov. (Figs 6.13, 6.59)

Material Examined
Holotype. ©, Queensland, '29 Km E of Texas, 27.xi.1976, E.M. Exley' (ANIC).

## Female

Length. 3.3 mm .

Colour. Head, scutum, scutellum and fore leg orange-yellow; metanotum, propodeum, mesosoma, hind coxa and hind femur black, mid leg, hind tibia and hind tarsus dark brown; antennae dark brown; labial and maxillary palps yellow; stigma dark brown.

Head. In dorsal view as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons weakly rugose-punctate to smooth; face at widest 1.4 x as wide as high, strigate-punctate; clypeus 0.3 x as high as face, 0.9 x as high as labrum, 3.3 x as wide as high; labrum 2.3 x as wide as high; temples smooth; in lateral view medial temples 0.7 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus passing in front lateral ocelli; distance between inner margin of lateral ocelli as much as distance from outer margin of lateral ocellus to edge of eye; antenna 0.6 x as long as body, pubescent, first flagellomere 1.9 x as long as wide, flagellomeres $10-12,1.2-1.4 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.5 x as wide as long, with sparse white pilosity, medial scutum smooth, lateral scutum weakly punctulate; notauli absent; scutellar sulcus shallow, with 12 weak longitudinal carinae; dorsal scutellum 1.1 x as wide as long, weakly punctate, sparsely pilose; lateral scutellum coarsely carinate, lateral band of scutellum smooth, with posterior margin closely impressed to metanotum; medial posterior band of scutellum smooth; metanotum coarsely crenulate, dorsellum smooth, glabrous, about as long as anterior width; propodeum 1.9 x as wide as long, convex, medial longitudinal carina strong; lateral fields of propodeum punctulate; propodeal spiracle surrounded by strong costula, space between spiracle and costula weakly sculptured; lateral pronotum smooth, glabrous, with weakly crenulate ventral groove; propleuron punctulate, without dorsal ridge; mesopleuron smooth, glabrous except for weak punctation antero-dorsally; epicnemial furrow deep; precoxal groove deep, smooth; metapleuron with weak punctation posteriorly, but smooth and glabrous medially; fore femur 0.4 x as wide as long; hind coxa 0.7 x as wide as long, 1.5 x as long as T1, weakly punctate, glabrous on outer surface, ventrally with dense white pilosity; inner hind tibial spur 1.5 x as long as outer spur, 0.9 x as long as hind basitarsus.

Wings. Fore wing with sparse pilosity over basal and sub-basal cells, evenly dense over rest of the wing; stigma 1.5 x as long as wide; 1-R1 0.7 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r}$ 0.6 x as long as width of stigma, meeting straight on $2-\mathrm{RS}$, forming a small quadrangular areolet; r-m and apex of $2-R S+M$ spectral; 1-CUa 0.6 x as long as $1-\mathrm{CUb}$; hind wing vannal
lobe weakly convex, without row of long hairs beyond its widest part; 2-SC+R 0.4 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 1.6 x as long as maximum apical width, broadened almost medially, then slightly narrowed at apex, anterior half smooth, glabrous, posterior half weakly punctate, with sparse pilosity, deep medial longitudinal groove present; T 2 in midline 0.4 x as long as T 1 , 0.8 x as long as T 3 , medial length 0.5 x as long as maximum anterior width, slightly broadening posteriorly, anterior margin slightly concave medially, posterior margin straight, smooth, with scattered white pilosity; median field absent; suture between T2 and T3 weak; T 3 in midline 0.5 x as long as wide across anterior margin, smooth, anterior and posterior margins straight; tergite with transverse row of hairs in posterior half; median field absent; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, 0.5 x as long as hind tibia; ovipositor sheaths 0.4 x as wide as long, 0.3 x as long as hypopygium, with hairs in apical half.

## Male

Unknown.

Host
Unknown.

## Comments

D. dichromus differs from other Australasian spretus-group and other Diolcogaster species in having T 1 bulging medially, T 2 without a median field, and T 2 and T 3 being poorly separated. This species is here named using Greek words di and chroma meaning two colours, after its black and orange-yellow body. This species is so far known only from south-eastern Queensland (Fig. 6.52).
6.5.6 Diolcogaster eclectes (Nixon) (Figs 5.9, 6.7-6.9, 6.58)

Protomicroplitis eclectes Nixon, 1965: 246; Shenefelt, 1973: 777.
Diolcogaster eclectes Mason, 1981: 114.

## Material Examined

Holotype. 〇, Philippines, 'Luzon, Mt Makiling' (USNM).
Other specimens examined. New Guinea: 2 O, Wabo, Gulf Province Papua, 1218.xi.1975, J.R. Pippet (CNCI); $1 O^{\prime \prime}$, Western Dist. Morehead, 20-30.ix.1972, J. Stibick (CNCI); 1 O', Wau, $^{2}$ 12-1400m, 9-17.ix.1972, J.V.D. Vecht (RMNH); 1 O, New Britain, Cape Hoskins, vi.1973, no collector (CNCI). Queensland: 1 ¢, 12.43S 143.17E, 9km ENE Mt Tozer, 5-10.vii.1986, J.C. Cardale (ANIC); 1 O, 12.44S 143.17E, 8km bN Mt Tozer, 7.vii.1986, J.C. Cardale, (ANIC); $1 O^{\prime}, 12.44 \mathrm{~S} 143.14 \mathrm{E}, 3 \mathrm{~km}$ ENE Mt Tozer. 28.vi4.vii.1981, J.C. Cardale (ANIC); $1 \bigcirc, 1 O^{\prime}, 15.50 \mathrm{~S} 145.20 \mathrm{E}$, Gap Ck, 5 km ESE Mt Finnigan, 13-16.v.1981, I.D. Naumann (ANIC); $2 O^{\prime \prime}$, 15.47S 145.14E, Shiptons Flat, 1618.v.1981, I.D. Naumann (ANIC); 1 O. Cairns, Crystal Cascades, 19.iv.1967, D.H. Colless (ANIC); 1 Q, Cooloola Nat Pk, 7.iii.1984, I.D. Galloway (ANIC).

## Female

Length. 3.1-4.1 mm.
Colour. Body generally black; scape and pedicle yellow, flagellum brown; labial and maxillary palps entirely yellow to basal two segments of labial and one of maxillary palps brown, rest yellow; fore and mid leg yellow to light brown, hind coxa black and ventrally with or without apical yellow spot, hind femur entirely dark brown to basal half yellow, apical half brown, hind trochantellus, basal half of tibia and hind tibial spurs yellow, apical half of hind tibia and hind tarsus dark brown; stigma dark brown, fore wing with brown apical spot; T1 yellow to brown, T2 entirely black to, basal half yellow, apical half black; T4-T7 and hypopygium dark brown to black

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons rugulose; face at widest 1.2-1.3 x as wide as high, acinose-striolate with faint medial longitudinal carina in dorsal half; temples striolate to striolate-punctate; in lateral view medial temples 0.6 x width of eye; eyes $0.5-0.6 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between inner margin of lateral ocelli 1.0-1.3 x distance from outer margin of lateral ocellus to edge of eye; antenna $0.9-1.0 \mathrm{x}$ as long as body, first flagellomere 2.7-3.1 x as long as wide.

Mesosoma. Scutum 1.4-1.7 x as wide as long, areolate-punctate with fine granulate background and sparse white pilosity; scutellar sulcus with 6-10 longitudinal carinae; dorsal scutellum 1.4-1.5 x as wide as long, areolate-punctate to punctate with fine granulate background, sparsely pilose; lateral scutellum generally coarsely carinate, smooth medially, lateral band of scutellum smooth with posterior margin carinate; medial posterior band of
scutellum interrupted by an excavated area with 1-2 longitudinal carinae, separated from scutellum by a strong transverse carina; metanotum coarsely crenulate except for smooth sub-margin, dorsellum about as long as anteriorly wide; propodeum 1.9-2.1 x as wide as long, weakly punctate, medial longitudinal carina with radiating short carinae on either side; propodeal spiracle oval, positioned medially, surrounded by costula which is joined with posterior margin of propodeum by a longitudinal carina; lateral pronotum smooth medially with weak punctation and sparse pilosity in dorsal and posterior half; propleuron with dorsal ridge; mesopleuron areolate to punctate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture, epicnemial furrow deep, precoxal groove shallow, weakly strigate; metapleuron areolate-carinate and dorsally pilose, except for smooth, glabrous antero-median area; hind coxa $0.6-0.7 \mathrm{x}$ as wide as long, $1.7-1.8 \mathrm{x}$ as long as T 1 , areolatepunctate with sparse pilosity, except weak, sparse punctation on outer surface mixed with background micro-punctation; inner hind tibial spur 1.2-1.6 x as long as outer spur, 0.7-0.9 x as long as hind basitarsus.

Wings. Fore wing without pilosity on basal two-third of sub-basal and plical cells, rest with evenly dense pilosity; stigma $2.5-3.0 \mathrm{x}$ as long as wide; 1-R1 0.8 x distance from stigma to 4-RS; r 0.9-1.1 x as long as width of stigma, forming an obtuse angle with RS; areolet slit-like, $\mathrm{r}-\mathrm{m}$ and apex of $2-\mathrm{RS}+\mathrm{M}$ unsclerotised; 1-CUa $0.8-0.9 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to slightly concave, without hairs beyond its widest part; 2SC+R 0.3-0.5 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 0.9-1.0 x as long as apical width, broadening posteriorly, anterior half smooth, glabrous, posterior half areolate to carinate-punctate with sparse pilosity, medial longitudinal groove diverging outward posteriorly, forming posterior margin of T 1 crenulate; T 2 in midline $0.7-0.8 \mathrm{x}$ as long as $\mathrm{T} 1,0.8-1.0 \mathrm{x}$ as long as T 3 , medial length $0.7-0.8 \mathrm{x}$ as long as anterior width, tergite parallel sided to slightly broadened posteriorly, anterior margin straight with few coarse crenulae, antero-median node absent, posterior margin weakly emarginate, lateral fields areolate to carinate-punctate; median field $0.1-0.2 \mathrm{x}$ as wide as tergite at anterior margin, smooth, bordered on either side by crenulate groove; T3 in midline $0.7-0.9 \mathrm{x}$ as long as wide across anterior margin, carinate with few scattered punctures, anterior margin medially convex and strongly crenulate, posterior margin rounded at corners, smooth; median field as long as T3, 0.3 x as wide as anterior width of tergite, smooth to
weakly carinulate posteriorly; suture between T 2 and T 3 deep and crenulate; T4-T7 smooth, with sparse row of hairs posteriorly; hypopygium with sparse pilosity; ovipositor sheaths rounded apically, with hairs in apical half, specialised sensilla present, which are spatulate, up-curved and obliquely truncate at apex.

## Male

As for females except as follows: Antennae 1.1-1.2 x as long as body; T 2 with anteromedian node slightly raised above level of anterior margin.

Host
Unknown.

## Comments

D. eclectes can be separated from other Australasian basimacula-group species by having a moderately elongate $\mathrm{M}+\mathrm{CU}$ vein, an elongate raised median field on T 3 and specialised sensilla on the ovipositor sheaths. Previously described from New Guinea (Nixon 1965), the species is here recorded from mainland Australia for the first time, from north to south coastal Queensland (Fig. 6.58).
6.5.7 Diolcogaster euterpus (Nixon) (Figs 4.8, 6.14, 6.60)

Protomicroplitis euterpe Nixon, 1965: 250; Shenefelt, 1973: 777.
Diolcogaster euterpe Mason, 1981: 114; Austin and Dangerfield, 1992: 27.

## Material Examined

Holotype. Q, Dutch New Guinea, 'Cyclops Mts., about 3,500 ft., iii.1936, L.E. Cheesman' (BMNH).

Other specimens examined. New Guinea: 1 ○, Bayier R. Jimmi Valley, 1800 m, 27.xii.1978-26.i.1979, J. Sedlacek (AEIC); 1 O゙, BayierR., 1100 m, 6-25.ii.1979, J. Sedlacek (AEIC)

Female
Length. 4.6 mm .

Colour. Head, propodeum, metasoma and legs light brown; scutum, scutellum and metanotum dark brown; propleuron dark brown on dorsal half, light brown on ventral; antennae dark brown; stigma and wing-venation dark brown, wings uniformly infuscate.

Head. In dorsal view 1.1 x as wide as scutum; vertex glabrous, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth; face at widest 1.4 x as wide as high, smooth with short faint medial longitudinal carina in dorsal half; temples smooth; in lateral view medial temples 0.9 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between lateral ocelli 0.9 x distance from lateral ocellus to edge of eye; antenna 1.3 x as long as body, last flagellomere 0.8 x as long as first.

Mesosoma. Scutum 1.4 x as wide as long, smooth to weakly punctate, with sparse white pilosity; notauli absent; scutellar sulcus with 6 longitudinal carinae; dorsal scutellum as wide as long, smooth, with sparse pilosity; lateral scutellum coarsely carinate; medial posterior band of scutellum smooth; metanotum coarsely crenulate; propodeum 2.0 x as wide as long, smooth, medial longitudinal carina weak; propodeal spiracle oval, positioned medially or slightly anterior to midline, without costulae; lateral pronotum excavated, smooth ventrally smooth; propleuron smooth without dorsal ridge; mesopleuron smooth; epicnemial furrow deep; precoxal groove shallow, weakly punctate; metapleuron smooth and glabrous; hind coxa 0.4 x as wide as long, 2.3 x as long as T 1 , with sparse punctation, glabrous on outer surface; inner hind tibial spur 1.8 x as long as outer spur.

Wings. Fore wing with evenly dense pilosity; $1-\mathrm{RS} 0.2 \mathrm{x}$ as long as $1-\mathrm{RS}+\mathrm{M}, 0.2 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.2 \mathrm{x}$ as long as $1-\mathrm{M}$; m-cu 1.3 x as long as $2-\mathrm{RS}+\mathrm{M}$; stigma 3.2 x as long as wide; 1-R1 0.9 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 1.2 \mathrm{x}$ as long as width of stigma, forming weakly acute angle with 2-RS; areolet slit-like; r-m dividing 2-RS in to $2-\mathrm{RSa}$ and 2-RSb; r-m and apex of 2-RS+M spectral; 1-CUa 0.6 x as long as 1-CUb; hind wing vannal lobe weakly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.1 x as long as maximum width, broadening posteriorly, tergite smooth and glabrous, weak medial longitudinal groove present in anterior three-quarters, absent in posterior one-quarter; T 2 smooth, in midline 0.8 x as long as T 1 , as long as T 3 , medial length 0.5 x as long as maximum width, broadening posteriorly, anterior margin straight, posterior margin strongly concave medially; median field 0.2 x as wide as maximum width of tergite,
slightly broadening anteriorly, bordered on either side by smooth grooves which continue postero-laterally and separate T 2 from T 3 distinctly; T 3 in midline 0.4 x as long as maximum width, anterior margin medially convex, straight posteriorly, tergite smooth with few hairs apically; T4-T7 smooth, with sparse hairs medially; hypopygium with sparse pilosity, medio-ventral length 0.4 x as long as hind basitarsus; ovipositor sheaths 0.2 x as long as hind basitarsus, truncate apically, with hairs in apical half, specialised sensilla absent.

## Male

As for females except as follows: Metasoma dark brown except anterior half of T1 which is light brown; head, mesosoma and mesopleuron light brown; hind trochantellus, femur, tibia and tarsus dark brown; median field of T2 parallel sided; stigma 3.9 x as long as wide; r 1.5 x as long as width of stigma; T 2 medially 0.7 x as long as T 3 .

## Host

Unknown.

## Comments

$D$. euterpus is close to $D$. nixoni sp. nov. with which it forms the euterpus-group. However, it can be separated from the latter species by T1 widening posteriorly and T2 divided into three fields. This species has only been recorded from New Guinea (Fig. 6.60).
6.5.8 Diolcogaster hadrommatus, sp. nov. (Figs 6.26, 6.27, 6.55)

## Material Examined

Holotype. O, Northern Territory, '23.41S 134.15E, 19 km E of Alice Springs, 25.ix.1978, J.C. Cardale' (ANIC).

Paratypes. New South Wales: 1 O, Wilton, 19.xii.1972, L.S. Willan (ANIC); 1 O, Fowlers Gap, 29.xi-20.xii.1981, J.C. Cardale (ANIC). Northern Territory: $7 \bigcirc$, same data as holotype, $25 . \mathrm{ix} .1978$ \& 1-5.x.1978, J.C. Cardale (ANIC). Queensland: 1 OT, Pistol Gap nr Byfield, 10.i.1970, G.A. Halloway (AMSA). South Australia: 1 Q, 45 km NE of Welbourn Hill, 20.ix.1978, J.C. Cardale (ANIC). Western Australia: 2 O, 29 km SEbyE of Coolgardie, 5.v.1983, E.S. Nielsen \& E.D. Edwards (ANIC); 1 ¢, 4 km WNW of Martin's Well, West Kimberley, 28.iv.1977, D.H. Colless (ANIC); $1 \bigcirc, 35 \mathrm{~km}$ N. of Mt Aloysius, 16.xi.1977, T.A. Weir (ANIC); 2 Q, 2 mi . SSW of Dongara, 15.x.1970, D.H. Colless (ANIC); 1 Q, 8 mi. ENE of Millstream, 20.x.1970, D.H. Colless (ANIC).

Other specimens examined. Queensland: $2 \bigcirc, 11 \mathrm{~km}$ WbyN Bald Hill, Mcllwraith Ra. $500 \mathrm{~m}, 26 . v i-13 . v i i .1989$, I.D. Naumann (ANIC);

## Female

Length. 3.0-4.0 mm.
Colour. Body generally light brown to dark brown or black; antennae dark brown; labial and maxillary palps light brown to yellow; mesosoma entirely light brown to dark brown, or scutum light brown, scutellum, metanotum and propodeum dark brown, to scutum and scutellum light brown, metanotum and propodeum dark brown; fore and mid leg light brown except mid coxa which is light brown to dark brown, hind leg light brown to dark brown except hind tibial spurs which are yellow; stigma dark brown, fore wing transparent; metasoma entirely light brown to dark brown, or T1 light brown and rest dark brown, to T1T3 light brown to yellow, rest dark brown.

Head. In dorsal view 1.1-1.2 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons weakly rugulose; face at widest $1.0-1.3 \mathrm{x}$ as wide as high, acinose-rugulose to rugulose-punctate with faint medial longitudinal carina in dorsal half; temples rugulose to rugulose-punctate; in lateral view medial temples $0.1-0.2 \mathrm{x}$ width of eye; eyes 0.7 x as wide as high; ocelli on a higher stammaticum; tangent to posterior margin of anterior ocellus passing above anterior margin of lateral ocelli; distance between inner margins of lateral ocelli 2.5-5.0 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.7-1.1 x as long as body.

Mesosoma. Scutum 1.4-1.6 x as wide as long, densely punctulate with white pilosity; notauli indicated by weakly-impressed punctulate depressions; scutellar sulcus with 6-10 longitudinal carinae; dorsal scutellum $0.9-1.1 \mathrm{x}$ as wide as long, with sparse punctation and smooth background, sparsely pilose; lateral scutellum generally smooth except for a few carinae posteriorly; medial posterior band of scutellum interrupted by weak rugosity; metanotum smooth to weakly crenulate, dorsellum about as long as anteriorly wide; propodeum 1.8-2.0 x as wide as long, smooth, medial longitudinal carina weak; propodeal spiracle oval, positioned medially or slightly anterior to midline, costulae absent; lateral pronotum smooth, with pilosity in dorsal half; propleuron smooth, without a dorsal ridge; mesopleuron smooth to weakly punctate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctate to smooth; metapleuron weakly rugulose and dorsally pilose, except for smooth glabrous antero-medial area; hind coxa $0.5-0.7 \mathrm{x}$ as wide as long, $1.5-1.8 \mathrm{x}$ as long as T 1 ,
generally smooth to weakly rugulose-punctulate with sparse pilosity; inner hind tibial spur 1.3-1.5 x as long as outer, 0.7 x as long as hind basitarsus.

Wings. Fore wing smooth to sparsely pilose over basal half of sub-basal and plical cells, rest with evenly dense pilosity; 1-RS 0.2 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.2-0.3 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-$ RS+M 1.1-1.3 x as long as $1-\mathrm{M}$; m-cu $0.9-1.2 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma 2.1-2.5 x as long as wide; 1-R1 0.8-0.9 x distance from stigma to $4-\mathrm{RS}$; $\mathrm{r} 0.6-0.9 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet in small quadrangular shape, r-m and apex of 2RS+M unsclerotised; 1-CUa 0.7-0.9 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to slightly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.5-2.0 x as long as maximum width, parallel-sided to slightly narrowed at apex, anterior three quarters smooth and glabrous, posterior one quarter with weakly scattered punctations, deep medial longitudinal groove present in anterior four-fifth, absent in posterior part; T 2 in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.6-0.9 \mathrm{x}$ as long as T 3 , medial length $0.3-0.5 \mathrm{x}$ as long as maximum width, parallel-sided, anterior margin straight, posterior margin slightly concave medially; median field $0.2-0.3 \mathrm{x}$ maximum width of tergite, smooth, indicated as a raised area; lateral sulci obliquely diverging postero-laterally along anterior one quarter; T3 in midline $0.5-0.6 \mathrm{x}$ as long as maximum width, anterior margin medially slightly convex, posterior margin straight; suture between T2 and T3 distinct; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, 0.7-0.8 x as long as hind basitarsus; ovipositor sheaths $0.3-0.5 \mathrm{x}$ as long as hind basitarsus, with hairs in apical half, specialised sensilla present, straight, rounded at apex.

Male
Unknown.

Host
Unknown.

## Comments

D. hadrommatus can be distinguished from all other members in the hadrommatusgroup and other Australasian Diolcogaster on its very large eyes and specialised sensilla on
the ovipositor sheaths. This species is here named by the Greek words hadros, meaning welldeveloped, and ommatos meaning eye, indicating its large eyes. It is broadly distributed across Australia from the west to east coasts, and is found both in arid and moderately wet habitats (Fig. 6.55).

The two specimens from Bald Hill, Queensland differ from specimens in the type series in having the body yellow in colour, the ocelli smaller, the lateral ocelli closer to the eyes, the frons smooth, the propodeum with short lateral carinae and a few punctures, and the propleuron with a dorsal ridge. For the time being these specimens are listed under this but as more material becomes available they may need to be treated as a separate new species.

### 6.5.9 Diolcogaster harrisi, sp. nov. (Figs 5.3, 5.5, 6.60)

## Material Examined

Holotype. O, New South Wales, '2 km NbyE Monga, 9.xi.1981, I.D. Naumann \& J.C. Cardale' (ANIC).

Paratypes. New South Wales: 1 O, Cann Valley High way, 25.ii.1980, I.D. Naumann \& J.C. Cardale (ANIC); 1 O, Brown Mt., 10.iii.1961, D.H. Colless (ANIC). Tasmania: 1 $\mathrm{O}^{\pi}$, Bronte Park, 27 .iii.no year, no collector (AEIC). Victoria: 1 O , Mount Bogong, 1600 m , 4-8.ii-no year, no collector (AEIC).

## Female

Length. 2.9-3.1 mm.
Colour. Body generally black; metasoma dark brown to black except lateral membranous area of T1-T2 which is yellow; labial and maxillary palps light to dark brown; antenna dark brown; fore leg light to dark brown; mid and hind leg dark brown to black; hind tibial spurs yellow; stigma and fore wing venation dark brown, fore wing transparent.

Head. In dorsal view 1.0-1.1 x as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons rugulose to punctate; face at widest $1.4-1.5 \mathrm{x}$ as wide as high, rugulose-punctate; temples punctate; in lateral view medial temples 0.7-0.8 x as wide as width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus touching the anterior margin of lateral ocelli; distance between lateral ocelli 0.9-1.1 x distance from lateral ocellus to edge of eye; antenna $0.8-0.9 \mathrm{x}$ as long as body, last flagellomere $0.5-0.7 \mathrm{x}$ as long as first, pre-apical antennal segment $1.4-2.0 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.4-1.7 x as wide as long, with white pilosity, punctate; scutellar sulcus with 6-7 longitudinal carinae; dorsal scutellum as wide as long, punctate, with sparse white pilosity; lateral scutellum weakly carinate; medial posterior band of scutellum interrupted by weak rugosity; metanotum rugose-carinate, posterior margin medially interrupted by strong rugosity; propodeum 1.7-2.3 x as wide as long, strongly rugosepunctate, medial longitudinal carina strong; propodeal spiracle oval, positioned medially or slightly anterior to midline, without costulae; lateral pronotum punctate, weakly pilose to glabrous medially, only ventral crenulate groove present; propleuron punctate, with weak dorsal ridge; mesopleuron pilose and punctate antero-dorsally and ventrally, glabrous and smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctate; metapleuron punctate and dorsally pilose, except for smooth glabrous antero-median area; hind coxa $0.7-0.8 \mathrm{x}$ as wide as long, 1.5-1.6 x as long as T 1 , weakly punctate and pilose on outer surface; inner hind tibial spur 1.3 x as long as outer spur, $0.6-0.7 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing sparsely pilose on basal and sub-basal cells, rest with evenly dense pilosity; 1-RS 0.2-0.3 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.3-0.4 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.3 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 0.8-0.9 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma $2.0-2.5 \mathrm{x}$ as long as wide; 1-R1 0.7-0.8 x distance from stigma to $4-\mathrm{RS}$; $\mathrm{r} 0.5-0.6 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; 3-RS absent; areolet triangular; part of r-m and apex of 2-RS+M spectral; 1CUa $0.6-0.7 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to weakly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.6-2.3 x as long as apical width, parallel-sided to weakly narrowed at apex, strigate, weakly pilose to glabrous, medial longitudinal groove strong in anterior half weak posteriorly; T 2 smooth, in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.7-1.0 \mathrm{x}$ as long as T 3 , medial length $0.3-0.4 \mathrm{x}$ as long as maximum width; median field indicated by broad darkbrown raised area; suture between T2 and T3 indistinct; T3 in midline $0.4-0.5 \mathrm{x}$ as long as maximum width, smooth, sparsely pilose to glabrous; T4-T7 smooth, pilose; hypopygium weakly pilose, medio-ventral length $0.6-0.8 \mathrm{x}$ as long as hind basitarsus; ovipositor sheaths $0.3-0.5 \mathrm{x}$ as long as hind basitarsus, narrowing apically, pilose in apical half, specialised sensilla absent.

## Male

As for female.

## Host

Unknown.

## Comments

D. harrisi is similar in some characters to $D$. ashmeadi but can be separated from the latter sand other connexus-group species on its triangular fore wing areolet. This species is here named after Paul Harris, founder of the Rotary International. It has been recorded from the south-east coast of New South Wales and Victoria, and Tasmania (Fig. 6.60).

### 6.5.10 Diolcogaster iqbali, sp. nov. (Figs 6.11, 6.12, 6.56)

## Material Examined

Holotype. O, Queensland, '24.24S 149.23E, Repulse Ck, 23 km NE of Bauhinla Downs, 22-23.iv.1981, I.D. Naumann' (ANIC).

Paratypes. New South Wales: 3 O, Narrabri, 24-25.i \& 25.iv.1961, M. Nikitin (CNCI); 1 Q, Minnamurra Falls, 19.i.1973, L.S. Willan (ANIC). Northern Territory: 2 Q, Kulgera, 21.ix.1978, J.C. Cardale (ANIC); 1 O, James Ranges, 22.ix.1978, J.C. Cardale (ANIC); 8 Q, Alice Springs, 24.ix-14.x.1978, J.C. Cardale (ANIC); 1 ○, Bessie Springs, 8 km ESE of Cape Crawford, 26.x.1975, J.C. Cardale (ANIC); 1 Q, Collibah Hs, 17.ix.1968, M. Mendum (ANIC); 3 ○, Areyonga, 28.ix, 10.xi \& 8.xii (no year), no collector (AEIC); 1 Q, Urandangi, 15.x.1978, J.C. Cardale (ANIC). Queensland: 1 Q, Hope Vale Mission, 710.v.1981, I.D. Naumann (ANIC); 1 Q, Boulia, 16.x.1978, J.C. Cardale (ANIC); 1 Q, Charleville, 21.x.1975, J.C. Cardale (ANIC); 1 ○, Mt Glorious, 28.ii-9.iii-1984, L. Masner (AEIC); $1 \bigcirc$, NW Paluma, 18.i.1970, G.A. Holloway (AMSA). South Australia: $3 \bigcirc$, Yalta Mission, 9.iv.1983, E.S. Nielsen \& E.D. Edwards (ANIC); 1 Q, Cooper Bore (Koppermanna No. 2), 20.ix.1972, Z. Liepa; 1 O, Mt Sarah Hs. N. of Oodnadatta, 24.ix.1972, Z. Liepa (ANIC); 1 Q, Edwards Ck, 19.ix.1978, J.C. Cardale (ANIC). Western Australia: 4 Q, 8 mi . ENE of Millstream, 20.x.1970, D.H. Colless (ANIC); 1 O, 15 km E of Millstream, 20.x.1970, J.C. Cardale (ANIC); 1 Q, Warburton, 15.xi.1977, J.A.L. Watson (ANIC); 2 Q, Cocklebiddy, 12.x.1981, J.C. Cardale (ANIC); 1 Q, Singleton, 28-29.ix.1981, I.D. Naumann \& J.C. Cardale (ANIC); 2 Q, Carson escarpment, 9-15.viii.1975, M.S. Upton (ANIC).

## Female

Length. 3.1-4.6 mm.
Colour. Body entirely light brown or propodeum and T4-T7 dark brown rest light brown to scutellum, metanotum and propodeum black rest light brown to dark brown;
antennae dark brown; labial and maxillary palps light brown to yellow; fore, mid and hind leg light brown except hind tarsi, apices of hind femur and hind tibia which are dark brown; hind tibial spurs yellow; stigma dark brown, fore wing transparent.

Head. In dorsal view 1.1-1.2 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth to weakly rugulose; face at widest 1.1-1.2 x as wide as high, weakly punctate to rugulose-punctate with faint medial longitudinal carina in dorsal half; temples weakly punctate to rugulose; in lateral view medial temples 0.2-0.4 x width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; ocelli on a higher stammaticum; tangent to posterior margin of anterior ocellus passing above the anterior margin of lateral ocelli; distance between inner margins of lateral ocelli 1.6-3.0 x distance from outer margin of lateral ocellus to edge of eye; antenna 1.1-1.2 x as long as body.

Mesosoma. Scutum 1.2-1.6 x as wide as long, weakly punctate to densely punctulate with white pilosity; notauli indicated by weakly-impressed punctulate depressions; scutellar sulcus with 3-8 longitudinal carinae; dorsal scutellum $0.8-0.9 \mathrm{x}$ as wide as long, with sparse punctation and smooth background, sparsely pilose; lateral scutellum generally carinate except for a little smooth area posteriorly; medial posterior band of scutellum interrupted by strong to weak rugosity; metanotum smooth to weakly crenulate, dorsellum about as long as anteriorly wide; propodeum 1.9-2.0 x as wide as long, smooth to weakly punctate medially, medial longitudinal carina weak to strong; propodeal spiracle oval, without costulae, positioned medially or slightly anterior to midline; lateral pronotum smooth, without pilosity in dorsal half; propleuron smooth, with a dorsal ridge; mesopleuron smooth to weakly punctate anteriorly and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, smooth to weakly punctate; metapleuron weakly punctate and dorsally pilose, except for smooth glabrous antero-median area; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long, $1.5-1.7 \mathrm{x}$ as long as T 1 , generally smooth to weakly punctate on outer surface; inner hind tibial spur 1.2-1.5 x as long as outer, $0.7-0.8 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing smooth to weakly pilose over basal half of sub-basal and plical cells, rest with evenly dense pilosity; 1-RS 0.2-0.3 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.1-0.2 \mathrm{x}$ as long as $1-\mathrm{M}$; 1-RS+M 1.2-1.3 x as long as $1-\mathrm{M}$; m-cu 0.9-1.1 x as long as $2-\mathrm{RS}+\mathrm{M}$; stigma 2.3-2.8 x as long as wide; 1-R1 0.8-0.9 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.6-0.8 \mathrm{x}$ as long as width of
stigma, forming an obtuse argle with 2-RS; areolet small quadrangular, 3-RS present; r-m and apex of $2-\mathrm{RS}+\mathrm{M}$ unsclerotised; 1-CUa $0.7-0.8 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to slightly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.9-2.3 x as long as maximum width, parallel-sided in anterior three quarters, to weakly narrowing in posterior one quarter; anterior three quarters smooth and glabrous, posterior one quarter weakly punctate and sparsely pilose, deep medial longitudinal groove complete; T 2 in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.8-1.0 \mathrm{x}$ as long as T 3 , medial length $0.4-0.6 \mathrm{x}$ as long as maximum width, parallel-sided, anterior margin slightly convex, posterior slightly concave medially, smooth; median field $0.2-0.3 \mathrm{x}$ maximum width of tergite, indicated as a raised area; lateral sulci obliquely diverging postero-laterally along anterior one quarter; suture between T 2 and T 3 distinct; T 3 in midline $0.5-0.7 \mathrm{x}$ as long as maximum width, anterior margin medially slightly convex, posterior margin straight; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, 0.4-0.6 x as long as hind basitarsus; ovipositor sheaths $0.3-0.4 \mathrm{x}$ as long as hind basitarsus, with hairs in apical half, specialised sensilla absent.

## Male

Unknown.

## Host

Unknown.

## Comments

This species similar to $D$. hadrommatus sp. nov. because of its large eyes, but can be separated from it and other hadrommatus -group species on the lack of specialised sensilla on the ovipositor sheaths. It is here named after Muhammad Iqbal. D. iqbali is widely distributed across mainland Australia where it is found in arid, tropical and subtropical habitats (Fig. 6.56).
6.5.11 Diolcogaster lucindae, sp. nov. (Figs 6.15, 6.16, 6.59)

## Material Examined

Holotype. Q, Tasmania, 'Catamaran, 7-27.ii', (no year), (no collector)' (AEIC).

Paratypes. Queensland: 1Q, Mt Glorius, ii-vi-1977, A. Hiller, (BMNH). Tasmania: 1 O, $1 O^{\prime}, 2 \mathrm{~km}$ NW Derwent $\mathrm{Br}, 730 \mathrm{~m}, 24-28 . \mathrm{i} .1980$, A. Newton and M. Thayer, (CNCI).

## Female

Length. 2.7-3.2 mm.
Colour. Body generally dark brown to black; legs dark brown to light brown, except for hind coxa which is dark brown to black; antennae light to dark brown; labial and maxillary palps pale-yellow; stigma light to dark brown.

Head. In dorsal view as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth to weakly rugose; face at widest $1.7-1.8 \mathrm{x}$ as wide as high, acinose-rugose to acinose-strigate; clypeus 0.3 x as high as face, 1.2 x as high as labrum, 2.8-3.2 x as wide as high; labrum 2.4-3.0 x as wide as high; temples smooth to weakly rugose; in lateral view medial temples $0.8-0.9 \mathrm{x}$ width of eye; eyes $0.5-0.6 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus passing in front of lateral ocelli; distance between inner margin of lateral ocelli 0.7-0.8 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.6 x as long as body, pubescent, first flagellomere 2.4-2.8 x as long as wide, flagellar segments $10-12$ as long as wide.

Mesosoma. Scutum 1.4-1.5 x as wide as long, weakly punctate to rugose with sparse white pilosity; notauli absent; scutellar sulcus with 7-9 longitudinal carinae; dorsal scutellum as wide as long, with few weak scattered punctures, sparsely pilose; lateral scutellum coarsely carinate, lateral band of scutellum smooth, with posterior margin weakly carinate; medial posterior band of scutellum smooth; metanotum coarsely crenulate, dorsellum smooth as long as anteriorly wide; propodeum 1.6 x as wide as long, convex, medial longitudinal carina weaker in anterior one-third, strong in posterior two-third, giving rise to short lateral carinae; lateral fields of propodeum smooth except for weak scattered punctation; propodeal spiracle surrounded by weak costulae, space between spiracle and costula coarsely sculptured; lateral pronotum smooth, glabrous, antero-ventral furrow weakly crenulate; propleuron smooth, without dorsal ridge; mesopleuron smooth, glabrous except for few punctures antero-dorsally; epicnemial furrow deep; precoxal groove shallow, smooth to weakly punctate; metapleuron smooth, with scattered white pilosity; fore femur 0.4-0.5 x as wide as long, swollen; hind coxa 0.7 x as wide as long, 1.3 x as long as T 1 , smooth,
glabrous, except for dense pilosity ventrally; inner hind tibial spur 1.0-1.3 x as long as outer spur, $0.6-0.7 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing with sparse pilosity over basal and subbasal cells, rest with evenly dense pilosity; stigma 2.5-3.0 x as long as wide; 1-R1 0.6 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r}$ $0.6-0.9 \mathrm{x}$ as long as width of stigma, meeting straight on 2-RS; areolet small quadrangular; $\mathrm{r}-\mathrm{m}$ and apex of $2-\mathrm{RS}+\mathrm{M}$ spectral; 1-CUa $0.7-0.9 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight with row of short and sparse hairs beyond its widest part.

Metasoma. T1 1.5-1.6 x as long as maximum apical width, parallel-sided, anterior half smooth and glabrous, posterior half weakly rugose and with sparse pilosity, medial longitudinal groove deep; T 2 in midline 0.5 x as long as $\mathrm{T} 1,0.9 \mathrm{x}$ as long as T 3 , medial length $0.5-0.6 \mathrm{x}$ as long as maximum anterior width, slightly broadening posteriorly, anterior margin sloping postero-laterally, posterior margin straight to slightly concave, lateral fields smooth with scattered pilosity; median field at most $0.3-0.5 \mathrm{x}$ as wide as T 2 at anterior margin, smooth, bordered on either side by smooth grooves which curves postero-laterally towards lateral margin so that tergite appears to be divided into three parts; suture between T2 and T3 distinct; T3 in midline 0.4-0.5 x as long as wide across anterior margin, smooth, anterior margin straight to medially convex, posterior margin straight; tergite with sparse pilosity in posterior half; T4-T7 smooth, medially with transverse sparse row of hairs; hypopygium with sparse pilosity, 1.8-2.2 x as long as medial length of $\mathrm{T} 3,0.5-0.6 \mathrm{x}$ as long as hind tibia; ovipositor sheaths 0.5 x as wide as long, $0.5-0.6 \mathrm{x}$ as long as hypopygium, with hairs in apical half.

## Male

As for female except as follows: Distance between inner margin of lateral ocelli 0.9 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.8 x as long as body, first flagellomere 3.0 x as long as wide, 10-12 antennal segments 2.2 x as long as wide; notauli indicated by weakly impressed depressions; dorsal scutellum 0.8 x as wide as long; fore femur 0.3 x as wide as long, flattened; T1 1.9 x as long as maximum apical width; T2 with medial length 0.9 x as long as maximum anterior width, not divided in to three parts.

## Host

Unknown.

## Comments

D. lucindae differs from all other spretus-group species in having broad ovipositor sheaths and T1 almost parallel-sided rather than broadening posteriorly. This species is named after Lucinda Deane. It is known only from two disjunct regions of Australia, viz. the south-east coast of Queensland and Tasmania (Fig. 6.59).
6.5.12 Diolcogaster masoni, sp. nov. (Figs 4.1, 4.2, 4.4, 4.5, 6.35, 6.55)

## Material Examined

Holotype. ©, Queensland, '13.44S 143.20E, 11 km WbyN Bald Hill, Mcllwraith Ra. $520 \mathrm{~m}, 27 . \mathrm{vi}-12 . v i i .1989$, I.D. Naumann' (ANIC).

Paratypes. New South Wales: 1 Ơ, Hrindle Ck Border Ras. NP., 14.ii.1984, I.D. Naumann (ANIC); $1 O^{*}$, Toloom Scrub, 1000 m, 14.ii.1984, L. Masner (CNCI). Queensland: 5 O, same data as holotype, 26.vi-13.vii.1989, I.D. Naumann (ANIC); 10 , Mt Webb National Park, 28-30.ix.1980, J.C. Cardale (ANIC).

## Female

Length. 4.2-5.1 mm.
Colour. Body generally light brown; antennae dark brown; labial and maxillary palps light brown; legs light brown except hind tarsi which are dark brown; fore wing blackish with stigma and veins dark brown.

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex glabrous, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth to weakly punctate; face at widest 1.1-1.2 x as wide as high, weakly punctate with faint medial longitudinal carina in dorsal half; temples weakly punctate; in lateral view medial temples $0.4-0.5 \mathrm{x}$ width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus touching anterior margin of lateral ocelli; distance between inner margins of lateral ocelli 0.8-1.1 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.9-1.0 x as long as body.

Mesosoma. Scutum 1.3-1.6 x as wide as long, weakly punctate with brown pilosity; notauli indicated by weakly impressed depressions; scutellar sulcus with 5-7 longitudinal carinae; dorsal scutellum 1.0-1.2 x as wide as long, smooth to weakly punctate, glabrous;
lateral scutellum generally carinate; medial posterior band of scutellum smooth to weakly depressed and continuous with dorsal scutellum; metanotum smooth to weakly crenulate; dorsellum smooth, excavated and rounded, about as long as anteriorly wide; propodeum 1.72.0 x as wide as long, smooth, medial longitudinal carina strong with short lateral carinae arising in posterior half; lateral carina strong; propodeal spiracle oval, touching lateral carina, with incomplete costulae, positioned medially or slightly anterior to midline; lateral pronotum smooth, without pilosity in dorsal half, with complete carinate ventral groove, dorsal groove very short; propleuron sparsely punctate, with a dorsal ridge; mesopleuron with sparse and weak punctations anteriorly and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, smooth to weakly punctate; metapleuron smooth; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long, $1.5-2.1 \mathrm{x}$ as long as T1, generally smooth; inner hind tibial spur 1.3-1.5 x as long as outer, $0.6-0.7 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing smooth to sparsely pilose over basal half of sub-basal and plical cells, rest with evenly dense pilosity; $1-\mathrm{RS} 0.1 \mathrm{x}$ as long as $1-\mathrm{RS}+\mathrm{M}, 0.1-0.2 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-$ RS+M 1.1-1.3 x as long as $1-\mathrm{M}$; m-cu 1.1-1.5 x as long as $2-\mathrm{RS}+\mathrm{M}$; stigma $2.6-2.9 \mathrm{x}$ as long as wide; 1-R1 0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet triangular; r-m intersecting 2-RS in distal half to form 2-RSa and $2-\mathrm{RSb} ; \mathrm{r}-\mathrm{m}$ and apex of $2-\mathrm{RS}+\mathrm{M}$ unsclerotised; 1-CUa $0.4-0.5 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing with vein $2-1 \mathrm{~A}$ in form of a stump; hind wing vannal lobe straight with row of short and sparse hairs beyond its widest part.

Metasoma. T1 1.4-1.5 x as long as maximum width, narrowest at base then broadened almost medially with maximum width at three quarters, slightly narrowed and parallel sided in apical one quarter, apex straight; tergite smooth, sparsely pilose on apical one-quarter along length, deep medial longitudinal groove strongly defined in basal half, shallow and weakly defined in apical half; T 2 smooth, in midline $0.4-0.6 \mathrm{x}$ as long as $\mathrm{T} 1,0.7-0.8 \mathrm{x}$ as long as T3, medial length $0.5-0.6 \mathrm{x}$ as long as maximum width, parallel-sided, anterior margin slightly convex medially, posterior margin regularly concave; median field absent; lateral sulci obliquely diverging postero-laterally in anterior one quarter giving triangular shape to tergite; suture between T2 and T3 distinct; T3 in midline $0.6-0.9 \mathrm{x}$ as long as maximum width of tergite, anterior margin medially slightly convex, posterior straight; T4-T7 smooth,
with sparse scattered pilosity; hypopygium with sparse scattered pilosity, 1.1-1.3 x as long as hind basitarsus; ovipositor sheaths $0.5-1.0 \mathrm{x}$ as long as hind basitarsus, with few reduced hairs at apex, specialised sensilla absent.

## Male

As for females except as follows: Antenna $1.3-1.4 \mathrm{x}$ as long as body; dorsellum broadly triangular; hind coxa with weaker punctations on outer margin; medial groove of T1 evenly deep.

## Host

Unknown.

## Comments

D. masoni is not closely related to any other species and can be separated from other Australasian Diolcogaster in having vein 2-1A of the hind wing stump-like. This species is here named after late Dr. W. R. M. Mason, braconid worker at the Canadian National Collection, Ottawa. It is known from east Queensland and New South Wales (Fig. 6.55).
6.5.13 Diolcogaster merata, sp. nov. (Figs 6.17, 6.52)

## Material Examined

Holotype. O, New Guinea, 'Baiyer R., New Guinea, 26.xii.1978-25.i.1979, 1100m. J.Sedlacek' (AEIC).

## Female

Length. 3.4 mm .
Colour. Body generally black; scape and pedicle light brown, flagellum dark brown; basal two maxillary and labial palps brown, rest yellow; fore trochantellus and femur dark brown, fore tibia and tarsus light brown, mid coxa and trochantellus yellow, mid tibia and tarsus light brown, hind legs with apex of coxa, trochantellus, sub-basal ring of tibia, and tibial spurs yellow, hind tarsus dark brown; stigma dark brown, fore wing with light brown apical spot; hypopygium dark brown.

Head. In dorsal view as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons rugulose; face at widest 1.3 x as wide as high, weakly rugulose with faint medial longitudinal carina in dorsal half; occiput smooth; temples striolate; in lateral view medial temples 0.6 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between inner margin of lateral ocelli equal to distance from outer margin of lateral ocellus to edge of eye; antenna 1.1 x as long as body, slender, first flagellomere 3.7 x as long as wide.

Mesosoma. Scutum 1.6 x as wide as long, areolate-punctate with fine granulate background microsculpture and sparse white pilosity; notauli not indicated; scutellar sulcus with 7 longitudinal carinae; dorsal scutellum 1.5 x as wide as long, weakly punctate, sparsely pilose; lateral scutellum generally coarsely carinate but smooth medially, lateral band of scutellum smooth, slightly convex medially with posterior margin carinate, medial posterior band of scutellum interrupted by strong punctation; metanotum with two carinae on either side of dorsellum, dorsellum as long as anteriorly wide; propodeum 2.3 x as wide as long, medial longitudinal carina with radiating short carinae on either side, rest of propodeum weakly punctate in anterior half, smooth posteriorly; propodeal spiracle oval, positioned medially, surrounded by costula; lateral pronotum areolate-punctate to smooth medially, pilose in dorsal half; propleuron with a dorsal ridge; mesopleuron areolate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture, epicnemial furrow deep; precoxal groove shallow, weakly punctate; metapleuron punctate and dorsally pilose, except for smooth glabrous antero-median area; hind coxa 0.5 x as wide as long, 1.9 x as long as T 1 , generally areolate-punctuate with sparse pilosity, except for weak sparse punctation on outer surface which merges with background micropunctation; inner hind tibial spur 1.5 x as long as outer spur, 0.7 x as long as hind basitarsus.

Wings. Fore wing with sparse pilosity over basal half, evenly dense in apical half; stigma 2.8 x as long as wide; $1-\mathrm{R} 10.7 \mathrm{x}$ distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 1.1 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet slit-like, r-m and apex of 2RS+M unsclerotised; 1-CUa 0.8 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe slightly concave, glabrous beyond its widest part; 2-SC+R 0.5 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 as long as apical width, broadening posteriorly, anterior half smooth and glabrous, posterior half areolate and pilose, medial longitudinal groove shallow and narrower
in anterior half, deep and broader in posterior half; posterior margin of T1 carinate and slightly concave; T2 in midline 0.9 x as long as $\mathrm{T} 1,2.6 \mathrm{x}$ as long as T 3 , medial length 0.9 x as long as anterior width, slightly broadening posteriorly, anterior margin straight with few coarse crenulae, antero-median node significantly raised above level of anterior margin, posterior margin straight, lateral fields carinate-punctate; median field smooth, longitudinally parallel-sided, bordered on either side by deep crenulate groove; T 3 smooth, in midline 0.3 x as long as wide across anterior margin; suture between T2 and T3 distinct; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, 1.7 x as long as length of medial T3; ovipositor sheaths rounded apically, with hairs in apical half, specialised sensilla present, rounded and up-curved at apex.

## Male

Unknown.

## Host

Unknown.

## Comments

Like the previous species, D. merata is apparently unrelated to any other members of the genus. It can be separated from other Australasian Diolcogaster in that T1 and T2 are similarly coarsely sculptured but T3 does not form a carapace with these tergites, and is much shorter than T2. This species is named after the aboriginal word merate meaning naked, because T3 does not form a carapace with T2. It is known from the holotype collected at Baiyer River, New Guinea.
6.5.14 Diolcogaster muzaffari, sp. nov. (Figs 6.20, 6.34, 6.57)

## Material Examined

Holotype. O., New Guinea, 'TariGap nr Mt Hagen, 2600 m, 29-31.xii.1978, J. Sedlacek' (AEIC).

Paratypes. New Guinea: $40^{\circ}$, 29.i-4.ii.1979, same data as holotype; $10^{\top}$, Mt Giluwe, $2800 \mathrm{~m}, 3 . \mathrm{i}-8 . \mathrm{ii} .1979$, J. Sedlacek (AEIC); $1 O^{\text {n, Jimmi Valley, } 1800 \mathrm{~m}, ~ 27 . x i i .1978-~}$ 26.i.1979, J. Sedlacek (AEIC).

## Female

Length. 3.7 mm .
Colour. Head, mesosoma and T1-T2 black, T3-T4 yellow to light brown, T5-T7 dark brown; antennae dark brown; labial and maxillary palps yellow; fore and mid leg light brown; hind coxa black, trochantellus and femur light brown except apex of femur which is dark brown, tibia dark brown except a sub-basal light brown ring, tarsi dark brown; stigma dark brown; hypopygium dark brown.

Head. In dorsal view as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons weakly punctulate; vertex smooth; face at widest 1.1 x as wide as high, poorly separated from clypeus, acinose with weak medial longitudinal carina in dorsal half; clypeus carinulate; temples weakly punctulate; in lateral view medial temples 0.5 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through anterior margin of lateral ocelli; distance between inner margin of lateral ocelli 0.8 x distance from outer margin of lateral ocellus to edge of eye; antenna 1.1 x as long as body, last flagellomere 0.6 x as long as first.

Mesosoma. Scutum 1.4 x as wide as long, punctate with sparse white pilosity; scutellar sulcus with 5 longitudinal carinae; dorsal scutellum 0.8 x as wide as long, punctate, sparsely pilose; lateral scutellum coarsely carinate; medial posterior band of scutellum strongly punctate; metanotum coarsely crenulate, dorsellum excavated, about as long as wide, anteriorly smooth, posteriorly with weak punctation; propodeum 1.6 x as wide as long, punctate, medial longitudinal carina weak; propodeal spiracle oval, positioned medially or slightly anterior to midline, without costulae; lateral pronotum punctate to smooth medially, with pilosity in dorsal half, ventral crenulate groove present; propleuron weakly punctulate without dorsal ridge; mesopleuron weakly punctulate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctate; metapleuron punctulate and dorsally pilose, except for smooth glabrous antero-median area; hind coxa 0.5 x as wide as long, 1.8 x as long as T 1 , weakly punctulate to smooth on outer surface; inner hind tibial spur 1.7 x as long as outer spur, 0.7 x as long as hind basitarsus.

Wings. Fore wing with dense pilosity; stigma 3.0 x as long as wide; $1-\mathrm{R} 10.9 \mathrm{x}$ distance from stigma to 4-RS; r 1.2 x as long as width of stigma, coming down straight from
stigma, forming an obtuse angle with 2-RS; areolet triangular, 2-RS intersected by r-m from middle, $\mathrm{r}-\mathrm{m}$ and apex of $2-\mathrm{RS}+\mathrm{M}$ spectral; 1-CUa 0.6 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe with row of long hairs and slightly convex distally beyond its widest part; 2-SC+R 0.4 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 3.5 x as long as apical width, parallel sided, anterior half smooth and glabrous, posterior weakly carinulate to carinulate-punctate with sparse pilosity, medial longitudinal groove present in anterior two-third along length, absent in posterior one-third along length; T 2 in midline 0.4 x as long as $\mathrm{T} 1,0.6 \mathrm{x}$ as long as T 3 , medial length 0.6 x as long as maximum width, anterior margin straight, posterior concave medially; median field strongly sclerotised, sub-triangular with anterior margin narrow, posterior emarginate, weakly carinulate-punctate, 0.7 x as wide as maximum width of tergite, bordered on either side by smooth groove; T3 in midline as long as its maximum width, smooth, glabrous; suture between T2 and T3 distinct; T4-T7 smooth, with sparse white pilosity; hypopygium with sparse pilosity, medio-ventrally 0.2 x as long as hind tibia; ovipositor sheaths with hairs in apical half.

## Male

As for females except as follows: T1 black to light brown; antenna 1.4-1.5 x as long as body; propodeal spiracle with or without a costula; T3 0.5-0.7 x as wide as long medially.

Host
Unknown.

## Comments

D. muzaffari sp. nov can be distinguished from other connexus-group species on the shape of the median field of T 2 and length of vein r in the fore wing. This species is here named after Muzaffar Saeed, my eldest brother who supported my studies financially for more than a decade. It is apparently endemic to New Guinea (Fig. 6.57).
6.5.15 Diolcogaster naumanni, sp. nov. (Figs 6.6, 6.22, 6.59)

## Material Examined

Holotype. ©, Western Australia, 'Augustus Island, CALM Site 26/1, 15.25S 124.38E, 11-16.vi.1988, I.D. Naumann' (ANIC).

## Female

Length. 2.7 mm .
Colour. Head and mesosoma black, metasoma light brown, except for T4-T7 which are dark brown, legs light brown except for hind tarsi and apex of hind tibia which are dark brown; antennae dark brown; labial and maxillary palps yellow; stigma dark brown.

Head. In dorsal view as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons strigate-punctate; face at widest 1.7 x as wide as high, acinose-strigate; clypeus 0.3 x as high as face, 0.9 x as high as labrum, 2.8 x as wide as high; labrum 2.1 x as wide as high; temples smooth; in lateral view medial temples 0.7 x width of eye; eyes 0.8 x as wide as high; tangent to posterior margin of median ocellus passing in front of anterior margin of lateral ocelli; distance between inner margin of lateral ocelli 1.2 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.6 x as long as body, pubescent, first flagellomere 1.6 x as long as wide; flagellar segments $10-12,1.0-1.2 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.6 x as wide as long, rugose-punctate with sparse white pilosity; notauli weakly indicated by impressed rugose depressions; scutellar sulcus with 10 longitudinal carinae; dorsal scutellum as wide as long, with weak few scattered punctures, sparsely pilose; lateral scutellum coarsely carinate, lateral band of scutellum smooth, with posterior margin carinate; medial posterior band of scutellum punctate; metanotum coarsely crenulate, dorsellum smooth, 1.3 x as long as anteriorly wide; propodeum 2.4 x as wide as long, strongly areolate-punctate; propodeal spiracle oval, surrounded by weak costula, space between spiracle and costula roughly sculptured; lateral pronotum smooth medially, with pilosity in dorsal half, only ventral crenulate groove present; propleuron rugulose, with weak dorsal ridge; mesopleuron weakly punctate antero-dorsally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, smooth; metapleuron smooth and glabrous, except for posterior margin which is rugose and pilose; fore femur 0.4 x as wide as long; hind coxa 0.8 x as wide as long, 1.7 x as long as T 1 ,
generally smooth glabrous, except for weak sparse punctation on outer surface and dense pilosity ventrally; inner hind tibial spur 1.7 x as long as outer spur, 0.9 x as long as hind basitarsus.

Wings. Fore wing with sparse pilosity over basal and sub basal cells, evenly dense over rest of the wing; stigma 2.0 x as long as wide; 1-R1 0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r}$ 0.7 x as long as width of stigma, vertical on 2-RS; areolet triangular, r-m and apex of 2RS+M spectral; 1-CUa 0.9 x as long as 1-CUb; hind wing vannal lobe straight, with row of short and sparse hairs beyond its widest part; 2-SC+R 0.5 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 smooth, 0.9 x as long as apical width, broadened posteriorly, anterior half glabrous, posterior half with scattered white pilosity, medial longitudinal groove deep; T 2 in midline 0.5 x as long as $\mathrm{T} 1,0.7 \mathrm{x}$ as long as T 3 , medial length 0.4 x as long as anterior width, slightly broadening posteriorly, anterior margin straight, antero-median node slightly raised above level of anterior margin, posterior margin concave medially, lateral fields smooth; median field 0.3 x as wide as tergite at anterior margin, smooth, bordered on either side by smooth grooves which curves posteriorly towards lateral margin so that tergite appears to be divided into three parts, suture between T 2 and T 3 distinct; T 3 in midline 0.6 x as long as width across anterior margin, smooth, anterior margin medially convex, posterior margin straight, with few hairs in posterior half; T4-T7 smooth, with transverse sparse row of hairs medially; hypopygium with sparse pilosity, 0.3 x as long as hind tibia; ovipositor sheaths 0.3 x as wide as long, 0.4 x as long as hypopygium, with pilosity on their entirety.

## Male

Unknown.

Host
Unknown.

## Comments

This species differs from other Australasian spretus-group species in having T1 very broad posteriorly. However, based on this character it is similar to D. tomentosa from India, but it can be separated from the latter species in having pubescent antennae, flagellomeres 10-

12 being less than 1.2 x as long as wide, the scutum rugose, and the propodeum punctate. In D. tomentosa the antennae are nearly glabrous, flagellomeres $10-12$ are more than 1.5 x as long as wide, the scutum is coarsely punctate, and the propodeum coarsely rugose. This species is named after its collector, Dr. Ian Naumann, hymenopterist at the Australian National Insect Collection. It is known only from the holotype collected from Augustus Island, north-western Australia.

### 6.5.16 Diolcogaster newguineaensis, sp. nov (Figs 6.24, 6.25, 6.54)

## Material Examined

Holotype. O, New Guinea, 'Wau, N. Guinea, x.1969, P. Shanahan' (AEIC).
Paratypes. New Guinea: 1 O, Jimmy Valley, 650 m, 7.ii-2.iii.1979, J. Sedlacek, (AEIC); 1 Ǫ, Baiyer, 1100 m, 26.xii.1978-25.i.1979, J. Sedlacek, (AEIC).

## Female

Length. $4.4-4.7 \mathrm{~mm}$.
Colour. Body generally black; Scape and pedicle yellow, flagellum brown; basal one segment of labial and maxillary palps brown, rest yellow; fore leg light to dark brown with trochantellus yellow, mid leg light to dark brown with coxa and trochantellus yellow, hind coxa and femur black, hind trochantellus, basal half of tibia and tibial spurs yellow, apical half of hind tibia and hind tarsus dark brown; stigma dark brown, fore wing with brown apical spot; metasoma dark brown to black with anterior three quarters of T1 yellow to dark brown.

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons acinose-carinate; face at widest $1.2-1.3 \mathrm{x}$ as wide as high, rugulose-acinose with faint medial longitudinal carina in dorsal half; temples striolate to striolate-punctate; in lateral view medial temples $0.5-0.7 \mathrm{x}$ width of eye; eyes $0.5-0.6 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between inner margin of lateral ocelli 1.0-1.1 x distance from outer margin of lateral ocellus to edge of eye; antenna $1.0-1.1 \mathrm{x}$ as long as body, first flagellomere $3.1-3.4 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.6-1.7 x as wide as long, areolate-punctate with fine granulate background and sparse white pilosity; scutellar sulcus with 7-8 longitudinal carinae; dorsal
scutellum 1.5-1.6 x as wide as long, punctate, background with micro-punctation, sparsely pilose; lateral scutellum coarsely carinate except for smooth median area, lateral band of scutellum smooth with posterior margin carinate; medial posterior band of scutellum interrupted by coarse punctation or longitudinal carinae; metanotum coarsely crenulate, dorsellum about as long as anteriorly wide; propodeum 2.1 x as wide as long, punctate anteriorly, smooth posteriorly, medial longitudinal carina with radiating short carinae on either side; propodeal spiracle oval, positioned medially or slightly anterior to midline, surrounded by costula which is joined to posterior margin of propodeum by a longitudinal carina; lateral pronotum punctate with sparse pilosity; propleuron with dorsal ridge; mesopleuron pilose-areolate antero-dorsally, smooth posteriorly beside carinate pleural suture, epicnemial furrow deep, precoxal groove shallow, weakly strigate to punctate; metapleuron areolate-carinate and dorsally pilose, except for smooth, glabrous antero-median area; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long, $1.6-1.8 \mathrm{x}$ as long as T1, punctate with sparse pilosity; inner hind tibial spur $1.5-1.6 \mathrm{x}$ as long as outer spur, 0.7 x as long as hind basitarsus.

Wings. Fore wing without pilosity in basal half of sub-basal and plical cells, rest with evenly dense pilosity; stigma $2.5-2.7 \mathrm{x}$ as long as wide; 1-R1 0.8 x distance from stigma to 4-RS; r 0.9-1.0 x as long as width of stigma, forming an obtuse angle with 2-RS; areolet slitlike, $\mathrm{r}-\mathrm{m}$ and apex of $2-\mathrm{RS}+\mathrm{M}$ unsclerotised; 1-CUa $0.6-0.7 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe slightly concave, glabrous, beyond its widest part; 2-SC+R 0.4-0.5 x as long as 1r-m.

Metasoma. T1 0.9-1.0 x as long as apical width, broadening posteriorly, anterior half smooth, glabrous, posterior half areolate with sparse pilosity, medial longitudinal groove smooth and straight anteriorly, crenulate and diverging outward posteriorly; T 2 in midline $0.7-0.9 \mathrm{x}$ as long as T1, 0.7-0.9 x as long as T3, medial length $0.7-0.8 \mathrm{x}$ as long as anterior width, tergite slightly broadening posteriorly, anterior margin straight to slightly convex medially with few coarse crenulae, antero-median node slightly raised above level of anterior margin, posterior margin weakly emarginate, lateral fields carinate-punctate; median field $0.1-0.2 \mathrm{x}$ as wide as tergite at anterior margin, smooth, bordered on either side by crenulate groove; T 3 in midline $0.7-0.9 \mathrm{x}$ as long as wide across anterior margin, costate with few scattered punctures, anterior margin medially convex, crenulate, posterior margin rounded on corners, smooth to costulate, median field 1.0 x as long as $\mathrm{T} 3,0.3-0.4 \mathrm{x}$ as wide as anterior
width of tergite, smooth, widened anteriorly; suture between T2 and T3 deep, crenulate; T4T7 smooth, with sparse row of hairs sub-apically; hypopygium with sparse pilosity; ovipositor sheaths rounded apically, with hairs in apical half, specialised sensilla absent.

## Male

Unknown.

## Host

Unknown.

## Comments

This species differs from other Australasian basimacula-group species in having ovipositor sheaths without specialised sensilla. It is known only from New Guinea (Fig. 6.54) after which it has been named.
6.5.17 Diolcogaster nixoni, sp. nov. (Figs 5.13, 6.41, 6.60)

## Material Examined

Holotype. O, New Guinea, 'Mt. Otto, 2000 m, 22.xii.1978-9.i.1979, J. Sedlacek' (AEIC).

Paratypes. New Guinea: 1 O, L. Sirunki, 2500 m, 5.ii.1979, J. Sedlacek (AEIC) (used for SEM); $1 \mathrm{O}^{*}$, data as holotype; $1 \mathrm{O}^{\prime \prime}$, Mt. Giluwe, 2800 m , 3.i-8.ii.1979, J. Sedlacek (AEIC)

Other specimens examined. New Guinea: $200^{\circ}$, BayierR., 24-26.xii.1978, 26.xii.1978-25.i.1979, 25.i-6.ii.1979, 6-25.ii.1979, 25.ii.9.iii.1979, 27.ii-7.iii.1979, J. Sedlacek (AEIC); $5 \mathrm{O}^{\circ}$, Bulolo., 15.i-14.ii.1979, 13.ii-13.iii.1979, J. Sedlacek (AEIC); $5 \mathrm{O}^{\circ}$, Kassam Pass, 1300 m, 20.xii.1978-10.i.1979, 10-23.i.1979, J. Sedlacek (AEIC); 2 O', W. Highl. Dist., Mt. Hagen, 1700 m, no date, no collector (CNCI); 1 O', E. Highl., Kainantu Yabunka, ii.1975, no collector (CNCI). Queensland: $1 O^{\prime}$, Atherton, 13.ii.1975, H. \& A. Howden (AEIC).

## Female

Length. 3.2 mm .
Colour. Head, antennae and basal two segments of labial palps dark brown; clypeus, labrum, labial palps and three apical segments of maxillary palps light brown; mesosoma and propodeum black; metasoma yellow except T7, hypopygium, ovipositor and ovipositor sheaths which are dark brown; legs yellow except for outer surface of hind coxa, hind
trochantellus, hind tibial spurs, hind tarsi and base and apex of hind femur and tibia which are dark brown; stigma and wing-venation dark brown, wings transparent.

Head. In dorsal view as wide as scutum; vertex glabrous, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth; face at widest 1.2 x as wide as high, weakly punctate with short faint medial longitudinal carina in dorsal half; temples smooth; in lateral view medial temples 0.6 x as wide as width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between lateral ocelli 1.1 x as much as distance from lateral ocellus to edge of eye; antenna 1.1 x as long as body, last flagellomere 0.7 x as long as first.

Mesosoma. Scutum 1.5 x as wide as long, weakly smooth on narrow median area otherwise punctate with sparse white pilosity; notauli absent; scutellar sulcus with 6 longitudinal carinae; dorsal scutellum as wide as long, smooth, glabrous; lateral scutellum weakly carinate, smooth medially; medial posterior band of scutellum smooth; metanotum coarsely crenulate; propodeum 2.3 x as wide as long, smooth, weakly curved and looking double faced, medial longitudinal carina weak; propodeal spiracle oval, positioned medially or slightly anterior to midline, without costulae; lateral pronotum smooth, glabrous, ventrally smooth; propleuron smooth with weak dorsal ridge; mesopleuron smooth except ventral punctation; epicnemial furrow deep; precoxal groove shallow, smooth; metapleuron smooth and glabrous; hind coxa 0.6 x as wide as long, 2.3 x as long as T 1 , smooth and glabrous on outer surface; inner hind tibial spur 1.7 x as long as outer spur, 0.9 x as long as hind basitarsus.

Wings. Fore wing with evenly dense pilosity; 1-RS 0.2 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.2 \mathrm{x}$ as long as $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.0 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 1.1 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma 3.2 x as long as wide; 1-R1 0.8 x distance from stigma to $4-\mathrm{RS}$; r 0.9 x as long as width of stigma, forming an obtuse angle with 2-RS; areolet in a small triangle; r-m intersecting 2-RS from middle to form 2-RSa and 2-RSb; r-m and apex of $2-\mathrm{RS}+\mathrm{M}$ spectral; 1-CUa 0.5 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe weakly convex with row of long hairs beyond its widest part.

Metasoma. T1 2.5 x as long as maximum width, parallel-sided, smooth and glabrous, medial longitudinal groove present in anterior three-quarters, absent in posterior one-quarter; T 2 smooth, broadening posteriorly, in midline 0.6 x as long as $\mathrm{T} 1,0.7 \mathrm{x}$ as long as T 3 , medial length 0.5 x as long as maximum width, lateral sulci posteriorly enclosing a sub triangular
area which is broadened on apex; median field indicated as a raised area; suture between T2 and T 3 indistinct; T 3 in midline 0.5 x as long as maximum width, smooth with few hairs apically; T4-T7 smooth, with sparse hairs medially; hypopygium sparsely pilose, medioventral length 0.6 x as long as hind basitarsus; ovipositor sheaths 0.4 x as long as hind basitarsus, with hairs in apical half, specialised sensilla absent.

## Male

As for females except for T4-T7 which are dark brown.

Host
Unknown.

## Comments

D. nixoni can be separated from D. euterpus (the only other species in the euterpusgroup) and all other Australasian Diolcogaster by its smooth lateral pronotum, posterior band of the scutellum interrupted by sculpturing, and elongate parallel-sided T1. This species is named after late Dr. G. E. J. Nixon, one of the great hymenopterist. It is apparently restricted to New Guinea and tropical north Queensland (Fig. 6.60).

All male specimens, except for the two included in the type series, are only provisionally placed in this species, because they differ in having the body dark brown to black, the propodeum strongly curved, T 2 longer than T 3 , and $1-\mathrm{RS}+\mathrm{M}$ shorter than $1-\mathrm{M}$. When further material is available to assess these characters, the males separated above may need to be treated as a distinct new species.
6.5.18 Diolcogaster notopecktos, sp. nov. (Figs 6.18, 6.19, 6.59)

Material Examined
Holotype. Q, Queensland, ‘Bamaga, 18.ii.1984, J. Sedlacek’ (AEIC).
Paratype. New Guinea: 1 O̧, Busu R., 20 m. 60 Km E. of Lae, 13.i-10.iii.1979, J. Sedlacek, (AEIC).

## Female

Length. 3.1-3.6 mm.

Colour. Body and legs light brown; antennae dark brown; labial and maxillary palps yellow; stigma dark brown.

Head. In dorsal view as wide as scutum; vertex, frons, temples, eyes and face with sparse white pilosity; dorsal and lateral frons weakly rugose-punctate; face at widest 1.3-1.5 x as wide as high, rugose-punctate; clypeus 0.3 x as high as face, $0.9-1.0 \mathrm{x}$ as high as labrum, 2.9-3.1 x as wide as high; labrum 2.1-2.3 x as wide as high; temples smooth to weakly punctate; in lateral view medial temples 0.6 x width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between inner margin of lateral ocelli 0.7-0.8 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.6 x as long as body, pubescent, first flagellomere $1.5-2.1 \mathrm{x}$ as long as wide, flagellar segments $10-12,1.0-1.2 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.6 x as wide as long, punctulate in anterior half, smooth in posterior half, sparsely pilose; notauli absent; scutellar sulcus shallow, with 8-10 strong longitudinal carinae; dorsal scutellum 1.0-1.1 x as wide as long, smooth, sparsely pilose; lateral scutellum coarsely carinate, lateral band of scutellum smooth, with posterior margin closely impressed to metanotum; medial posterior band of scutellum smooth; metanotum coarsely crenulate, dorsellum smooth, about as long as anterior width; propodeum 1.8-1.9 x as wide as long, weakly convex, medial longitudinal carina strong; lateral fields of propodeum punctate; propodeal spiracle oval, surrounded by strong costula, surface between spiracle and costula weakly sculptured; lateral pronotum smooth, glabrous, crenulate ventral groove present; propleuron weakly punctate, without dorsal ridge; mesopleuron smooth, except for weak punctations antero-dorsally; epicnemial furrow deep; precoxal groove deep, smooth; metapleuron medially smooth except for 3-4 punctures, glabrous, carinate to carinate-punctate along margins with scattered white pilosity; fore femur 0.4 x as wide as long; hind coxa 0.8-0.9 x as wide as long, 1.6-1.7 x as long as T 1 , glabrous, smooth except for few weak punctations on outer surface, with dense white pilosity; hind femur 0.4 x as wide as long; inner hind tibial spur $1.5-1.7 \mathrm{x}$ as long as outer spur, 0.9 x as long as hind basitarsus.

Wings. Fore wing with pilosity evenly dense throughout; stigma 2.4 x as long as wide; 1-R1 0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.7-0.8 \mathrm{x}$ as long as width of stigma, meeting straight on 2-RS; areolet in small quadrangular shape, r-m and apex of 2-RS+M spectral; 1-

CUa $0.7-0.9 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight, glabrous beyond its widest part; 2-SC+R 0.2-0.4 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 1.4 x as long as maximum apical width, broadening posteriorly with maximum width apically, then slightly narrowed at apex, smooth, glabrous in anterior half, sparsely pilose in posterior half, deep medial longitudinal groove present; T 2 in midline 0.4 0.6 x as long as $\mathrm{T} 1,0.7-1.0 \mathrm{x}$ as long as T 3 , medial length $0.4-0.5 \mathrm{x}$ as long as maximum anterior width, slightly broadening posteriorly, anterior and posterior margins straight, tergite smooth, with scattered white pilosity; median field absent; suture between T2 and T3 indistinct; T3 smooth, in midline $0.5-0.6 \mathrm{x}$ as long as wide across anterior margin, anterior and posterior margin straight, with few hairs on posterior margin; T4-T7 smooth, each with transverse row of hairs on posterior margin; hypopygium sparsely pilose, 0.5 x as long as hind tibia; ovipositor sheaths 0.1 x as wide as long, 0.8 x as long as hypopygium, with few reduced hairs at apex.

## Male

Unknown.

## Host

Unknown.

## Comments

D. notopecktos differs from other Australasian spretus-group species in having the tangent to the posterior margin of median ocellus cutting through the lateral ocelli, the suture between T2 and T3 indistinct, the ovipositor sheaths long and thin. This species is here named using Greek words noton and pecktos meaning glued back, indicating the part fusion of T2 and T3. It is apparently restricted to New Guinea and tropical far north Queensland (Fig. 6.59).
6.5.19 Diolcogaster perniciosus (Wilkinson) (Figs 4.7, 4.10, 5.20, 6.10, 6.28, 6.29, 6.53)

Microgaster perniciosa Wilkinson, 1929: 112.
Protomicroplitis perniciosa Nixon, 1965: 248; Shenefelt, 1973: 781.

## Material Examined

Holotype. ©, 'Victoria, undated, C. French' (BMNH).
Other specimens examined. Australian Capital Territory: 1 O, Black Mt, 1.vi12.vii.1982, I.D. Naumann \& J.C. Cardale (ANIC). New South Wales: 15 Q, $3 O^{\text {n }}$, Berala, 24.xii.1969, G. Daniels, (UQBA); 1 O, Kurrajong, nr Richmond, 8.ix.1970, D.K. McAlpine \& G.A. Holloway (AMSA); 2 O. Mt Wilson, Blue Mountains, 22.iv. 1970 and 9.v.1974, (AMSA); 1 Q, Rydalmere, 6.xii.1985, G.R. Brown, H.M. Holmes \& S.G. Hunter, (NSWA); $1 O^{\prime \prime}$, Rydalmere, 5.i.1986, S.G. Hunter (NSWA); 1 Q, 20 mi Glen Inns to Grafton H'way, 20.1 iv .1970 , D.H. Colless (NSWA); 1 O, Clorelly, 16.ix.1950, W.E. Wright (NSWA); 1 O", Mossy Pt, 1.ii.1957, E.F. Riek (?); $1 O^{\text {h }}$, Barrington House, 26-28.xii.1965, T. Weir (UQBA). South Australia: $133 \bigcirc, 78 O^{7}$, Waite Inst, Glen Osmond, 10.viii.1961, D.A. Maelzer (reared from larvae of Ardices glatignyi Le Guil.), (WARI); 1 ○, Waterfall Gully, Adelaide, 7.xii.1975, I.D. Naumann (UQBA); 1 O', Glen Osmond, 25.xi.1977, D.K. McAlpine \& M.A. Schneider (UQBA); 3 O', Nat Pk Belair, viii.1974, E. Heddle (Em. ex. Spilosoma galtignyi) (WARI). Queensland: $3 \bigcirc, 2 O^{\prime}$, Hugh Nelson Ra, 1.v-21.vi.1984, Storey \& Brown (WARI); 1 Q, $10^{\text {a }}$, Mt Glorious, $630 \mathrm{~m}, 28 . i i-9 . i i i .1984$, L. Masner (CNCI); 2 Q, Mt Glorious, ii-iii.1982, Hiller, (QDPI); 1 Q, Mt Glorious, iii.1982, Storey \& Brown (WARI); 2 ○, Mt Glorious, 17.xi, no collector, (AEIC); 3 Q, Mt Tambourine, 3.iii.1984, x.1977, G.A. Galloway (WARI \& BMNH); 1 Q, Mt Tamborine, 15.ii.1960, F.A. Perkins (UQBA); 3 Q, Wongabel, 10.vi-3.xii.1983, 9.i-10.ii.1984, Storey \& Brown (WARI); 1 ○, nr Wilson's Peak, $700-800 \mathrm{~m}, 12 . \mathrm{v} .1974$, I.D. Naumann (UQBA); 1 O, Bald Mt area, 27-31.i.1972, S.R. Monteith (UQBA); 1 Q̨, Cuningham Pass, 6-20.iii, no collector, (AEIC); 3 Q, Stanthorpe, 1982, J. Sedlacek (BMNH); 1 O', Crystal Cascades, Cairns, 19.iv.1967, D.H. Colless; 1 O', $^{7}$, Mt Webb Nat Pk, 28-30.ix.1980, J.C. Cardale, (ANIC). Tasmania: $30^{\circ}$, Waldheim, 300 m , 25.i-9.ii, no collector, (AEIC); 4 Q, $6 O^{\prime \prime}$, Bunker Research Labs, New Town, 6.iii.1979, G. Anderson (larvae on ragwort) (TDPI); 3 O, Blackmans Bay, 23.i.1985, R. Bochford (TDPI). Victoria: 10 Q, $5 \bigcirc^{\prime}$, Greensborough, 23.vii.1956, no collector, (Anthelid parasite), (MVMA); 2 Q, Melbourne, no date, G.F. Hill (MVMA); 11 Q, (bred from larvae of Drerasia caverceus), iv.1911, no collector, (MVMA); 1 ○, Wilson Prom, no date, S. \& J. Peck (CNCI); $1 \bigcirc, 10^{\prime}$, Mt Dandenong, $300 \mathrm{~m}, 13$-29.ii, no collector, (AEIC); $1 O^{7}$, Club Terrace, 120m., 5.xii.1974, I.D. Naumann (UQBA); 6 O, 2 O', Heyfield, 7 km , 10.iv.1990, I.G. Faithful \& D. Crawford, (Anthelid host, swept from Lucern) (AEIC). Westran Australia: 1 O̧, Serpentine Falls, Darling Ranges, 20.i.1971, G.A. Holloway (AMSA). New Zealand: 31 Ǫ, $18 O^{*}$, Wainnuiomata, Wellington, iii.1985, D.S. Parker (ex Nyctemera annulata) (ANIC); 1 Q, Canterbury, 11.ii.1976, Ph. Pronk (RMNH).

## Female

Length. 3.2-3.9 mm.
Colour. Body dark brown to black; antennae dark brown; labial and maxillary palps yellow to light brown; fore and mid leg light brown; hind leg light brown but with ventral surface of coxa, apex of femur and tibia dark brown, tarsi dark brown, dorsal surface of coxa
black; stigma dark brown but basally with yellow to light brown spot; T1 and median field of T2 black, T3-T7 light to dark brown; hypopygium dark brown to black.

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth to weakly punctate; face at widest 1.4-1.7 x as wide as high, distinctly separated from clypeus, punctate with weak medial longitudinal carina in dorsal half; clypeus punctate; temples weakly striolate-punctate; in lateral view medial temples $0.6-0.8 \mathrm{x}$ width of eye; eyes $0.5-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus passing in front of anterior margin of lateral ocelli; distance between inner margin of lateral ocelli 0.8-1.3 x distance from outer margin of lateral ocellus to edge of eye; antenna 1.0-1.3 x as long as body, last flagellomere $0.5-0.8 \mathrm{x}$ as long as first.

Mesosoma. Scutum 1.4-1.6 x as wide as long, punctate with sparse white pilosity; scutellar sulcus with 3-5 longitudinal carinae; dorsal scutellum $0.9-1.0 \mathrm{x}$ as wide as long, punctate, sparsely pilose; lateral scutellum coarsely carinate; medial posterior band of scutellum strongly punctate to carinate-punctate; metanotum coarsely crenulate, dorsellum excavated, anteriorly smooth, posteriorly with strong rugosity; propodeum 1.7-2.0 x as wide as long, strongly carinate-punctate, medial longitudinal carina strong; propodeal spiracle oval, positioned medially or slightly anterior to midline, surrounded by costula; lateral pronotum punctate to smooth medially, with pilosity in dorsal half, ventral crenulate groove present; propleuron carinate-punctate without dorsal ridge; mesopleuron weakly punctate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctate; metapleuron rugose and dorsally pilose, except for smooth glabrous antero-median area; hind coxa $0.4-0.9 \mathrm{x}$ as wide as long, $1.2-1.6 \mathrm{x}$ as long as T 1 , punctate with sparse pilosity; inner hind tibial spur 1.3 x as long as outer spur, $0.4-0.6 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing with dense pilosity; stigma $2.5-2.8 \mathrm{x}$ as long as wide; 1-R1 0.8 x distance from stigma to 4-RS; $\mathrm{r} 0.8-0.9 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet in small quadrangular shape, $\mathrm{r}-\mathrm{m}$ and apex of 2-RS+M spectral; 1-CUa 0.4 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe slightly convex and with row of long hairs beyond its widest part; 2-SC+R 0.3-0.5 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 1.9-2.0 x as long as apical width, parallel sided except slightly narrowed apical margin, anterior half smooth and glabrous, posterior areolate-punctate and sparsely
pilose, medial longitudinal groove present in anterior half, absent in posterior; T 2 in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.7-0.9 \mathrm{x}$ as long as T 3 , medial length $0.5-0.6 \mathrm{x}$ as long as maximum width, anterior and posterior margins slightly concave medially; median field strongly sclerotised, rugose, indicated as a raised area, narrow in anterior half then sulci enclosing median field curve postero-laterally making it almost as broad as tergite in posterior half; T3 in midline 0.6 x as long as its maximum width, smooth; suture between T 2 and T 3 distinct; T4-T7 smooth, with transverse sparse row of hairs medially; hypopygium with sparse pilosity, medio-ventrally $0.7-0.8 \mathrm{x}$ as long as hind tibia; ovipositor sheaths with hairs in apical half, specialised sensilla absent.

## Male

As for females except as follows: Propodeum strongly carinate-punctate to weakly punctate and posteriorly smooth; suture between T3 and T4 distinct.

Host
Ardices glatignyi, Nyctemera amica, Nyctemera annulata, Spilosoma glatignyi Le Guillemot (Arctiidae) and unknown anthelids.

## Comments

D. perniciosus can be easily distinguished from other Australasian connexus-group and other species on have the median field of T2 rugulose and 1-CUa very short compared to 1CUb. It is the most abundantly collected species in the Australasian region, and is found along the eastern coastal part of Australia, Tasmania, south-western Western Australia, and is here recorded from New Zealand for the first time (Fig. 6.53).

### 6.5.20 Diolcogaster rixosus (Wilkinson) (Fig. 6.58)

Microgaster rixosa Wilkinson, 1929: 108; Shenefelt, 1973: 725.
Diolcogaster rixosus Austin and Dangerfield, 1992: 27.

## Material Examined

Holotype. New South Wales: ©, 'Moree, 1918, W.W.F' (BMNH).

Other specimens examined. Australian Capital Territory: $110^{\prime \prime}$, (two cocoons \& one larva additional), Black Mountain, 24.x. 1988 (emerged, ex Doratifera oxleyi), W.J Waujura (ANIC); 2 ○, 3 O' $^{\prime}$, Canberra, 18.iv.1960, E.F. Riek (ANIC); 3 ○, Canberra, 16.xii.1958, 3.xi. 1959 \& 10.iii.1961, E.F. Riek (ANIC); $1 O^{\prime}$, Black Mountain, 2-10.iv.1968, no collector (ANIC). New South Wales: 1 Q, Queanbeyan, 5.iv.1980, I.F.B. Common (ANIC); 2 Q, Royal National Park, 4.xii. 1970 \& 13.vii.1971, D.K. McAlpine (ANIC \& AMSA); 5 Q, 1 $O^{\prime \prime}$, (on two points), (cup moth caterpillar, Doratifera: Limacodidae), Moree, 2.ii.1918, no collector (NSWA); $1 O^{3}, 3$ points with cocoons (cup moth caterpillar, Doratifera: Limacodidae), Moree, no date, W.W.F (NSWA); 1 O", Kangaroo Valley, 22.iii.1961, E.F. Riek (ANIC). Queensland: 15 Q, (ex Doratifera larva) (one used for SEM), Long Pocket, Brisbane, i.1971, B. Doube (ANIC). South Australia: 7 O, $26 \mathrm{O}^{\prime \prime}$, (parasite of Limacodidae, on Euc fasciculosa), Coorong, 25.ix. 1965 (collected) (pupate 12.x.1965; adults emerged 25.x.1965), N.C Stuart (WARI); 1 O, Mannum, 28.i.1990, G.W. Howard (ANIC). Victoria: $1 \bigcirc, 3 \odot^{\prime \prime}$, (on one point) (ex cup moth caterpillar, Doratifera sp.), Durham Ox, i.1962, no collector (MVMA); $4 \bigcirc, 1 O^{\text {n }}$, (bred from Limacodid larva: longcrans), Melbourne, 3.xii, F.R.S. (MVMA) . Western Australia: 1 Q, 24 mi. E pinjarra, 19.i.1971, G.A. Holloway \& H. Hughes (ANIC).

## Female

Length. 3.3-4.2 mm .
Colour. Generally head, mesosoma and T1 light brown to head dark brown rest light brown; T2-T7 dark brown to light brown; fore, mid and hind leg light brown to hind leg dark brown rest light brown or only hind tarsi dark brown rest light brown; antenna dark brown; labial and maxillary palps light brown; stigma and fore wing veins dark brown, wing transparent to smoky brown.

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons smooth; face at widest $1.2-1.3 \mathrm{x}$ as wide as high, weakly punctulate with faint medial longitudinal carina in dorsal half; temples smooth; in lateral view medial temples $0.4-0.5 \mathrm{x}$ width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; ocelli on a higher stammaticum; tangent to posterior margin of anterior ocellus touching anterior margin of lateral ocelli; distance between inner margin of lateral ocelli 1.0-1.3 x distance from outer margin of lateral ocellus to edge of eye; antenna 1.1-1.2 x as long as body.

Mesosoma. Scutum 1.4-1.7 x as wide as long, weakly punctate with sparse white pilosity; notauli absent; scutellar sulcus with 4-7 longitudinal carinae; dorsal scutellum as wide as long, with few weak punctations, sparsely pilose; lateral scutellum rugose-carinate; lateral bands of scutellum strongly convex; medial posterior band of scutellum weakly rugose-punctate, continuous with dorsal scutellum; metanotum smooth to weakly crenulate;
dorsellum smooth, excavated, broadly triangular, about as long as anteriorly wide; propodeum 1.8-1.9 x as wide as long, smooth, medial longitudinal carina strong; propodeal spiracle almost rounded, without costulae, positioned medially or slightly anterior to midline; lateral pronotum smooth, pilose in dorsal half, ventral and dorsal groove completely smooth to weakly carinate; propleuron weakly punctulate, with a dorsal ridge; mesopleuron sparsely punctate anteriorly and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctate; metapleuron smooth; hind coxa $0.6-0.7 \mathrm{x}$ as wide as long, 1.2-1.5 x as long as T 1 , generally smooth; inner hind tibial spur 1.3 x as long as outer, 0.6 x as long as hind basitarsus.

Wings. Fore wing smooth to sparsely pilose over basal half of sub-basal and plical cells, rest with evenly dense pilosity; 1-RS 0.2-0.3 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.2-0.3 \mathrm{x}$ as long as $1-\mathrm{M}$; $1-\mathrm{RS}+\mathrm{M} 1.1-1.2 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 0.9-1.1 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma 2.2-2.5 x as long as wide; 1-R1 0.8-0.9 x distance from stigma to $4-\mathrm{RS}$; $\mathrm{r} 0.7-0.8 \mathrm{x}$ as long as width of stigma, straight, forming an obtuse angle with 2-RS; areolet triangular; r-m and apex of 2RS + M unsclerotised; 1-CUa 0.4-0.8 x as long as 1-CUb; hind wing vannal lobe straight and with a row of long hairs beyond its widest part.

Metasoma. T1 1.6-1.8 x as long as maximum width, parallel-sided to weakly rounded in apical one quarter, apex straight, anterior three quarters smooth to weakly punctulate and sparsely pilose, posterior one quarter smooth, glabrous, deep medial longitudinal groove complete; T 2 smooth, in midline $0.3-0.4 \mathrm{x}$ as long as $\mathrm{T} 1,0.5-0.7 \mathrm{x}$ as long as T 3 , medial length 0.3 x as long as maximum width, slightly widened posteriorly, anterior margin straight to slightly convex medially, posterior margin strongly concave medially; median field indicated by raised square area; lateral sulci obliquely diverging postero-laterally in anterior one quarter; suture between T 2 and T 3 distinct; T 3 in midline $0.4-0.5 \mathrm{x}$ as long as maximum width of tergite, anterior margin medially strongly convex, posterior margin straight; T4-T7 smooth with row of hairs medially; hypopygium with sparse pilosity, $0.8-1.1 \mathrm{x}$ as long as hind basitarsus; ovipositor sheaths 0.6 x as long as hind basitarsus, polished-smooth with few reduced hairs at apex, specialised sensilla absent.

## Male

As for females except for propodeum which is weakly punctate posterior to spiracle.

Doratifera oxleyi (Limacodidae).

## Comments

D. rixosus is apparently unrelated to any other species, but is similar to D. tearae and D. vulpinus in some characters. It but can be separated from these and other Australasian Diolcogaster by having the lateral bands of the scutellum strongly convex and T2 relatively short compared with T3. This species is known from eastern and south-eastern Australia, and south-western Western Australia (Fig. 6.58).
6.5.21 Diolcogaster robertsi, sp. nov. (Figs 6.23, 6.32, 6.33, 6.57)

## Material Examined

Holotype. ©, Queensland, '12.44S 143.17E, 8 km EbyN Mt Tozer, 7.vii.1986, J.C. Cardale' (ANIC).

Paratypes. Queensland: $1 \bigcirc$ with same data as holotype; $4 \bigcirc, 10 O^{7}$, Mt Web Nat Pk, 28-30.ix.1980, J.C. Cardale (ANIC); $1 O^{\prime \prime}$, Mt Web Nat Pk, 20-27.iv.1981, I.D. Naumann (WARI); $1 \circ^{\text {T}}$, Cedar Ck, 14.v.1980, I.D. Naumann \& J.C. Cardale (WARI); $20^{*}$, Kuranda, 16-17.v.1980, I.D. Naumann \& J.C. Cardale (WARI); 1 Ơ, Shiptons Flat, 17-19.x.1980, J.C. Cardale (WARI); 2 Ơ, Mt Cook Nat Pk Cooktown, 11-13.x.1980, J.C. Cardale (ANIC); 1 $0^{7}$, Kuranda, 11.iii.1964, I.F.B. Common \& M.S. Upton (WARI); 1 Q, $16 O^{7}$, Bamaga, 3-15.i-3-20.ii.1984, J. Sedlacek (AEIC); 1 Q, Cow Bay, 29.iii.1983, Storey \& Cunningham (ANIC); 1 O., St Paul Moa Is, 11-16.ii.1986, Nousrer \& Hovrucek (WARI).

## Female

Length. 2.3-2.9 mm.
Colour. Body generally dark brown to black; antennae white on segments 5-8, rest dark brown; basal segment of labial and maxillary palps brown, rest yellow; legs light brown with apices of hind femur and hind tibia dark brown, hind coxa light to dark brown; stigma dark brown but basally with yellow to light brown spot; hypopygium dark brown to black

Head. In dorsal view 1.2-1.3 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth to weakly punctate; vertex weakly punctate; face at widest 1.2-1.4 x as wide as high, distinctly separated from clypeus, punctate with weak medial longitudinal carina in dorsal half; clypeus punctate; temples weakly punctate; in lateral view medial temples 0.3-0.5 x width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus passing in front of anterior margin of lateral ocelli;
distance between inner margin of lateral ocelli 0.8-1.0 x distance from outer margin of lateral ocellus to edge of eye; antenna 1.2-1.3 x as long as body, last flagellomere $0.6-0.7 \mathrm{x}$ as long as first.

Mesosoma. Scutum 1.7-1.9 x as wide as long, punctate with sparse white pilosity; scutellar sulcus with 6-8 longitudinal carinae; dorsal scutellum 1.0-1.1 x as wide as long, punctate, sparsely pilose; lateral scutellum coarsely carinate; medial posterior band of scutellum strongly punctate to carinate-punctate; metanotum coarsely crenulate, dorsellum excavated, as long as wide, anteriorly smooth, posteriorly with strong rugosity; propodeum $1.9-2.3 \mathrm{x}$ as wide as long, strongly rugose-punctate, medial longitudinal carina strong; propodeal spiracle oval, positioned medially or slightly anterior to midline, surrounded by a costula; lateral pronotum entirely punctate to medially smooth rest punctate, ventral groove present; propleuron punctate, without dorsal ridge; mesopleuron weakly punctulate anterodorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctulate; metapleuron weakly rugose and dorsally pilose, except for smooth glabrous antero-median area; hind coxa $0.6-0.7 \mathrm{x}$ as wide as long, 1.5-1.8 x as long as T1, weakly punctulate to smooth on outer surface; inner hind tibial spur $1.3-1.5 \mathrm{x}$ as long as outer spur, $0.4-0.6 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing with dense pilosity; stigma $2.6-2.8 \mathrm{x}$ as long as wide; $1-\mathrm{R} 10.8-0.9 \mathrm{x}$ distance from stigma to 4-RS; r 0.7-0.9 x as long as width of stigma, forming an obtuse angle with 2-RS; areolet triangular, r-m and apex of 2-RS+M spectral; 1-CUa $0.4-0.6 \mathrm{x}$ as long as 1-CUb; hind wing vannal lobe slightly convex and with row of long hairs beyond its widest part; 2-SC+R 0.3 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 1.5-2.0 x as long as apical width, anterior half smooth and glabrous, parallel sided, posterior carinulate to carinulate-punctate with sparse pilosity weakly narrowing, medial longitudinal groove present in anterior half, absent in posterior half; T2 in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.7-0.9 \mathrm{x}$ as long as T 3 , medial length $0.4-0.7 \mathrm{x}$ as long as maximum width, anterior and posterior margin slightly concave medially; median field strongly sclerotised, indicated as a raised area, carinulate, sulci enclosing median field curve outwards postero-laterally, posteriorly making it almost as broad as tergite; T3 in midline $0.4-0.6 \mathrm{x}$ as long as its maximum width, carinulate to carinulate-punctate medially with white pilosity; suture between T2 and T3 distinct; T4-T7 smooth, with sparse white pilosity;
hypopygium with sparse pilosity, medio-ventrally $0.3-0.5 \mathrm{x}$ as long as hind tibia; ovipositor sheaths with hairs in apical half, specialised sensilla absent.

## Male

As for females except as follows: Head and mesosoma black to dark brown and metasoma light to dark brown; or head black and mesosoma and metasoma light brown; antenna brown; T2 carinate to carinulate-punctate; T3-T7 with sparse to dense pilosity.

## Host

Unknown.

## Comments

D. robertsi can be distinguished from other connexus-group members and other Australasian Diolcogaster by having white banded antennae (flagellomeres 5-8), and T2 and T3 being carinulate. This species is named after John Roberts, my Rotary Counsellor in Australia. It is known only from northern Queensland (Fig. 6.57).
6.5.22 Diolcogaster sons (Wilkinson) (Figs 4.3, 5.7, 5.8, 5.19, 6.30, 6.31, 6.36-6.39, 6.52)

Microgaster sons Wilkinson, 1932: 87.
Protomicroplitis sons Nixon, 1965: 247; Shenefelt, 1973: 781.
Diolcogaster sons Mason, 1981: 114; Austin and Dangerfield, 1992: 27.

## Material Examined

Holotype. $0^{\prime \prime}$, Australian Capital Territory, 'Brindabella F.C.T., about $4,000 \mathrm{ft}$., 23.iii.1930, J.F. Evans' (BMNH).

Other specimens examined. Queensland: $5 \bigcirc, 10^{7}$, Stanthorpe, 700 m and 1000 m , Mar. and Dec., no collector (ANIC); $4 \bigcirc^{7}$, Stanthorpe, 6.v-13.vii, no collector (ANIC); $1 \bigcirc$, Mt Tamborine, 10.x.1979, J.F. Donaldson (QDPI). Tasmania: 1 Q, $1 O^{\prime \prime}$, Frenchmans Cap. Franklin River, 22.ii-26.iii and 14-21.ii, no collector (AEIC). Western Australia: 10 , Yanchep, 32 mi . N. of Perth, 16.x.1969, H. Evans \& R.W. Matthews (ANIC). New Caledonia: 1 Q, Dumbea 100 m 7.ix.1972, J.F. McAlpine (CNCI). Sulawesi Utara: 1 Q, Dumoga Bone Nat. Pk. nr Toraut, rainforest, vi.1985, MT, A.D. Austin (WARI).

## Female

Length. 3.0-4.0 mm.
Colour. Body generally black; antennae brown; basal two segments of labial and maxillary palps brown, rest yellow or brown; fore leg light to dark brown, fore coxa black, mid leg dark brown, hind leg black but with hind trochantellus and basal half of hind femur dark brown, sub-basal tibial ring and hind tibial spurs yellow; stigma dark brown, fore wing with brown apical spot; basal half of T1 and entire T2 yellow except for apical half of median field which is black; T4-T7 and hypopygium dark brown to nearly black

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons rugulose; face at widest $1.2-1.3 \mathrm{x}$ as wide as high, acinose-striolate with faint medial longitudinal carina in dorsal half; temples striolate or striolate-punctate; in lateral view medial temples $0.5-0.6 \mathrm{x}$ width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus cutting through lateral ocelli; distance between lateral ocelli 1.4-1.6 x distance from lateral ocellus to edge of eye; antenna $1.0-1.2 \mathrm{x}$ as long as body, slender, first flagellomere $3.0-3.4 \mathrm{x}$ as long as wide.

Mesosoma. Scutum 1.4-1.6 x as wide as long, alveolate-punctate with fine granulate background microsculpture and sparse white pilosity; notauli indicated by dark weaklyimpressed alveolate-punctate depressions; scutellar sulcus with 7-9 longitudinal carinae; dorsal scutellum 1.4-1.5 x as wide as long, alveolate-punctate with fine granulate microsculpture, sparsely pilose; lateral scutellum generally coarsely carinate but smooth medially; medial posterior band of scutellum interrupted by variable sculpturing (depressed with 1-2 longitudinal carinae to almost smooth with few very weak punctures); metanotum coarsely crenulate except for smooth sub-margin, dorsellum about as long as anteriorly wide; propodeum 1.7-2.0 x as wide as long, medial longitudinal carina with radiating short carinae on either side, rest of propodeum sparsely punctate; propodeal spiracle oval, positioned medially or slightly anterior to midline, surrounded by costula; lateral pronotum rugulose to smooth medially, with pilosity in dorsal and posterior half; propleuron with a dorsal ridge; mesopleuron pilose-alveolate to punctate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly strigate to punctate; metapleuron areolate-carinate and dorsally pilose, except for smooth glabrous antero-median area; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long, $1.4-1.8 \mathrm{x}$ as long as T 1 ,
generally alveolate-punctate with sparse pilosity, except for weak sparse punctation on outer surface which merges with background micropunctation; inner hind tibial spur 1.2-1.5 x as long as outer spur, $0.6-0.8 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing with scattered pilosity over basal half, evenly dense in apical half; stigma 2.1-2.7 x as long as wide; 1-R1 0.7 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.7-1.0 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with $2-\mathrm{RS}$; areolet slit-like, r-m and apex of 2-RS+M unsclerotised; 1-CUa 0.7-0.8 x as long as 1-CUb; hind wing vannal lobe straight to slightly concave, glabrous beyond its widest part; 2-SC+R 0.4-0.6 x as long as $1 \mathrm{r}-\mathrm{m}$.

Metasoma. T1 1.0-1.3 x as long as apical width, broadening posteriorly, anterior half smooth and glabrous, posterior half areolate and sparsely pilose, medial longitudinal groove shallow in anterior half, deeper in posterior half; T 2 in midline $0.6-0.7 \mathrm{x}$ as long as $\mathrm{T} 1,0.9-$ 1.0 x as long as T3, medial length $0.7-0.9 \mathrm{x}$ as long as anterior width, slightly broadening posteriorly, anterior margin straight or slightly convex medially with few coarse crenulae, antero-median node slightly raised above level of anterior margin, posterior margin broadly emarginate, lateral fields carinate to carinate-punctate; median field $0.4-0.6 \mathrm{x}$ as wide as tergite at anterior margin, smooth, bordered on either side by deep crenulate groove in anterior one third, crenulations becoming weaker or absent in posterior two third; T3 in midline 0.7 x as long as wide across anterior margin, carinulate with a few scattered punctures, anterior margin medially convex and strongly crenulate, posterior margin rounded at corners, smooth with few hairs, median field of T3 0.4-0.7 x as long as medial length, 0.50.7 x as wide as anterior width of tergite, smooth, diamond-shaped in anterior half; suture between T2 and T3 deep, crenulate; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, $0.5-0.7 \mathrm{x}$ as long as medial length of T 3 ; ovipositor sheaths rounded apically, with hairs in apical half and a single thickened hair sub-apically, specialised sensilla present, truncate at apex.

## Male

As for females except as follows: Fore and mid legs, hind trochantelli and hind femora light brown to reddish-brown (except for black apices of hind femora); head 0.8-0.9 x as wide as scutum; antennae more robust, first flagellomere $2.0-2.8 \mathrm{x}$ as long as wide; T 20.9 x as long as T3; T3 carinulate or cristulate with few scattered punctures.

Unknown.

## Comments

D. sons can be distinguished from all Australasian basimacula-group and other Diolcogaster species by the presence of a black spot in the posterior half of T1, and the shape of the median field of T3. Previously this species was known only from the male holotype collected in the A.C.T. However, the female is recorded here and described for the first time, and its distribution extended to include south-east Queensland, south-western Western Australia, Tasmania, New Caledonia and Sulawesi (Fig. 6.52).

The two specimens from Tasmania differ the other Australasian material in having the medial posterior band of scutellum with very weak sculpturing, the lateral fields of propodeum smooth, and the T2 extensively black. The specimens from Sulawesi Utara and New Caledonia differ from the Australian material by having T1 entirely black, T2 black except for the lateral margins which are yellow, and the hind tibia lacking a yellow ring subbasally. However, until further specimens are available these differences are best considered as intra-specific variability associated with its wide geographic distribution.

### 6.5.23 Diolcogaster tearae (Wilkinson) (Fig. 6.58)

Microgaster tearae Wilkinson, 1929: 107; Shenefelt, 1973: 732.
Diolcogaster tearae Austin and Dangerfield, 1992: 27.

## Material Examined

Holotype. ○̧, 'Victoria, undated, no collector' (BMNH).
Other specimens examined. New South Wales: 1 Ọ, Cabbage Tree Ck, 8.ii.1961, N. Dobrotworsky (AMSA). South Australia: 1 O , Waite Agricultural Research Institute, 2.iii.1994, P.C. Dangerfield (WARI). Victoria: 1 O, Cann River, E. Gippsland, 6.ii.1961, N. Dobrotworsky (AMSA). Western Australia: $1 O^{\prime \prime}$, Porongurups, 10.xii.1970, G.A. Holloway \& H. Hughes (Unknown).

## Female

Length. 3.0-3.6 mm.

Colour. Head dark brown to black; antennae dark brown; basal two segments of labial palps dark brown, rest light brown; maxillary palps light brown; fore tibia and fore tarsi light brown to smoky brown; mid femur and mid tarsi light brown to smoky brown; hind coxa, hind trochantellus and hind tibia light brown, hind femur and hind tarsi dark brown or basal half of hind coxa light brown, apical half of hind coxa, hind trochantellus, hind femur, hind tibia, and hind tarsi smoky brown; stigma and veins dark brown, wing transparent to smoky black; T1-T3 light brown, T4-T7 dark brown.

Head. In dorsal view 0.9-1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons smooth to weakly punctulate; face at widest 1.3-1.4 x as wide as high, weakly punctulate with faint medial longitudinal carina in dorsal half; temples smooth; in lateral view medial temples $0.5-0.6 \mathrm{x}$ width of eye; eyes 0.6 x as wide as high; tangent to posterior margin of anterior ocellus touching anterior margin of lateral ocelli; distance between inner margin of lateral ocelli 1.0 x distance from outer margin of lateral ocellus to edge of eye; antenna 1.1 x as long as body.

Mesosoma. Scutum $1.5-1.6 \mathrm{x}$ as wide as long, weakly punctate with sparse white pilosity; notauli absent; scutellar sulcus with 3-5 longitudinal carinae; dorsal scutellum 0.91.0 x as wide as long, smooth to with a few weak punctations, sparsely pilose; lateral scutellum generally carinate; lateral bands of scutellum weakly convex; medial posterior band of scutellum rugose-punctate continuous with dorsal scutellum; metanotum smooth to weakly crenulate; dorsellum anteriorly smooth, excavated, broadly triangular, posteriorly with a pilose-punctate area about as long as anteriorly wide; propodeum 1.8-2.2 x as wide as long, smooth, medial longitudinal carina strong; propodeal spiracle rounded, without costulae, positioned medially or slightly anterior to midline; lateral pronotum smooth, pilose in dorsal half, with smooth ventral groove; propleuron weakly punctulate, with a dorsal ridge; mesopleuron smooth anteriorly, ventrally and posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, smooth; metapleuron smooth; hind coxa 0.6 x as wide as long, $1.5-1.7 \mathrm{x}$ as long as T 1 , generally smooth; inner hind tibial spur 1.3 x as long as outer, $0.5-0.7 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing smooth to sparsely pilose over basal half of sub-basal and plical cells, rest with evenly dense pilosity; $1-\mathrm{RS} 0.2-0.3 \mathrm{x}$ as long as $1-\mathrm{RS}+\mathrm{M}, 0.2-0.4 \mathrm{x}$ as long as $1-\mathrm{M}$; $1-\mathrm{RS}+\mathrm{M} 1.2-1.4 \mathrm{x}$ as long as $1-\mathrm{M}$; m-cu 0.9-1.0 x as long as $2-\mathrm{RS}+\mathrm{M}$; stigma $2.0-2.7 \mathrm{x}$ as
long as wide; 1-R1 0.8-0.9 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.8-0.9 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet triangular; r-m and apex of 2-RS+M unsclerotised; 1-CUa $0.7-0.8 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight, with short and sparse row of hairs beyond its widest part.

Metasoma. T1 smooth, 1.7-2.0 x as long as maximum width, parallel-sided, then weakly narrowed on posterior one quarter, apex straight; anterior three quarters glabrous, posterior one quarter sparsely pilose, deep medial longitudinal groove complete; T 2 smooth, in midline 0.5 x as long as $\mathrm{T} 1,0.6-0.8 \mathrm{x}$ as long as T 3 , medial length $0.5-0.6 \mathrm{x}$ as long as maximum width, parallel sided, anterior margin slightly convex medially, posterior margin regularly concave; median field indicated by raised oval area; lateral sulci obliquely diverging postero-laterally in anterior one quarter giving a triangular shape to tergite; suture between T2 and T3 distinct; T 3 in midline $0.7-0.8 \mathrm{x}$ as long as maximum width, anterior margin medially slightly convex, posterior margin straight; T4-T7 smooth, glabrous; hypopygium with sparse scattered pilosity, 1.0-1.1 x as long as hind basitarsus; ovipositor sheaths 0.6 x as long as hind basitarsus, specialised sensilla absent.

## Male

As for females except that metanotum, propodeum. metasoma and hind leg are smoky brown.

## Host

Epicoma tristis (Donovan) (Thaumetopoeidae).

## Comments

The presence of weakly convex to almost parallel-sided lateral bands of the scutellum and a smooth mesopleuron distinguish $D$. tearae from other Australasian species. Previously known only from the holotype collected in Victoria, the species is here recorded from northern NSW, South Australia, and south-western Western Australia (Fig. 6.58).

Microgaster vulpina Wilkinson, 1929: 109; Shenefelt, 1973: 736.
Diolcogaster vulpinus Austin and Dangerfield, 1992: 27.

## Material Examined

Holotype. Victoria: 'O, undated, no collector' (BMNH).
Other specimens examined. New South Wales: 2 Q, Packsaddle, 111 mi . N. of Broken Hill, 21-26.xi.1969, H.E Evans \& R.W Mathews (MCZC). Northern Territory: 1 O, Row Ck Alice Springs, 27.ix.1978, J.C. Cardale (ANIC); $4 \bigcirc$ (one used for SEM), Waterhouse Range, Alice Springs, i1.x.1978, J.C. Cardale (ANIC); 5 ¢, $1 \bigcirc^{\circ}$, Alice Springs, 3-5.x.1978, J.C. Cardale (ANIC); $130^{\circ}$, Areyonga, 28.ix, 30.x, 10.xi \& 8.xii, (no collector) (AEIC); 10 $O^{\top}$, Plenty Highway, 268 km ENE of Alice Springs, 14.x.1978, J.C. Cardale (ANIC); $30^{*}$, Entire Ck, 155 NEbyE of Alice Springs, 13.x.1978, J.C. Cardale (ANIC); 1 O', Illungnarra, 90 km SWbyS of Alice Springs, 25.ix.1978, J.C. Cardale (ANIC); $10^{\circ}$, Todd River Alice Springs, 1.x.1978, J.C. Cardale (ANIC); $1 O^{7}$, Old Andado Hs, Simpson Desert, 30.ix.1972, Z. Liepa (ANIC). Queensland: $1 \bigcirc, 3 O^{7}$, Boulia, 16 x.1978, J.C. Cardale (ANIC); $1 O^{*}$, Bald Hill Mcllwraith Ra. 500 m , 26.vi-13.vii.1989, I.D. Naumann (ANIC). South Australia: $1 \bigcirc, 10 O^{7}$, Mt. Barr, 24 km SSE of Abminga, 25.ix.1972, Z. Liepa (ANIC); 2 O, Yalata Mission, 9.iv.1983, E.S. Nielsen \& E.D. Edwards (ANIC); $3 O^{\text {® }}$ (one damaged), Mt. Sarah Hs., N. of Odnatta, 24.ix.1972, Z. Liepa (ANIC). Victoria: 2 Q, Hamilton, 27.xi.1947, G. Stephens (MVMA); Western Australia: 1 O, Millstream, 17-20.iv.1972, N.R. Mitchell (ANIC); $1 \bigcirc$, Argyle Dimond Mine, 7-13.v.1985, A. Postle (ANIC); 1 O, Nedlands, xii.1960, M.M.H. Wallace (?), (used for SEM); $1 O^{\prime \prime}$, Norseman, 6.v.1983, E.S. Nielsen \& E.D. Edwards (ANIC).

## Female

Length. 2.5-3.7 mm.
Colour. Head and scutum light brown to head light brown, scutum dark brown; scutellum, metanotum and propodeum black; metasoma entirely dark brown to T1-T3 yellow rest dark brown; fore leg light brown, mid leg light brown to dark brown, hind leg dark brown to black; antenna dark brown; labial and maxillary palps light brown; stigma and fore wing veins dark brown, wing transparent to smoky brown.

Head. In dorsal view 1.0-1.1 x as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons smooth; occiput rounded; face at widest 1.31.5 x as wide as high, weakly rugose-punctulate to punctulate with faint medial longitudinal carina in dorsal half; temples smooth to weakly punctulate; in lateral view medial temples $0.5-0.6 \mathrm{x}$ width of eye; eyes 0.6 x as wide as high; ocelli on a higher stammaticum; tangent to posterior margin of anterior ocellus touching anterior margin of lateral ocelli; distance
between inner margin of lateral ocelli 1.0-1.1 x as distance from outer margin of lateral ocellus to edge of eye; antenna $0.9-1.1 \mathrm{x}$ as long as body.

Mesosoma. Scutum 1.3-1.5 x as wide as long, with weak to strong punctulation, sparsely pilose; notauli absent; scutellar sulcus with 5-11 longitudinal carinae; dorsal scutellum 0.9 x as wide as long, weakly punctate laterally, smooth to weakly punctate medially, sparsely pilose; lateral scutellum carinate; lateral bands of scutellum strongly convex; medial posterior band of scutellum with weak to strong rugosity continuous with or separated by a smooth band from dorsal scutellum; metanotum smooth to weakly crenulate; dorsellum anteriorly excavated, broadly triangular, posteriorly smooth with a few hairs, about as long as anteriorly wide; propodeum 1.8-2.2 x as wide as long, smooth, glabrous to sparsely pilose, medial longitudinal carina weak; propodeal spiracle rounded, without costulae, positioned medially or slightly anterior to midline; lateral pronotum smooth, glabrous, ventral and dorsal groove smooth; propleuron weakly punctulate, with or without a dorsal ridge; mesopleuron entirely smooth to sparsely punctate anteriorly and ventrally, smooth posteriorly beside carinate pleural suture; pleural suture weak; epicnemial furrow deep; precoxal groove shallow, smooth to weakly punctulate; metapleuron smooth; hind coxa $0.6-0.7 \mathrm{x}$ as wide as long, 1.3-1.6 x as long as T1, generally smooth; inner hind tibial spur 1.2-1.3 x as long as outer, 0.7 x as long as hind basitarsus.

Wings. Fore wing smooth to sparsely pilose over basal half of sub-basal and plical cells, rest with evenly dense pilosity; $1-\mathrm{RS}$ 0.1-0.3 x as long as $1-\mathrm{RS}+\mathrm{M}, 0.2-0.4 \mathrm{x}$ as long as $1-\mathrm{M}$; $1-\mathrm{RS}+\mathrm{M} 1.2-1.3 \mathrm{x}$ as long as $1-\mathrm{M}$; m-cu $1.0-1.1 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma $2.2-2.7 \mathrm{x}$ as long as wide; 1-R1 0.7-0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.7-0.9 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet in small triangle, 2-RS intersected by r-m from middle dividing it into $2-\mathrm{RSa}$ and $2-\mathrm{RSb} ; \mathrm{r}-\mathrm{m}$ and apex of $2-\mathrm{RS}+\mathrm{M}$ unsclerotised; 1CUa $0.6-0.8 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight, with short and sparse row of hairs beyond its widest part.

Metasoma. T1 1.9-2.5 x as long as maximum width, parallel-sided in basal three quarters, weakly narrowing in apical one quarter; anterior three quarters smooth, glabrous, posterior one quarter smooth to weakly punctate and sparsely pilose, deep medial longitudinal groove complete; T 2 smooth, in midline $0.4-0.6 \mathrm{x}$ as long as $\mathrm{T} 1,0.7-0.9 \mathrm{x}$ as long as T 3 , medial length $0.4-0.5 \mathrm{x}$ as long as maximum width, slightly widened posteriorly, anterior
margin slightly convex medially, posterior margin straight to weakly concave medially; median field indicated by raised elongate area; lateral sulci obliquely diverging posterolaterally in anterior one quarter; suture between T 2 and T 3 distinct; T 3 in midline 0.4-0.6 x as long as maximum width, anterior margin medially straight to weakly convex, posterior margin straight; T4-T7 smooth, with sparse row of hairs medially; hypopygium with sparse pilosity, 1.3-1.8 x as long as hind basitarsus, acute on apex; ovipositor sheaths $0.3-0.5 \mathrm{x}$ as long as hind basitarsus, polished-smooth, with few reduced hairs at apex, specialised sensilla absent.

## Male

As for female.

Host
Unknown.

## Comments

D. vulpinus is not closely related to any other species and it can be distinguished from other Australasian Diolcogaster by the presence of a weak scutellar sulcus, weak medial longitudinal carina of the propodeum, and T2 with an almost straight apical margin. This species is widely distributed across western, central and southern Australia(Fig. 6.58).
6.5.25 Diolcogaster walkerae, sp. nov. (Figs 6.40, 6.55)

## Material Examined

Holotype. O, Western Australia, 'Lake Violet, 6 mi. S. Wiluna, 23-27.ix.1969, H.E. Evans \& R.W. Matthews' (MCZC).

Paratypes. New South Wales: 1 O, Brindle Ck Border Ranges NP, 3-14.x.1984, I.D. Naumann \& J.C. Cardale, (ANIC). Western Australia: 1 Q, Comet Vale Siding, 715.iii.1979, T.F. Houston et al. (WAMP).

## Female

Length. 2.9-4.3 mm.
Colour. Head and scutum light brown, scutellum to propodeum black, metasoma dark brown; antennae dark brown; labial and maxillary palps light brown; fore and mid leg light
brown except mid coxa which is dark brown, hind leg dark brown except hind tibial spurs which are yellow; stigma dark brown, fore wing transparent.

Head. In dorsal view 1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons weakly punctate to smooth; face at widest 1.3-1.5 x as wide as high, weakly rugulose-punctate with faint medial longitudinal carina in dorsal half; temples smooth to weakly rugulose-punctate; in lateral view medial temples $0.4-0.5 \mathrm{x}$ width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; ocelli on a higher stammaticum; tangent to posterior margin of anterior ocellus just touching the anterior margin of lateral ocelli; distance between inner margins of lateral ocelli 1.7-2.0 x distance from outer margin of lateral ocellus to edge of eye; antenna 0.8-1.1 x as long as body.

Mesosoma. Scutum 1.3-1.9 x as wide as long, densely punctulate with white pilosity; notauli indicated by weakly-impressed depressions; scutellar sulcus with 10-11 longitudinal carinae; dorsal scutellum $0.6-0.8 \mathrm{x}$ as wide as long, with sparse punctation, sparsely pilose; lateral scutellum generally smooth except for few carinae posteriorly; medial posterior band of scutellum interrupted by weak rugosity; metanotum smooth to weakly crenulate, dorsellum about as long as anteriorly wide; propodeum 1.8-2.1 x as wide as long, smooth to weakly punctate; propodeal spiracle oval, positioned medially or slightly anterior to midline, without costulae; lateral pronotum smooth, with pilosity in dorsal half; propleuron smooth to weakly striolate-punctate, without a dorsal ridge; mesopleuron punctate antero-dorsally and ventrally, smooth posteriorly beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, weakly punctate to smooth; metapleuron weakly rugulose and dorsally pilose, except for smooth glabrous antero-median area; hind coxa 0.6 x as wide as long, $1.5-1.6 \mathrm{x}$ as long as T1, weakly punctulate on outer margin with sparse pilosity; inner hind tibial spur 1.3 x as long as outer, 0.7 x as long as hind basitarsus.

Wings. Fore wing entirely smooth to sparsely pilose; 1-RS 0.2 x as long as $1-\mathrm{RS}+\mathrm{M}$, 0.3 x as long as $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.3-1.4 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 0.7-0.8 \mathrm{x}$ as long as $2-\mathrm{RS}+\mathrm{M}$; stigma 2.3-2.5 x as long as wide; 1-R1 0.8 x distance from stigma to $4-\mathrm{RS} ; \mathrm{r} 0.7 \mathrm{x}$ as long as width of stigma, forming an obtuse angle with 2-RS; areolet triangular; r-m and apex of 2RS +M unsclerotised; 1-CUa 0.6 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight, with row of long hairs beyond its widest part.

Metasoma. T1 1.6-1.7 x as long as maximum width, parallel-sided to slightly narrowing in posterior one quarter, anterior three quarters smooth and glabrous, posterior one quarter punctate, pilose, deep medial longitudinal groove complete; T 2 in midline $0.4-0.5 \mathrm{x}$ as long as $\mathrm{T} 1,0.6-0.7 \mathrm{x}$ as long as T 3 , medial length 0.3 x as long as maximum width, slightly broadened posteriorly, anterior margin straight, posterior margin slightly concave medially; median field 0.2-0.3 x maximum width of tergite, smooth, indicated as a raised parallel sided area; lateral sulci obliquely diverging postero-laterally along anterior one quarters; T3 in midline 0.5 x as long as maximum width, anterior margin medially slightly convex, posterior margin straight; suture between T2 and T3 distinct; T4-T7 smooth, with row of sparse hairs to glabrous; hypopygium glabrous to sparsely pilose, $0.6-0.7 \mathrm{x}$ as long as hind basitarsus; ovipositor sheaths 0.4 x as long as hind basitarsus, with hairs in apical half, specialised sensilla present, straight, rounded at apex.

## Male

Unknown.

## Host

Unknown.

## Comments

D. walkerae can be separated from other hadrommatus-group species by its smaller eyes. The species is here named after Dr Annette K Walker from the International Institute of Entomology, London. The species has been recorded from the east coast of New South Wales and inland Western Australia (Fig. 6.55).
6.5.26 Diolcogaster yousufi, sp. nov. (Figs 4.6, 6.21, 6.43, 6.57)

## Material Examined

Holotype. O, Western Australia, 'Crowea st. For. nr Pemberton, 29.x-20.xii.1979, S.J. Curry' (ANIC).

Paratypes. Australian Capital Territory: 4 O, Black Mt, 9.xi-7.xii.1979, D.H. Colless (ANIC); $1 O^{\prime \prime}$, Uriarra Forrest, 20.xi.1960, D.H. Colless, (ANIC); 1 O, Wombat Ck, 750 m , iv.1985, Lawrence, Weir \& Johnson, (ANIC); $1 \bigcirc^{\prime}$, Canberra, 3.i.1961, E.F. Riek, (ANIC); $1 \bigcirc^{\text {O }}$, Honeysuckle Ck, 11-22.iv.1985, I.D. Naumann \& J.C. Cardale, (ANIC). New South Wales: 1 O, Clyde Mt, 26.x.1960, D.H. Colless (ANIC); 10 , Eastern Slopes, Clyde

Mt, 12.i.1961, D.H. Colless, (ANIC); 1 Ơ, Mt Boyce, Blue Mts, 14.iv.1964, D.K. McAlpine, (AMSA); $1 O^{\prime}$, Creel-Sawpit Ck, Snowy Mts, 15.ii.1963, D.K. McAlpine, (AMSA); $1 O^{*}$, Gibralter Range, 27-29.xii.1972, S.R. Monteith, (UQIC); 2 Q, 2 O', Taralga, Jan., no collector, (AEIC); $10^{\prime \prime}$, Creel Kosciusko, 8.xi.1961, E.F. Riek, (ANIC). Queensland: 5 Q, Windsor T'land, 10.x-26.xii.1983, Storey \& Titmarsh, (WARI); $1 \bigcirc, 3$ O', Windsor T'land, iii.1981, R. Storey, (BMNH); 1 O, Windsor T'land, 26.xii.1983-24.i.1984, no collector,
 5.xi-1.xii.1983, Storey Brown, (WARI); 1 Q, Mt Glorious, 17.xi., no collector (AEIC); 1 Q, $3 \mathrm{O}^{7}$, Stanthorpe, 1000 m , Dec., no collector, (AEIC); 2 O', Stanthorpe, 6.v.-13.vii., no $^{\text {n }}$
 Boucek, (AEIC); $10^{\prime \prime}$, Mt Glorious, i.1983, Boucek, (BMNH); $30^{\circ}$, Mt Glorious, x-7.xii, no collector, (AEIC); $1 \bigcirc^{*}$, Mt Edith Forest, 6.v.1967, D.H. Colless, (ANIC); $1 Q$, Ipswich, Feb., no collector, (AEIC). South Australia: $1 \mathrm{O}^{*}$, Waite Inst, 27.ii-3.iii.1989, P.C. Dangerfield, (WARI); 1 Ơ, E Kimba, 28.xi.1958, E.F. Riek, (ANIC). Tasmania: 1 Q, 1 O", Roseberry, 8-24.i., no collector, (AEIC); 1 O, Strahan, 20.ii.1963, I.F.B. Common \& M.S. Upton (ANIC); $7 \mathrm{O}^{\prime}$, Strahan, $14 . \mathrm{ii}-8 . \mathrm{iii}$., no collector, (AEIC); $60^{\circ}$, Collinsville, 300 m , iiiii.1983, I. Gauld, (BMNH); $20^{\prime \prime}$, Mt Barrow, $1000 \mathrm{~m}, 28$. iii., no collector, (AEIC); $10^{\text {r }}$, Togari, 2.iv., no collector, (AEIC); $1 \bigcirc^{7}$, Waldheim, 800 m ., 9.ii-4.iii., no collector, (AEIC). Victoria: $3 \bigcirc, 1 \bigcirc^{\top}$, Noorinbee, 12.xi.1969, A. Neboiss, (MVMA); $1 \bigcirc$, Glenelg Riv., 25.xi.1966, (MVMA); $1 \bigcirc, 6 O^{\prime}$, Warburton, 22.ii-1.iii., no collector, (AEIC). Western Australia: $50^{\circ}$, Crowea St. For., xi-xii.1978, S.J. Curry, (ANIC); $1 \bigcirc, 1 O^{\circ}$, Crowea, 29.x20.xii.1979, S.J. Curry, (ANIC); 3 O, $1 \bigcirc^{7}$, Ludlow, 4.xi-22.xii.1980, S.J. Curry, (ANIC); 3 $O^{*}$, Waren Riv., 16-17.i.1971, G.A. Halloway, (AMSA); $1 \bigcirc^{\prime}$, Norseman, 17.v.1984, E.S. Neilsen \& E.D. Edwards, (ANIC); $1 O^{\text {n }}$, Torndirrup, 7.x.1981, I.D. Naumann \& J.C. Cardale, (ANIC).

## Female

Length. 2.7-3.1 mm.
Colour. Body generally black to dark brown; antennal segments 1-6 light brown, rest dark brown; labial and maxillary palps yellow; fore leg light brown; mid leg dark brown except coxa which is light brown; hind leg dark brown except yellow basal ring on tibia, tibial spurs yellow; stigma dark brown; hypopygium dark brown.

Head. In dorsal view 1.0 x as wide as scutum; vertex, temples, eyes and face with sparse pilosity; dorsal and lateral frons strongly punctate; face at widest $1.3-1.5 \mathrm{x}$ as wide as high, punctate with weak medial longitudinal carina in dorsal half; clypeus smooth to punctate; temples weakly punctate; in lateral view medial temples $0.6-0.7 \mathrm{x}$ width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of median ocellus cutting through anterior margin of lateral ocelli; distance between inner margin of lateral ocelli 1.0-1.1 x distance from outer margin of lateral ocellus to edge of eye; antenna $1.0-1.4 \mathrm{x}$ as long as body, last flagellomere $0.6-0.7 \mathrm{x}$ as long as first.

Mesosoma. Scutum 1.7-1.9 x as wide as long, strongly punctate with fine granulate background sparsely pilose; notauli indicated by depressed punctation; scutellar sulcus with 6-9 longitudinal carinae; dorsal scutellum as wide as long, punctate, sparsely pilose; lateral scutellum coarsely carinate; medial posterior band of scutellum punctulate; metanotum coarsely crenulate, dorsellum excavated, about as long as wide, posteriorly with weak punctation, anteriorly smooth; propodeum 1.7-1.9 x as wide as long, rugose-punctate, medial longitudinal carina strong; propodeal spiracle oval, positioned medially or slightly anterior to midline; lateral pronotum punctate medially, with pilosity in dorsal half, ventral groove present; propleuron punctate without dorsal ridge; mesopleuron punctate antero-dorsally and ventrally, smooth medially beside carinate pleural suture; epicnemial furrow deep; precoxal groove shallow, punctate; metapleuron rugose-punctate and pilose, except for smooth pilose antero-median area; hind coxa $0.5-60 \mathrm{x}$ as wide as long, $1.5-1.7 \mathrm{x}$ as long as T 1 , rugosepunctate on outer surface; inner hind tibial spur 1.3 x as long as outer spur, 0.6 x as long as hind basitarsus.

Wings. Fore wing with dense pilosity except for the basal half of sub-basal and plical cell where it is sparse; stigma 2.1-2.6 x as long as wide; 1-R1 0.8-0.9 x distance from stigma to 4-RS; r 0.6-0.9 x as long as width of stigma, sloping down obliquely towards apex of wing, forming an obtuse angle with $2-\mathrm{RS}$; areolet in small quadrangular shape, 2-RS intersected by r-m from middle to divide it into $2-\mathrm{RSa}$ and $2-\mathrm{RSb}$; r-m and apex of $2-\mathrm{RS}+\mathrm{M}$ spectral; 1-M 0.7-0.8 x as long as $1-\mathrm{RS}+\mathrm{M} ; 1$-CUa $0.5-0.6 \mathrm{x}$ as long as $1-\mathrm{CUb}$; hind wing vannal lobe slightly convex and with row of long hairs beyond its widest part.

Metasoma. T1 2.0-2.5 x as long as apical width, parallel sided, anterior half rugosecarinulate and glabrous, posterior weakly punctate with sparse pilosity, medial longitudinal groove present; T 2 in midline 0.4 x as long as $\mathrm{T} 1,0.8 \mathrm{x}$ as long as T 3 , medial length 0.4 x as long as maximum width, anterior margin straight to slightly concave medially, posterior straight; median field sclerotised, sub-triangular, indicated as a raised area, weakly rugosepunctate, $0.8-0.9 \mathrm{x}$ as wide as maximum width of tergite; T 3 in midline $0.4-0.5 \mathrm{x}$ as long as its maximum width with sparse pilosity; suture between T2 and T3 distinct; T4-T7 smooth, with sparse white pilosity; hypopygium with sparse pilosity, medio-ventrally 0.3 x as long as hind tibia; ovipositor sheaths with hairs in apical half, specialised sensilla absent.

## Male

As for females except as follows: Antennae dark brown; fore and mid legs light brown to dark brown; hind femur and hind tibia light brown to dark brown; T3 smooth to weakly punctate.

## Host

Unknown.

## Comments

D. yousufi is not closely related to any other members of the genus, and it is best separated from other Australasian species by a complex of characters given in the key. This species is here named after Dr. Muhammad Yousuf, odontologist at the University of Agriculture Faisalabad, Pakistan. This is one of the most abundantly collected species of Australasian Diolcogaster. It is found throughout coastal mainland Australia, inland NSW and Tasmania, but not the arid interior, and northern and north-western coastal areas (Fig. 6.57).

Most Queensland specimens ( $13 \mathrm{Q}, 18 \mathrm{O}^{7}$ ) vary from the rest in that T 1 is yellow and, within this group, those from northern and north-east Queensland have T1 slightly narrowing posteriorly, while those from southern Queensland have virtually T1 parallel-sided. However, this variation seems well within the limits of the species as defined here.

### 6.6 The genus Neodiolcogaster gen. nov.

## Neodiolcogaster gen. nov.

Type species: Neodiolcogaster whiffieldi sp. nov.

## Description

Body. Generally dark brown to black; hind tibial spurs yellow.
Head. In dorsal view wider than scutum, pilose except frons which are smooth; face almost twice as wide as high, weakly punctate; temples smooth; ocelli in higher triangle, i.e. tangent to posterior margin of median ocellus passing in front of anterior margin of lateral ocelli; antenna as long as to longer than body.

Mesosoma. Scutum 1.5-2.0 x as wide as long, sparsely punctulate to smooth posteromedially, with white pilosity; notauli absent to weakly indicated by change in scutum coloration; medial posterior band of scutellum smooth, continuous with dorsal scutellum; propodeum smooth except for a few weak carinae diverging from postero-median node, medial longitudinal carina absent; hind coxa $1.2-1.5 \mathrm{x}$ as long as T 1 , smooth, pilose on outer surface; inner hind tibial spur 1.1-1.2 x as long as outer spur, $0.4-0.5 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing sparsely pilose on basal and sub-basal cells, rest with evenly dense pilosity; stigma 2.5-3.3 x as long as wide; r straight, forming an obtuse angle with 2-RS; hind wing with vein $2-R S$ concave towards anterior margin making first marginal cell (1a) wider than second marginal cell (1b); hind wing vannal lobe straight to weakly convex, with a row of hairs beyond its widest part.

Metasoma. T1 about twice as long as maximum width, narrowing posteriorly, smooth to weakly rugose and glabrous, without medial longitudinal groove but with weak depression anteriorly; T2 smooth, triangular to sub-triangular; medial field absent; lateral sulci complete, meeting suture between T2 and T3 and separating T2 from membranous laterotergite; suture between T2 and T3 distinct; hypopygium pilose, evenly sclerotised; ovipositor sheaths of variable shape and pilosity, without specialised sensilla.

## Biology

Unknown.

## Distribution

The genus is endemic to Australia and has been recorded from New South Wales, Queensland, Tasmania and Western Australia.

## Comments

The species tegularis was first described based on a single male in 1905 under the genus Microgaster, however, Nixon (1965) placed the species in Protomicroplitis giving it separate species-group status. When Mason (1981) transferred most of the Protomicroplitis species-groups (sensu Nixon) to Diolcogaster, he did not mention tegularis. More recently,

Austin and Dangerfield (1992) transferred tegularis into Choeras Mason based on the absence of a medial longitudinal carina on the propodeum and the shape of the first metasomal tergite. However, during this study female specimens were found that were deemed to be conspecific with tegularis. These specimens revealed the presence of an evenly sclerotised hypopygium for the species and, thus, its placement in Choeras by Austin and Dangerfield (1992) cannot be supported. Further, females of this and the new species, whitfieldi, will not run to any genus in Austin and Dangerfield (1992) as they will not run any further than couplet 9 .

As discussed above, the genus Diolcogaster, although not monophyletic, is best defined by a series of characters including the presence of a medial longitudinal carina on the propodeum. The species tegularis has a completely smooth propodeum and, based mainly on this character, it is assigned to a new genus, Neodiolcogaster, along with the new species whitfieldi (designated as the type species). These two species were resolved as sister taxa in the phylogenetic analysis undertaken here (see Chapter 5). The name of the genus indicates its general similarity to members of Diolcogaster..

### 6.7 Key to the species of Neodiolcogaster gen. nov. based on females

Antenna 1.3-1.5 x as long as body; two apical flagellar segments together longer than basal flagellar segment (Fig. 6.51); placodes missing on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.9); medio-apical flagellomeres with fluted bent-tipped sensilla in oblique row (Figs 5.6-5.8); apical T1 0.4 x as wide as basal width (Fig. 6.49); medial T2 1.1-1.2 x as long as maximum width (Fig. 6.49); vein 1a of fore wing present (as in Fig. 6.28); fore wing vein M+CU 0.57-0.72 x as long as $1-\mathrm{M}$; inner hind tibial spur $0.59-0.74 \mathrm{x}$ as long as hind basitarsus; hypopygium 0.19-0.33 x as long as hind tibia; ovipositor sheaths with pilosity reduced and at apex only (Fig. 6.50), $0.05-0.24 \mathrm{x}$ as long as hind tibia $N$. whitfieldi sp. nov.

Antenna 1.0 x as long as body; two apical flagellar segments together shorter than basal flagellar segment (Fig. 6.46); placodes intact on ventro-lateral surface of medio-apical flagellomeres (as in Fig. 5.2); medio-apical flagellomeres without flute bent-tipped sensilla; apical T1 $0.6-0.7 \mathrm{x}$ as wide as basal width (Fig. 6.44);
medial T2 $0.5-0.8 \mathrm{x}$ as long as maximum width (Fig. 6.44); vein 1 a of fore wing absent (as in Fig. 4.4); fore wing vein $\mathrm{M}+\mathrm{CU} 0.88-1.02 \mathrm{x}$ as long as $1-\mathrm{M}$; inner hind tibial spur 0.43-0.58 x as long as hind basitarsus; hypopygium 0.34-0.47 x as long as hind tibia; ovipositor sheaths with uniform pilosity on their entire length (Fig. 6.45), 0.25-0.43 x as long as hind tibia $\qquad$ N. tegularis (Szépligeti)

### 6.8 Treatment of Neodiolcogaster species

6.8.1 Diolcogaster tegularis (Szépligeti) comb. nov. (Figs 6.44-6.48, 6.54)

Microgaster tegularis Szépligeti, 1905: 49.
Protomicroplitis tegularis Nixon, 1965: 235; Shenefelt, 1973, 781.
Diolcogaster tegularis Mason, 1981: 114.
Choeras tegularis Austin and Dangerfield, 1992: 21.

## Material Examined

Holotype. O’, ‘Australia, Mount Victoria, 1900, Biro’ (HNHM), LOST.
Other specimens examined. New South Wales: $10^{\top}$, Thirlmere Lake National Park, 18.ix.1985, G.R. Brown \& H.M. Holmes, (NSWA). Tasmania: 1 O, Mount Barrow, 1100 m , 1.ii-3.iii.no year, no collector (AEIC); $1 \bigcirc$, data as holotype; $1 \bigcirc$, Waldheim, 800 m , 9.ii-4.iii.no year, no collector (AEIC); $10^{\prime \prime}$, Collinsville, 300 m , ii.1983, I. Gauld (BMNH); $4 \bigcirc^{\circ}$, W. sided, St. Clair L., $750 \mathrm{~m}, 25-29.1 .1980$, A. Newton \& M. Thayer (CNCI). Western Australia: $1 O^{\prime \prime}$, Mt. Chudalup S. Of Northcliffe, 22.xi.1975, K.A. Spencer (WAMP).

## Female

Length. 2.7-3.1 mm.
Colour. Head and mesosoma black; metasoma dark brown except lateral membranous area of T1-T3 which is yellow; labrum and mandibles light brown; labial and maxillary palps yellow; antenna dark brown; legs light brown except for hind coxa, hind tarsi, apex of hind femur and hind tibia which are dark brown; hind tibial spurs yellow; stigma and fore wing venation dark brown, fore wing transparent.

Head. In dorsal view 1.1-1.2 x as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons smooth; face at widest $1.5-1.6 \mathrm{x}$ as wide as high, weakly punctate; temples smooth; in lateral view medial temples $0.5-0.6 \mathrm{x}$ as wide as width of eye; eyes $0.6-0.7 \mathrm{x}$ as wide as high; tangent to posterior margin of medial ocellus passing in front of anterior margin of lateral ocelli; distance between lateral ocelli 0.7 x
distance from lateral ocellus to edge of eye; antenna 1.0 x as long as body, last flagellomere 0.5 x as long as first, pre-apical antennal segment 1.4 x as long as wide.

Mesosoma. Scutum 1.2-1.3 x as wide as long, sparsely punctulate, with white pilosity; scutellar sulcus with 6-8 longitudinal carinae; dorsal scutellum $0.8-0.9 \mathrm{x}$ as wide as long, smooth with sparse pilosity; lateral scutellum carinate; medial posterior band of scutellum smooth, continuous with dorsal scutellum; metanotum carinate; propodeum 1.6-1.8 x as wide as long, anterior half smooth, posterior half with few weak carinae diverging from postero-median node; medial longitudinal carina absent, costulae absent; propodeal spiracle round, positioned medially or slightly anterior to midline, without costulae; lateral pronotum smooth, glabrous, ventral groove crenulate; propleuron without dorsal ridge, weakly punctulate; mesopleuron smooth except weakly punctulate area anteriorly and ventrally; epicnemial furrow deep; precoxal groove shallow, smooth; metapleuron smooth; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long, 1.2-1.4 x as long as T 1 , smooth, pilose on outer surface; inner hind tibial spur 1.1-1.2 x as long as outer spur, $0.4-0.5 \mathrm{x}$ as long as hind basitarsus.

Wings. Fore wing sparsely pilose on basal and sub-basal cells, rest with evenly dense pilosity; 1-RS $0.1-0.2 \mathrm{x}$ as long as $1-\mathrm{RS}+\mathrm{M}$ and $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.0 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu}$ 1.6-2.0 x as long as 2-RS+M; stigma 2.5-2.9 x as long as wide; 1-R1 0.9 x distance from stigma to 4-RS; r 0.7-0.8 x as long as width of stigma, straight, forming an obtuse angle with 2-RS; areolet in small triangle; r-m and apex of 2-RS+M spectral; 1-CUa 0.6-0.7 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to weakly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.6-1.9 x as long as maximum width, narrowest posteriorly, so that posterior margin $0.6-0.7 \mathrm{x}$ width of anterior margin, smooth to weakly rugose and glabrous, without medial longitudinal groove but with weak depression anteriorly; T 2 smooth, triangular, anteriorly as wide as apex of T 1 , in midline 0.4 x as long as $\mathrm{T} 1,0.5-0.7 \mathrm{x}$ as long as T3, medial length $0.5-0.8 \mathrm{x}$ as long as maximum width; lateral sulci complete, meeting suture between T2 and T3 and separating T2 from lateral membranous area; median field bordered on either side by smooth groove; suture between T2 and T3 distinct; T3 in midline $0.5-0.6 \mathrm{x}$ as long as maximum width, smooth, sparsely pilose apically; T4-T7 smooth, pilose; hypopygium pilose, medio-ventral length $0.9-1.0 \mathrm{x}$ as long as hind basitarsus; ovipositor
sheaths $0.6-0.7 \mathrm{x}$ as long as hind basitarsus, narrow at base broadened apically with pointed apex, with hairs on their entirety, specialised sensilla absent.

## Male

As for females except as follows: Body generally dark brown to black; legs dark brown to black; pre-apical antennal segment about twice as long as wide.

Host
Unknown.

## Comments

Neodiolcogaster tegularis differs from $N$. whiffieldi in having a short robust pre-apical antennal flagellomere and basally narrow and apically broad ovipositor sheaths. This species was described on the basis of the male type only (Nixon, 1965), which was lost recently in the post when returning the specimen to Budapest (A.D. Austin pers. comm.). However, detailed drawings of the type undertaken by P.C. Dangerfield and specimens compared with the type in WARI before it was lost, have allowed for the recognition of conspecific specimens, including the female sex which is described here for the first time. This species has been recorded from the central coast of NSW, Tasmania and south-western Western Australia (Fig. 6.54).
6.8.2 Diolcogaster whitfieldi, sp. nov. (Figs 6.49-6.51, 6.54)

## Material Examined

Holotype. Q, Queensland, 'Stanthorpe, 6.v-13.vii.no year, no collector' (AEIC). Paratype. Queensland: $1 \bigcirc, 1 O^{\prime}$, data as holotype.
Other specimens examined. Western Australia: $1 \bigcirc^{7}$, Yarragil via Dwellingup, 1927.x.1981, no collector (QDPI).

## Female

Length. 2.4-2.7 mm..
Colour. Body generally dark brown to black; head dark brown with occiput black; labial and maxillary palps light brown; antenna dark brown; dorsal pronotum, lateral pronotum and propleuron dark brown; scutum dark brown to black; scutellum, metanotum,
propodeum, mesopleuron and metapleuron black; metasoma dark brown except lateral membranous area of T1-T2 which is light brown; fore and mid leg light brown; hind leg dark brown except hind coxa which is dark brown to black; hind tibial spurs yellow; stigma and fore wing venation dark brown, fore wing transparent.

Head. In dorsal view 1.1-1.2 x as wide as scutum; vertex, temples, eyes and face with sparse white pilosity; dorsal and lateral frons smooth; face at widest $1.3-1.4 \mathrm{x}$ as wide as high, weakly punctulate; temples weakly punctulate; in lateral view medial temples 0.5-0.6 x as wide as width of eye; eyes 0.7 x as wide as high; tangent to posterior margin of median ocellus passing in front of anterior margin of lateral ocelli; distance between lateral ocelli 0.7 x distance from lateral ocellus to edge of eye; antenna 1.3-1.5 x as long as body, last flagellomere 0.6 x as long as first, pre-apical antennal segment 2.2 x as long as wide.

Mesosoma. Scutum 1.5-2.0 x as wide as long, sparsely punctate antero-medially and laterally, smooth postero-medially, with white pilosity; notauli weakly indicated by smooth depressed areas; scutellar sulcus with 5-6 longitudinal carinae; dorsal scutellum 0.8 x as wide as long, smooth with sparse pilosity; lateral scutellum carinate; medial posterior band of scutellum smooth, continuous with dorsal scutellum; metanotum carinate; propodeum $1.6-1.7 \mathrm{x}$ as wide as long, smooth except a few weak carinae diverging from postero-median node; medial longitudinal carina absent, costulae absent; propodeal spiracle round, positioned medially or slightly anterior to midline, without costulae; lateral pronotum smooth, glabrous, ventral groove weakly crenulate; propleuron without dorsal ridge, weakly punctulate; mesopleuron smooth; epicnemial furrow deep; precoxal groove shallow, smooth; metapleuron smooth; hind coxa $0.5-0.6 \mathrm{x}$ as wide as long, 1.3-1.5 x as long as T1, smooth, pilose on outer surface; inner hind tibial spur 1.1-1.2 x as long as outer spur, 0.4-0.6 x as long as hind basitarsus.

Wings. Fore wing sparsely pilose on basal and sub-basal cells, rest with evenly dense pilosity; 1-RS 0.2 x as long as $1-\mathrm{RS}+\mathrm{M}$ and $1-\mathrm{M} ; 1-\mathrm{RS}+\mathrm{M} 1.0 \mathrm{x}$ as long as $1-\mathrm{M} ; \mathrm{m}-\mathrm{cu} 1.4 \mathrm{x}$ as long as 2-RS+M; stigma 2.5-3.3 x as long as wide; 1-R1 0.8 x distance from stigma to 4RS; r 0.6-0.7 x as long as width of stigma, straight, forming an obtuse angle with 2-RS; areolet in small quadrangular shape; r-m and apex of 2-RS+M spectral; 1-CUa 0.4 x as long as $1-\mathrm{CUb}$; hind wing vannal lobe straight to weakly convex, with row of long hairs beyond its widest part.

Metasoma. T1 1.9-2.0 x as long as maximum width, narrowest posteriorly so that posterior margin 0.4 x width of anterior margin, smooth and glabrous, without medial longitudinal groove but with weak depression anteriorly; T2 smooth, sub-triangular, anterior margin as wide as apex of T1, median field encircled by smooth grooves, in midline 0.4-0.5 x as long as T1, 0.7-0.9 x as long as T 3 , medial length $1.1-1.2 \mathrm{x}$ as long as maximum width; lateral sulci complete, meeting suture between T 2 and T 3 and separating T 2 from lateral membranous area; suture between T 2 and T 3 distinct; T 3 in midline $0.6-0.7 \mathrm{x}$ as long as maximum width, smooth, sparsely pilose apically; T4-T7 smooth, with apical pilosity; hypopygium pilose, medio-ventral length 0.7 x as long as hind basitarsus; ovipositor sheaths $0.4-0.6 \mathrm{x}$ as long as hind basitarsus, tapering posteriorly, with few reduced hairs at apex, specialised sensilla absent.

## Male

As for females except as follows: Lateral pronotum light brown; lateral sulci of T 2 not complete.

Host
Unknown.

## Comments

The species is here named after Dr. James B. Whitfield from the University of Arkansas. The holotype female was collected in south-eastern Queensland, while a male specimen, apparently conspecific with the type, comes from south-western Western Australia (Fig. 6. 54).

### 6.9 New Genus

## Comments

While examining non-Australasian material of Diolcogaster during this project, two female specimens from Brazil were encountered (sent by J.B. Whitfield) which cannot be easily accommodated in any existing microgastrine genera. The salient characters of this taxon are: body uniformly light-yellow; surface generally smooth; $4.0-4.5 \mathrm{~mm}$ in length;
medial posterior band of scutellum smooth; propodeum with strong medial longitudinal carina; T1 weakly narrowing posteriorly and greatly excavated in basal half; T2 with weakly defined median field; fore wing areolet open; cu-a of hind wing meeting 1A at an angle much wider than $90^{\circ}$; hind tibial spur subequal; hypopygium evenly sclerotised, almost half the length of hind tibia; ovipositor sheaths pilose in apical half, less than 0.2 x of the length of hind tibia.

The evenly sclerotised hypopygium of this taxon places it among the Cotesiine group of genera (sensu Mason 1981), and the open areolet of the fore wing, presence of a medial longitudinal carina on the propodeum, and posteriorly narrowing T 1 align it with Glyptapanteles (to where it keys out in Austin and Dangerfield 1992). However, this taxon is distinguishable from at least the described Glyptapanteles based on the subequal hind tibial spurs, smooth lateral fields of the propodeum, median field of T 2 present, $\mathrm{cu}-\mathrm{a}$ of hind wing meeting 1 A at an angle which is much wider than $90^{\circ}$, and its larger size. The latter characters fit at least some species of Diolcogaster and so the Brazilian species appears to be intermediate between these two genera, Glyptapanteles and Diolcogaster. Because the species is extra-limital to the region under study here, it has not been formally described, although it was included in the phylogenetic analysis in an attempt to shed some light on its relationships. Unfortunately, its position relative to other cotesiine genera was completely unresolved (see Chapter 5).

Figs 6.1-6.4. Diolcogaster alkingara sp. nov. paratype $O^{x}: 6.1$, scutellum, metanotum and propodeum; 6.2 , hind coxa; 6.3 , metasomal tergite $1 ; 6.4$, metasomal tergites 2 and 3. Scale lines $=100 \mu \mathrm{~m}$.



Fig 6.5-6.6. 6.5, Diolcogaster dangerfieldi sp. nov. holotype $\bigcirc$, dorsal habitus; 6.6, Diolcogaster naumanni sp. nov. holotype $Q$, dorsal habitus. Scale line $=0.5 \mathrm{~mm}$. Both figures showing tangent to posterior margin of median ocellus.

Figs 6.7-6.10. 6.7-6.9, Diolcogaster eclectes (Nixon) $\cap: 6.7$, medial posterior band of scutellum to propodeum; 6.8, metasomal tergite $1 ; 6.9$, metasomal tergites 2 and 3; 6.10, Diolcogaster perniciosus (Wilkinson) $\bigcirc$, propodeum, metasomal tergites 1 and 2 . Scale lines $=100 \mu \mathrm{~m}$.



Figs 6.11-6.14. 6.11, 6.12, Diolcogaster iqbali sp. nov. holotype $Q: 6.11$, head to scutum showing tangent to posterior margin of median ocellus; 6.12, metasomal tergites 1-3; 6.13, Diolcogaster dichromus sp. nov. holotype $Q$, dorsal metasoma; 6.14, Diolcogaster euterpus (Nixon) Q, metasomal tergites 1-4. Scale lines $=0.5 \mathrm{~mm}$.


6.16

Figs 6.15, 6.16. Diolcogaster lucindae sp. nov. holotype $Q: 6.15$, dorsal habitus showing tangent to posterior margin of median ocellus; 6.16, lateral view of hypopygium and ovipositor. Scale line $=0.5 \mathrm{~mm}$.


Figs 6.17-6.19. 6.17, Diolcogaster merata sp. nov. holotype $\mathcal{O}$, dorsal habitus; 6.18, 6.19, Diolcogaster notopecktos sp. nov. holotype $¢: 6.18$, antenna; 6.19, dorsal habitus. Scale line $=1 \mathrm{~mm}$.


Figs 6.20-6.23. Fore wings: 6.20, Diolcogaster muzaffari sp. nov. holotype $Q ; 6.21$, Diolcogaster yousufi sp. nov. holotype $\odot ; 6.22$, Diolcogaster naumanni sp. nov. holotype $Q$; 6.23, Diolcogaster robertsi sp. nov. holotype $Q$. Scale lines $=0.5 \mathrm{~mm}$.

Figs 6.24-6.27. 6.24, 6.25, Diolcogaster newguineaensis sp. nov. holotype $Q: 6.24$, dorsal view of head showing tangent to posterior margin of median ocellus; 6.25, metasomal tergites 2 and 3;6.26, 6.27, Diolcogaster hadrommatus sp. nov. holotype $Q: 6.26$, propleuron, arrow showing absence of propleural flange; 6.27 , ovipositor sheaths, arrow showing specialised sensilla. Scale lines: $6.24=200 \mu \mathrm{~m} ; 6.25,6.26=100 \mu \mathrm{~m} ; 6.27=20 \mu \mathrm{~m}$.


6.29


Figs 6.28-6.31. 6.28, 6.29, Diolcogaster perniciosus (Wilkinson) $Q: 6.28$, fore wing showing vein $3-1 \mathrm{~A} ; 6.29$, hind wing showing straight, pilose vannal lobe; $6.30,6.31$, Diolcogaster sons (Wilkinson) $Q: 6.30$, fore wing showing vein 1a and position of brown spots; 6.31 , hind wing showing position of brown spots and concave, glabrous vannal lobe. Scale lines $=0.5 \mathrm{~mm}$.


6.34

6.35

Figs 6.32-6.35. 6.32, 6.33, Diolcogaster robertsi sp. nov. holotype $Q: 6.32$, head and scutum; 6.33, propodeum to metasomal tergite 3; 6.34, Diolcogaster muzaffari sp. nov. holotype $\odot$, propodeum to metasomal tergite 3; 6.35, Diolcogaster masoni sp. nov. holotype $Q$, lateral view of posterior metasoma. Scale lines: $6.32-6.34=0.5 \mathrm{~mm} ; 6.35=0.7 \mathrm{~mm}$.

Figs 6.36-6.39. Diolcogaster sons (Wilkinson) $Q: 6.36$, lateral habitus; 6.37, metasomal tergites 1-3; 6.38, (scuto-scutellar sulcus arrowed); 6.39, arrow showing propleural flange. Scale lines: $6.36=400 \mu \mathrm{~m} ; 6.37,6.38=100 \mu \mathrm{~m} ; 6.39=40 \mu \mathrm{~m}$.



### 6.41

6.40


Figs 6.40-6.43. 6.40, Diolcogaster walkerae sp. nov. holotype $Q$, head and scutum; 6.41, Diolcogaster nixoni sp. nov. holotype $\varnothing$, propodeum to metasomal tergite 4; 6.42, Diolcogaster vulpinus (Wilkinson) Q, propodeum to metasomal tergite 4; 6.43, Diolcogaster yousufi sp. nov. holotype $Q$, propodeum and metasoma. Scale lines $=0.5 \mathrm{~mm}$.


Figs 6.44-6.48. Neodiolcogaster tegularis (Szépligeti), $Q: 6.44$, propodeum to metasomal tergite $3 ; 6.45$, ovipositor sheaths; 6.46 , antenna; 6.47 , fore wing; 6.48 , hind wing showing cell 1a wider than cell 1 b . Scale lines: $6.44,6.45=250 \mu \mathrm{~m} ; 6.46-6.48=0.5 \mathrm{~mm}$.


Figs 6.49-6.51. Neodiolcogaster whitfieldi sp. nov. holotype $Q: 6.49$, propodeum to metasomal tergite $4 ; 6.50$, ovipositor sheaths, 6.51 , antenna. Scale lines: $6.49,6.50=250 \mu \mathrm{~m}$; $6.51=0.5 \mathrm{~mm}$.




Figs 6.52, 6.53. Distributional maps of Diolcogaster spp.
6.54
А = Diolcogaster alkingara sp. nov.
$\square=$ D. newguineaensis sp. nov.

- Neodiolcogaster tegularis (Szépligeti)
$\star=N$. whitfieldi sp. nov.



Figs 6.54-6.56. Distributional maps of Diolcogaster and Neodiolcogaster spp.


Figs 6.57-6.60. Distributional maps of Diolcogaster spp.

## Chapter 7

## General Discussion

This project has demonstrated the inability of a detailed morphological data set to clearly resolve the phylogenetic relationships among the microgastrine genera that comprise the Cotesia-complex of genera, and the species-groups of Diolcogaster. The major reason for this was the very high level of homoplasy among characters. Even minor changes in any parameters associated with the analyses undertaken caused substantial changes in the resultant tree topologies, in particular when the character set was analysed as unpolarised versus polarised and ordered. Homoplasy occurs due to frequent reversals and parallel development of characters during evolution. When the level of homoplasy is very high, different taxa appear to be defined by the recombination of characters, rather than specific taxon groups being defined by the appearance of 'new' synapomorphies. This certainly appears to be the case within the braconid subfamily Microgastrinae but it is certainly not unique to this group. For instance, Gauld and Mound (1982) discussed in general terms the level of homoplasy found in some large groups of insects, such as the Ichneumonidae and fungus-feeding Phaleothripidae (Thysanoptera). They highlighted the problem of defining monophyletic genera in such groups, and favoured the recognition of 'polythetic' classifications. Implicit in their approach was the possibility that the natural relationships among such groups may never be found. However, these ideas were published 15 years ago at a time that was at the beginning of the 'cladistics revolution'. In the intervening time two important developments have occurred that directly impinge on the problems outlined by Gauld and Mound (1982). One is the development of very powerful parsimony-based computer programs, such as PAUP, to extract the optimal amount of informative information from 'messy' data sets, and the parallel development of equally powerful desk-top hardware. The second is the advent of a completely new area of phylogenetic study, i.e. molecular systematics. At the time Gauld and Mound (1982) published their paper, the parsimony programs available were crude and could only handle relatively small data sets. In the present study which used PAUP 3.1.1, a data set of 68 taxa by 43 characters was analysed and certainly this program is capable of handling a data set of this size However, ultimately the resolution obtained by parsimony-based programs is limited by the quality, not necessarily its size.

Molecular systematics has the ability to generate a completely independent set of data that can be analysed separately or together with morphological data. The comparison of

DNA sequences, such as those produced for a range of mitochondrial genes by the direct sequencing of amplified DNA segments using the polymerase chain reaction, provides the means for examining phylogenetic problems that have not be easily amenable to analysis using morphological data. For example, Dowton and Austin (1994, 1995, in press; Dowton et al. in press), using mitochondrial sequence data for the 16 S and COI genes, have recently been able to successfully generate robust phylogenies for the major groups of parasitic Hymenoptera and the proctotrupoid families, while Cameron (1993) has been able to examine the evolution of eusociality in the Apidae using a similar approach. The fact that three major studies including this one (Mason 1981; Walker et al. 1992) have not been able to provide a stable generic-level classification for the Microgastrinae, also makes this group a likely target for molecular systematic studies, and at least one such program has been initiated recently ( J . B. Whitfield, pers. comm.).

Comparison of the phylogenetic results produced in this study with those of Mason (1991) and Walker et al. (1992) show that the pattern of relationships within the Microgastrinae has become less clear with time. Why is this? As discussed in Chapter 2, the phylogeny for the Microgastrinae proposed by Mason (1981) was fully resolved because it was a 'hand-generated' or intuitive tree. It was not produced by a cladistic-based parsimony analysis. Walker et al. (1992) then reanalysed Mason's characters and showed that the data did not resolve relationships within the group very well at all. Although they reinterpreted and recoded several characters, they did not question the monophyly of any genera. In fact, the phylogenies proposed by Mason (1981) and Walker et al. (1992) are for generic groups (see Table 2.5), not genera alone. Several of these generic groups, such as the ones that contain Cotesia, Glyptapanteles, Apanteles s.str. and Dolichogenidea contain hundreds if not thousands of species and are akin in size and status to the tribes of other braconid subfamilies. Neither Mason nor Walker et al. have tested the monophyly of these groups and, indeed, Mason himself provided substantial evidence that Dolichogenidea is paraphyletic with respect to Apanteles s.str., even though he placed these two genera in separate genus groups.

The present study has attempted to approach this problem in what may be a more realistic way; that is by coding characters for exemplar species for each genus and species group, rather that coding characters in a more global way for large groups that are assumed to be monophyletic. The potential problem with this approach is that the exemplar species may
not be truly representative of the taxon in question, but then if they are not, PAUP should not resolve them as monophyletic. Even if the species chosen as exemplars are not the ' best' ones, the resultant phylogeny should at least accurately reflect the phylogeny for those species included. Intuitively, this would seem to be a better option than treating large assemblages of species as monophyletic, when this may not be the case. Therefore it seems realistic to assume that phylogenetic trees generated in this study represent a more accurate reflection of microgastrine relationships than the previous more resolved hypotheses. Indeed, how may microgastrine genera are demonstrably monophyletic? The answer to this question is not known. Certainly several of the smaller genera such as Miropotes, Parenion, Wilkinsonellus and Buluka are probably natural groups, but the results of this study show that Diolcogaster is not, nor are probably Dolichogenidea, Cotesia, Sathon and Choeras as presently defined (see Mason 1981; Dangerfield and Austin 1992).

When examining the relationships among higher taxa, inevitably it is impossible to avoid assuming the monophyly of at least some lower groups. However, in such studies it is important to at least be aware of this problem or, alternatively, to use exemplar taxa. Clearly, some phylogenetic studies on the Braconidae have faced up to this problem while others have avoided it. Two examples highlight the problems with the latter approach. In a study of relationships among the cyclostome braconids, Whitfield (1992) used exemplar genera for tribes and subfamilies. This approach quite rightly allows these genera to be placed independent of each other in a parsimony analysis. That is, three exemplar genera for groups like the Rogadini and Exothecini are sorted independently by PAUP and they come together, thus confirming their monophyly. This then represents an internal test of the robustness of the data set. If the data cannot resolve groups known or suspected to be monophyletic, then little confidence can be gained from the relationships postulated among them. The same is true moreso in molecular systematics where truly exemplar species are used for the groups being compared. In molecular studies the number of in-group taxa are limited by the cost of DNA sequencing and the size of the data-set. More importantly, the sequencing of a particular gene yields an objective set of data in that the observer cannot chose which characters can be included, as they are determined automatically by the process of sequencing. Whereas, in morphological systematics the observer chooses which characters to score and which ones not to include.

Where this study has taken the same philosophical approach as Whitfield (1992) in using exemplar taxa, albeit a lower ranked problem, much of the work to date on the relationships among braconid subfamilies seems to be flawed, at least in part, because characters have been coded in a global way for subfamilies as a whole. Studies by Quicke and van Achterberg (1990) and more recently van Achterberg $(1993,1995)$ assume the monophyly of numerous subfamilies where there is substantial doubt as to their status. In particular this impinges on two important Australian groups, the Betylobraconinae and the Mesostoinae. There is good reason to suspect that these subfamilies render the Rogadinae and Dorcytinae, respectively, as paraphyletic (see Austin and Wharton 1992; Wahl and Sharkey 1993). However, without coding generic exemplars for these subfamilies, one group can never fall inside the other and they will always be resolved as separate. The more times this approach is used, the danger is that their monophyly is accepted by default. For this reason, the approach of using exemplar species is strongly advocated here.

A second aspect of the current research that is worth considering in a more general way is the size of the Australasian Diolcogaster fauna and its bearing on the make-up of the microgastrine fauna for this and other regions. Prior to this study only six species of Diolcogaster were recognised for Australasia, and this has been increased to 26 species, with an additional three species recognised on limited material but not formally described. This represents a four- to five-fold increase in the number of species, but is substantially less than the 70 plus estimated by Austin and Dangerfield (1992). However, future collecting in the remote areas of mainland Australia and forested regions of New Guinea and adjacent islands is likely to generate a substantial number of additional species, but the total is unlikely to reach the figure estimated by Austin and Dangerfield (1992). This discrepancy highlights the difficulty of estimating the size of poorly known groups. In terms of described species, Diolcogaster is now the second largest microgastrine genus for Australasia, after Apanteles with 33 species, while Dolicogenidea has 24, Microplitis 20 and the relatively minor genus Miropotes has 10 . These figures simply reflect that these genera have been exposed to recent taxonomic revision (Nixon 1965, 1967; Austin 1990; Austin and Dangerfield 1993), while supposedly large genera, like Cotesia with 15 species (several of which are introduced biological control agents) and Glyptapanteles with nine species, have not been revised and undoubtedly contain many new species. Whether or not the 100 plus species estimated for
the latter two genera (Austin and Dangerfield 1992) is relatively accurate, will only be determined when they are critically revised. Further, any comparison between the size of the Australasian microgastrine fauna with other regions would seem to be a futile exercise, given that the faunas of the three adjacent regions (Ethiopian, Oriental and Neotropical) are as poorly studied as Australia.

Finally, it is hoped that the present study will serve as a useful basis for future studies on the phylogeny of the Microgastrinae, and revisionary work on this and other groups of parasitic Hymenoptera for Australasia. There is yet much to be done!

## References

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 (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 Parasitic Hymenoptera Research 1988, 85-115.
Achterberg, C. van (1993). Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 283, 1-189.
Achterberg, C. van (1995). Generic revision of the subfamily Betylobraconinae (Hymenoptera: Braconidae) and other groups with modified fore tarsus. Zoologische Verhandelingen 298, 1-242.
Achterberg, C. van, and Quicke D. L. J. (1992). Phylogeny of the subfamilies of the family Braconidae: A reassessment assessed. Cladistics 8, 237-64.
Allen, W. W. (1958). The biology of Apanteles medicaginis Muesebeck (Hymenoptera: Braconidae). Hilgardia 27, 515-41.
Almeida, M. T., and Bisby, F. A. (1984). A simple method for establishing taxonomic characters from measurement data. Taxon 33, 405-9.
Anderberg, A., and Tehler, A. (1990). Consensus trees, a necessary taxonomic practice. Cladistics 6, 399-402.
Arakawa, T., and Kitano, H. (1989). A possible reason for the decrease of the number of teratocytes in the body cavities of Pieris rapae crucivora Boisduval (Lepidoptera: Pieridae) parasitised by Apanteles glomeratus L. (Hymenoptera: Braconidae). Applied Entomology and Zoology 24, 229-31.
Archie, J. W. (1985). Methods for coding variable morphological features for numerical taxonomic analysis. Systematic Zoology 34, 326-45.
Archie, J. W. (1989). A randomization test for phylogenetic information in systematic data. Systematic Zoology 38, 239-52.
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. (E. J. Brille: Gainesville) 220 pp .
Arthur, A. P., and Mason, P. G. (1986). Life history and immature stages of the parasitoid Microplitis mediator (Hymenoptera: Braconidae), reared on the bertha armyworm Mamestra configurata (Lepidoptera: Noctuidae). Canadian Entomologist 118, 487-91.
Ashmead, W. H. (1900a). (In: Smith, J. B.) Insects of New Jersey. Report New Jersey Agricultural Experiment Station 27 (1899) Suppl., 755 pp.
Ashmead, W. H. (1900b). Classification of the ichneumon-flies, or the superfamily Ichneumonoidea. Proceedings of the United States National Museum 23, 127-58.

Askew, R. R. (1990). Species diversities of Hymenoptera taxa in Sulawesi. pp. 255-60. In 'Insects and the Rainforests of South-East Asia (Wallacea)'. (Eds W. J. Knight and J. D. Halloway), (The Royal Entomological Society: London).

Austin, A. D. (1987). A review of the Braconidae (Hymenoptera) that parasitise Limacodidae in South-east Asia, particularly those associated with coconut and oil-palm. pp. 13964. In 'Slug and nettle caterpillars'. (Eds M. J. W. Cock, H. C. J. Godfray and J. D. Holloway). (C.A.B. International: Wallingford).
Austin, A. D. (1989). Revision of the genus Buluka De Saeger (Hymenoptera: Braconidae: Microgastrinae). Systematic Entomology 14, 149-63.
Austin, A. D. (1990). Revision of the enigmatic 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 Wharton, R. A. (1992). New records of subfamilies, tribes and genera of Braconidae (Hymenoptera) from Australia, with descriptions of seven new species. Transactions of the Royal Society of South Australia 116, 41-63.
Austin, A. D., and Dangerfield, P. C. (1989). The taxonomy of new world microgastrine braconids (Hymenoptera) parasitic on Diatraea spp. (Lepidoptera: Pyralidae). Bulletin of Entomological Research 79, 131-44.
Austin, A. D., and Dangerfield, P. C. (1992). Synopsis of Australian 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., Quicke, D. L. J., and Marsh, P. M. (1994). The hymenopterous parasitoids of eucalypt longicorn beetles, Phoracantha spp. (Coleoptera: Cerambycidae) in Australia. Bulletin of Entomological Research 84, 145-74.
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, 57181.

Brown, R. W. (1954). Composition of Scientific Words. George W. (Privately published: Baltimore) 882 pp .
Cameron, P. (1891). Hymenopterological Notices. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 4 (Series, 4), 182-95.
Cameron, P. (1904). On the Hymenoptera of the Albany Museum, Grahamstown, South Africa. Records of Albany Museum 1, 161-75.
Cameron, S. A. (1993). Multiple origins of advanced eusociality in bees inferred from mitochondrial DNA sequences. Proceedings of the National Academy of Sciences of the United States of America 90, 8687-91.

Carpenter, J. M. (1988). Choosing among multiple equally parsimonious cladograms. Cladistics 4, 291-96.
Chappill, J. A. (1989). Quantitative characters in phylogenetic analysis. Cladistics 5, 21734.

Colless, D. H. (1981). Predictivity and stability in classification: some comments on recent studies. Systematic Zoology 30, 325-31.
Cresson, E. T. (1865). On the Hymenoptera of Cuba. Proceedings of the Entomological Society of Philadelphia 4, 1-200.
Dangerfield, P. C. (1995). The systematics of the genera of Cardiochilinae (Hymenoptera: Braconidae) with a revision of Australasian species. PhD Thesis, The University of Adelaide, 233 pp .
Dangerfield, P. C., and Austin, A. D. (1990). Revision of the Oriental genus Hartemita Cameron (Hymenoptera: Braconidae: Cardiochilinae). Journal of Natural History 24, 137-58.
Dangerfield, P. C., and Austin, A. D. (1995). Revision of the Australasian species of Cardiochilinae (Hymenoptera: Braconidae). Invertebrate Taxonomy 9, 387-445.

Dangerfield, P. C., Whitfield, J. B., and Austin, A. D. (in press). The systematics of the genera of Cardiochilinae (Hymenoptera: Braconidae). Systematic Entomology.
De Saeger, H. (1937). L'Apanteles sagax Wilk. parasite de la pyrale du cotonnier. Bulletin Agricole du Congo Belge 28, 47-52.
De Saeger, H. (1944). Microgastrinae (Hymenoptera: Apocrita). Exploration du Parc National Albert. Mission G. F. de Witte 47, 1-389.
Dowton, M., and Austin, A. D. (1994). Molecular phylogeny of the insect order Hymenoptera - apocritan relationships. Proceedings of the National Academy of Sciences of the United States of America 19, 9911-9915.
Dowton, M., and Austin, A. D. (1995). Increased genetic diversity in mitochondrial genes is correlated with the evolution of parasitism in the Hymenoptera. Journal of Molecular Evolution 41, 958-965.
Dowton, M., and Austin, A. D. (in press). Evidence for AT-transversion bias in the Symphyta: Hymenoptera and its implications for the origin of parasitism in the wasps. Evolution.

Dowton, M., Austin, A. D., Dillon, N., and Bartowsky, E. (in press). Molecular phylogeny of the apocritan wasps with particular reference to the Proctotrupomorpha and Evaniomorpha. Systematic Entomology.
Eady, R. D. (1968). Some illustrations of microsculpture in the Hymenoptera. Proceedings of the Royal Entomological Society of London, Series A 43, 66-72.
Eady, R. D. (1974). The present state of nomenclature of wing venation in the Braconidae (Hymenoptera), its origin and comparison with related groups. Journal of Entomology (B) 43, 63-72.

Edson, K. M., and Vinson, S. B. (1976). The function of the anal vesicle in respiration and excretion in the braconid wasp, Microplitis croceipes. Journal of Insect Physiology 22, 1037-43.
Edson, K. M., and Vinson, S. B. (1977). Nutrient absorption by the anal vesicle of the braconid wasp, Microplitis croceipes. Journal of Insect Physiology 23, 5-8.
Fabricius, J. C. (1798). Supplementum Entomologiae Systematicae. Hafniae, Proft et Storch. pp. 572.
Fabricius, J. C. (1804). Systema Piezatorum. Brunsvigae, Reichard. pp. 439.
Fahringer, J. (1937). Opuscula Braconologica. 4. Palaerktische Region. Lieferung 4-6, 257520.

Fallis, A. M. (1942). The life cycle of Apanteles carpatus (Say) (Hymenoptera: Braconidae), a parasite of the webbing clothes moth, Tineola bisselliella Hum. Canadian Journal of Research (D) 20, 13-19.
Farris, J. S. (1970). Methods for computing Wagner trees. Systematic Zoology 19, 83-92.
Farris, J. S. (1972). Estimating phylogenetic trees from distance matrices. The American Naturalist 106, 645-68.

Farris, J. S. (1979). The information content of the phylogenetic system. Systematic Zoology 28, 483-519.
Farris, J. S. (1988). Hennig86, version 1.5. Computer program and documentation distributed by A. G. Klug, Museum of Zoology. The University of Michigan, Ann Arbor, Michigan.
Farris, J. S. (1989). The retention index and the rescaled consistency index. Cladistics 5, 417-9.

Forster, A. (1862). Synopsis der Familien und Gattungen der Braconen. Verhandlungen des Naturhhistorischen Vereins preussischen Rheinlande und Westfalens 19, 225-88.
Gahan, A. B. (1918). Four new African parasitic Hymenoptera belonging to the subfamily Microgastrinae. Proceedings of the United States National Museum 54, 587-90.

Gámez, R., and Gauld, I. D. (1993). Costa Rica: an innovative approach to the study of tropical biodiversity. pp. 329-36. In 'Hymenoptera and Biodiversity'. (Eds J. Lasalle and I. D. Guald.), (The Natural History Museum: London).
Gatenby, J. B. (1919). Notes on the bionomics, embryology, and anatomy of certain Hymenoptera Parasitica, especially of Microgaster connexus (Nees). Journal of the Linnean Society (Zoology) 33, 387-416.
Gauld, I. D., and Mound, L. A. (1982). Homoplasy and the delineation of holophyletic genera in some insect groups. Systematic Entomology 7, 73-86.
Gauld, I. D., and Bolton, B. (Eds) (1988). The Hymenoptera. (British Museum (Natural History) London and Oxford University Press: Oxford) 332 pp.
Godfray, H. C. J. (1994). Parasitoids: Behavioural and Evolutionary Ecology. (Princeton University Press: Princeton, New Jersey) 473 pp.
Goloboff, P. A. (1991). Homoplasy and the choice among cladograms. Cladistics 7, 215-32.

Goulet, H., and Huber, J. T. (Eds) (1993). Hymenoptera of the World: An identification guide to families. (Research Branch Agriculture Canada Publication: Ottawa) 1-668 pp.
Granger, C. (1949). Braconides de Madagascar. Mémoires de l'Institute Scientifique de Madagascar (A) 2, 1-428.
Greathead, D. J. (1986). Parasitoids in classical biological control. pp. 289-318. In 'Insect Parasitoids'. (Eds J. K. Waage, and D. J. Greathead.), (Academic Press: London).
Hanson, P. and Gauld, I. D. (Eds) (1995). The Hymenoptera of Costa Rica. (Oxford University Press: Oxford) 893 pp.
Harris, R. A. (1979). A glossary of the surface sculpturing. California Department of Food and Agriculture, Bureau of Entomology, occasional papers 28, 1-31.
Hauser, D. L., and Presch. W. (1991). The effect of ordered characters on phylogenetic reconstruction. Cladistics 7, 243-65.
Hegazi, E. M., and Fuhrer, E. (1985). Instars of Microplitis rufiventris (Hymenoptera: Braconidae) and their relative developmental speed under different photoperiods. Entomophaga 30, 231-43.
Hennig, W. (1966). Phylogenetic Systematics. (University of Illinois Press: Urabana). 263 pp.
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 the Entomological Research 78, 435-61.
Iqbal, M., and Austin, A. D. (in press). Species richness and endemism of Baeini wasps (Hymenoptera: Scelionidae) in Australia. Memoirs of the Museum of Victoria.
Johansson, A. S. (1951). Studies on the relation between Apanteles glomeratus L. (Hymenoptera: Braconidae) and Pieris brassicae L. (Lepidoptera: Pieridae). Norsk Entomologisk Tidsskrift 8, 145-86.
King, P. E., Ratcliffe, N. A., and Copland, M. J. W. (1969). The structure of the egg membrane in Apanteles glomeratus (L.) (Hymenoptera: Braconidae). Proceedings of the Royal Entomological of London (A) 44, 137-42.
Kluge, A. G. and Farris, J. S. (1969). Quantitative phyletics and the evolution of Anurans. Systematic Zoology 18, 1-32.
Lasalle, J. (1993). Parasitic Hymenoptera, biological control and biodiversity. pp. 197-215. In 'Hymenoptera and Biodiversity'. (Eds J. Lasalle and I. D. Guald.), (The Natural History Museum: London).
Lasalle, J., and Guald, I. D. (Eds ) (1993). Hymenoptera and Biodiversity. (The Natural History Museum: London) pp. 348.
Latreille, P. A. (1804). Histoire naturelle, générale et particuliére des crustacés et des insects. Ouvrage faisant suite aux oevres de Leclerc de Buffon et partie du cours complet d'Histoire naturelle rédigé p. C.S. Sonnini. Paris, Dufort, vol. 24.

Laving, J. E., and Levin, D. B. (1982). A review of the biology and a bibliography of Apanteles glomeratus (L.) (Hymenoptera: Braconidae). Biocontrol News and Information 3, 7-23.
Lewis, W. J. (1970). Life history and anatomy of Microplitis coreceipes (Hymenoptera: Braconidae) a parasite of Heliothis spp. (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 63, 67-70.
Lyle, G. T. (1918). Contributions to our knowledge of the British Braconidae. No. 3Microgastrinae (continued). Entomologist 50, 104-11, 129-37.
Maddison, W. P., and Maddison, D. R. (1992). MacClade version 3: Analysis of Phylogeny and Character Evolution. Computer program (Sinauer Associates Inc.: Massachusetts).
Marshall, T. A. (1872). A catalogue of British Hymenoptera: Chrysididae, Ichneumonidae, Braconidae and Evaniidae. part 4. Braconidae. Entomological Society of London, A, 96-132.
Marshall, T. A. (1885). Monograph of British Braconidae. Transactions of Royal Entomological Society of London 1, 1-280.
Masner, L., and Huggert, L. (1989). World review and keys to genera of the subfamily Inostemmatinae with reassignment of the taxa to the Platygastrinae and Sceliotrachelinae (Hymenoptera: Platygastridae). Memoirs of the Entomological Society of Canada 47, 1-214.
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 American Entomological Institute 20, 49-62.
Memmott, J., and Godfray, C. J. (1993). Parasitoid webs. pp. 217-34. In 'Hymenoptera and Biodiversity'. (Eds J. Lasalle and I. D. Guald.), (The Natural History Museum: London).
Mickevich, M. F., and Johnson, M. S. (1976). Congruence between morphological and allozyme data in evolutionary inference and character evolution. Systematic Zoology 25, 260-70.

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 classifications. Cladistics 1, 186-89.

Muesebeck, C. F. W. (1918). Two important introduced parasites of the brown-tail moth. Journal of Agricultural Research 14, 191-206.
Muesebeck, C. F. W. (1922). A revision of the North American ichneumon-flies belonging to the subfamilies Neoneurinae and Microgastrinae. Proceedings of the United States National Museum 61, 1-76.

Muesebeck, C. F. W., and Walkley. (1951). Braconidae. pp. 90-184. In 'Hymenoptera of America, North of Mexico, Synoptic Catalogue'. (Eds C. F. W. Muesebeck, K. V. Kranbein, and H. K. Townes), (United States Department of Agriculture: Washington, D. C.)

Naumann, I. D., Weir, T. A., and Edwards, E. D. (1991). Insects of Kimbley rainforests. pp. 299-332. In 'Kimbley Rainforests'. (Eds N. L. McKienzie, R. B. Johnston, and P. G. Kendrich), (Surrey Betty and Sons: Chipping Norton).
Nees von Esenbeck, C. G. (1834). Hymenopterorum Ichneumonibus affinium monographiae, genera Europea et species illustrantes. Stuttgart, Tübingen, Cotta 1, 320 pp.; 2, 448 pp .
Nixon, G. E. J. (1961). Two new European species of Apanteles (Hymenoptera: Braconidae). Proceedings of the Royal Entomological Society of London (B) 30, 50-2.
Nixon, G. E. J. (1965). A reclassification of the Tribe Microgastrini (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History) Entomology, Supplement 2, 1-284.
Nixon, G. E. J. (1967). The Indo-Australian species of the Ulter-group of Apanteles Forster (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History) Entomology 21, 1-34.
Nixon, G. E. J. (1968). A revision of the genus Microgaster Latreille (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History) Entomology 22, 31-72.
Nixon, G. E. J. (1970). A revision of the north-western European species of Microplitis Forster (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History) Entomology 25, 1-30.
Nixon, G. E. J. (1972). A revision of the north-western European species of the laevigatusgroup of Apanteles Forster (Hymenoptera, Braconidae). Bulletin of Entomological Research 61, 701-743.
Nixon, G. E. J. (1973). A revision of the north-western European species of the vitripennis, pallipes, octonarius, triangulator, fraternus, formosus, parasitellae, metacarpalis and circumscriptus-groups of Apanteles Forster (Hymenoptera, Braconidae). Bulletin of Entomological Research 63, 169-228.
Nixon, G. E. J. (1974). A revision of the north-western species of the glomeratus-group of Apanteles Forster (Hymenoptera, Braconidae). Bulletin of Entomological Research 64, 453-524.
Nixon, G. E. J. (1976). A revision of the north-western European species of the merula, lacteus, vipio, ultor, butalidis, popularis, carbonarius and validus-groups of Apanteles Forster (Hymenoptera, Braconidae). Bulletin of Entomological Research 65, 687-732.
Norton, W. N., and Vinson, S. B. (1974). Antennal sensilla of three parasitic Hymenoptera. International Journal of Morphology and Embryology 3, 305-16.
Noyes, J. S. (1989). The diversity of Hymenoptera in the tropics with special reference to parasitica in Sulawesi. Ecological Entomology 14, 197-207.
Noyes, J. S., and Hayat, M. (1994). Oriental Mealybug Parasitoids of the Anagyrini (Hymenoptera: Encytridae). (British Museum (Natural History): London) 554 pp .

Page, R. D. M. (1992). Comments on the information content of classifications. Cladistics 8, 87-95.
Papp, J. (1976). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae), I. The species-groups. Annales Historico-naturales Musei Nationalis Hungarici 68, 251-74.
Papp, J. (1978). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae). II. The laevigatus-group, 1. Annales Historico-naturales Musei Nationalis Hungarici 70, 265-301.
Papp, J. (1979). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae). III. The laevigatus-group, 2. Annales Historiconaturales Musei Nationalis Hungarici, 71, 235-50.
Papp, J. (1980a). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae). IV. The lineipes-, obscurus- and ater-group. Annales Historico-naturales Musei Nationalis Hungarici 72, 241-72.
Papp, J. (1980b). On the genus Fornicia Brulle with two new Oriental species (Hymenoptera: Braconidae: Microgastrinae). Folia Entomologica Hungarica 41, 30511.

Papp, J. (1981). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae), V. The lacteus-, longipalpis-, ultor- and vipio-group. Annales Historico-naturales Musei Nationalis Hungarici 73, 263-91.
Papp, J. (1982). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae), VI. The laspeyresiella-, merula-, falcatus- and validusgroup. Annales Historico-naturales Musei Nationalis Hungarici 74, 255-67.
Papp, J. (1983a). A survey of the European species of the Apanteles Forst (Hymenoptera, Braconidae, Microgastrinae), vii. The carbonarius-, circumscriptus-, fraternus-, pallipes-, parisitallae-, vitripennis-, lipardis-, octonarius- and thompsoni-group. Annales Historico-naturales Musei Nationalis Hungarici 75, 247-83.
Papp, J. (1983b). Contribution to the braconid fauna of Hungary. IV. Microgastrinae (Hymenoptera: Braconidae). Folia Entomologica Hungarica 44, 125-38.
Papp, J. (1984a). Contributions to braconid fauna of Hungary, VI. Microgastrinae (Hymenoptera: Braconidae). Folia Entomologica Hungarica 45, 157-68.
Papp, J. (1984b). Palaearctic species of Microgaster LATREILLE (= Microplitis Forster) with description of seven new species. (Hymenoptera, Braconidae, Microgastrinae). Entomologische Abhandlungen Staatliches Museum für Tierkunde Dresden 47, 95-140.
Papp, J. (1984c). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae, Microgastrinae), viii. The metacarpalis-, formosus-, popularis- and suevus-group. Annales Historico-naturales Musei Nationalis Hungarici 76, 265-95.
Papp, J. (1986a). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae) IX. The glomeratus-group, 1. Annales Historiconaturales Musei Nationalis Hungarici 78, 225-47.

Papp, J. (1986b). First survey of Glabromicroplitis Papp species of the Holarctic region, with taxonomic remarks of three Microgaster Latreille species (Hymenoptera, Braconidae: Microgastrinae). Annales Historico-naturales Musei Nationalis Hungarici 78, 249-53.
Papp, J. (1987). A survey of the European species of Apanteles Forst (Hymenoptera, Braconidae: Microgastrinae) X. The glomeratus-group 2 and the cutellatus-group. Annales Historico-naturales Musei Nationalis Hungarici 79, 207-58.
Papp, J. (1988). A survey of the European species of Apanteles Forst (Hymenoptera, Braconidae: Microgastrinae) XI. Homologization of the species groups of Apanteles s.l. with Mason's generic taxa. Checklist of genera. Parasitoid/host list 1. Annales Historico-naturales Musei Nationalis Hungarici 80, 145-75.
Papp, J. (1990). A survey of the European species of Apanteles Forst. (Hymenoptera, Braconidae: Microgastrinae) XII. Supplement to the key of glomeratus-group. Parasitoid/ host list 2. Annales Historico-naturales Musei Nationalis Hungarici 81, 159-203.
Parker, D. L. (1935). Apanteles solitarius (Ratzeburg), an introduced braconid parasite of the satin moth. Technical Bulletin, United States Department of Agriculture 477, 1-17.
Pimentel, R. A. and Riggins, R. (1987). The nature of cladistic data. Cladistics 3, 201-9.
Porter, K. (1983). Multivoltinism in Apanteles bignellii and the influence of weather on sunchronization with its host Euphydryas aurinia. Entomologia Experimentalis et Applicata 40, 285-92.
Provancher, L. (1886). Additions et Corrections a la Faune hyménoptérologique de la province de Québec. Québec, 15-164.
Puttler, B., and Thewke, S. E. (1970). Biology of Microplitis feltiae (Hymenoptera: Braconidae), a parasite of black cutworm Agrotis ipsilon. Annals of the Entomological Society of America 63, 645-48.
Quicke, D. L. J. (1993a). The polyphyletic origin of endoparasitism in the cyclostome lineage of Braconidae (Hymenoptera): a reassessment. Zoölogische Mededeelingen 67, 159-77.
Quicke, D. L. J. (1993b). Principles and Techniques of Contemporary Taxonomy. (Blackie Academic and Professional: London) 311 pp.
Quicke, D. L. J., and Achterberg, C. van. (1990). Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 258, 1-95.
Quicke, D. L. J., Ficken, L., and Fitton, M. G. (1992). New diagnostic ovipositor characters for doryctine wasps (Hymenoptera, Braconidae). Journal of Natural History 26, 103546.

Reed, A. W. (1988). Aboriginal Words of Australia. (Reed Books: Forester) 144 pp.
Reinhard, H. (1880). Beiträge zur Kenntnis einiger Braconiden-Gattungen. Fünftes Stück. XVI. zur Gattung Microgaster Latr. (Microgaster, Microplitis, Apanteles). Deutsche Entomologische Zeitschrift 24, 353-70.
Rohlf, F. J. (1982). Consensus indices for comparing classifications. Mathematical Biosciences 59, 131-44.

Sato, Y. (1980). Experimental studies on parasitisation by Apanteles glomeratus V. Relationships between growth rate of parasitoid and host age at the time of oviposition. Entomophaga 25, 123-8.
Shaw, M. R. and Huddleston, T. (1991). Classification and biology of braconid wasps (Hymenoptera). 'Handbooks for the identification of British insects'. 7(11). (Royal Entomological Society: London) pp. 126.
Shenefelt, R. D. (1973). Braconidae 5, Microgastrinae and Ichneutinae. In 'Hymenopterorum Catalogus'. (Eds J. Van der vecht and R. D. Shenefelt.) Part 9, pp. 669-812.
Shestakov, A. (1932). Zur Kenntnis der asiatischen Braconiden. Zoologischer Anzeiger 99, 255-63.
Short, J. R. T. (1952). The morphology of the head of larval Hymenoptera with special reference to the head of the Ichneumonoidea, including a classification of the final instar larvae of the Braconidae. Transactions of the Royal Entomological Society of London 103, 27-84.
Short, J. R. T. (1954). A grouping by larval characters of some species of the genus Apanteles (Hymenoptera: Braconidae). Bulletin of Entomological Research 44, 32732.

Simon, C. (1983). A new coding procedure for morphometric data with an example from periodical cicada wing veins. Nato ASI series, Vol. G1. pp. 378-82. In Numerical Taxonomy. (Ed. J. Felsenstein), (Springer-Verlag: Berlin).
Stoltz, D. B. (1986). Interactions between parasitoid-derived products and host insects: an overview. Journal of Insect Physiology 32, 347-50.
Stoltz, D. B. and Whitfield, J. B. (1992). Viruses and virus like entities in the parasitic Hymenoptera. Journal of Hymenoptera Research 1, 125-39.
Strand, M. R., Johnson, J. A. and Culin, J. D. (1988). Developmental interactions between the parasitoid Microplitis demolitor (Hymenoptera: Braconidae) and its host Heliothis virescens (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 81, 822-30.
Swofford, D. L. (1991). PAUP: Phylogenetic Analysis Using Parsimony, version 3.1 Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
Swofford, D. L. and Begle, D. P. (1993). PAUP: Phylogenetic Analysis Using Parsimony, version 3.1, User's Manual. (Centre for Biodiversity, Illinois Natural History Survey: Champaign, Illinois). 257 pp .
Szépligeti, G. V. (1899). Magyarországi Braconidak. Rovart. Lapok, 6, 98-102.
Szépligeti, G. V. (1904). Hymenoptera Fam. Braconidae(Premíer partie). Genera Insectorum, 22 and 23, pp 255.
Szépligeti, G. V. (1905). Exotische Braconiden aus den aethiopischen, orientalischen Regionen. Annales Historico-Naturales Musei Nationalis Hungarici 3, 25-55.

Tadic', M. D. (1958). Apanteles hyphantriae Riley, an egg parasite of the fall webworm. Proceedings of the X International Congress of Entomology, Montreal 4, 859-61.
Thorpe, R. S. (1984). Coding morphometric characters for constructing distance Wagner networks. Evolution 38, 244-55.
Tobias, V. I. (1964). New species and a new genus of Braconidae from Kazakhstan. Trudy Zoologicheskogo Insttituta Akademiya Nauk SSSR 34, 177-234.
Tobias, V. I. (1967). A review of the classification, phylogeny and evolution of the family Braconidae (Hymenoptera). Entomological Review 46, 387-99.
Tobias, V. I. (1986). Subfamily Microgastrinae. pp. 344-459. In 'Identification of Insects of European USSR, Volume III, Part IV, Hymenoptera, Braconidae'. (Ed. V. I. Tobias), (Publishing House of Science: Leningrad) [In Russian].
Tower, D. G. (1915). Biology of Apanteles militaris. Journal of Agricultural Research 5, 495-507.
Vance, A. M. (1931). Apanteles thompsoni Lyle, a braconid parasite of the European corn borer. Technical Bulletin, United States Department of Agriculture 233, 1-28.
Viereck, H. L. (1910). Hymenoptera for the New Jersey list of insects, and other Hymenoptera. Proceedings of the Entomological Society of Washington 11, 208-11.
Viereck, H. L. (1911). Hymenoptera in Smith's Insects of New Jersey. Proceedings of Entomological Society of washington 13, 93-9.
Viereck, H. L. (1912). Descriptions of five new genera and twenty-six new species of ichneumon-flies. Proceedings of the United States National Museum 42, 139-53.
Viereck, H. L. (1913). Descriptions of twenty-three new genera and thirty-one new species of ichneumon flies. Proceedings of the United States National Museum 46, 359-86.

Viereck, H. L. (1917). The Hymenoptera or wasp-like insects of Connecticut. Guide to the Insects of Connecticut, part III. Bulletin Connecticut State Geological and Natural History Survey 22, 824 pp.
Waage, J. K. (1991). Biodiversity as a resource for biological control. pp. 149-62. In 'The Biodiversity of Microorganisms and Invertebrates: Its Role in sustainable Agriculture'. (Ed. D. L. Hawksworth), (C.A.B. International: Wallingford).
Wahl, D. B. (1991). The status of Rhimphoctona, with special reference to the higher categories within Campopleginae and the relationships of the subfamily (Hymenoptera: Ichneumonidae). Transactions of the American Entomological Society 117, 193-213.
Wahl, D. B., and Sharkey, M. J. (1993). Superfamily Ichneumonoidea. pp. 358-509. In 'Hymenoptera of the World: An identification guide to families'. (Eds H. Goulet, and J. T. Huber), (Research Branch Agriculture Canada Publication: Ottawa).

Walckenaer, C. A. (1802). Faune Parisienne. Insects. Paris, Dentu 1, 303 pp and 2, 438 pp.
Walker, A. K., Kitching, I. J., and Austin, A. D. (1990). A reassessment of the Phylogenetic relationships within the Microgastrinae (Hymenoptera: Braconidae). Cladistics 6, 291306.

Watanabe, C. A. (1937). contribution to the knowledge of the braconid fauna of the Empire of Japan. Japanese Journal of the Facculty of Agriculture, Hokkaido University 42, 188.

Watrous, L. E., and Wheeler, Q. D. (1981). The out-group comparison method of character analysis. Systematic Zoology 30, 1-11.
Weed, C. M. (1888). Descriptions of some new or little known Microgastrinae. Transactions of American Entomological Society 15, 294-97.
Wesmael, C. (1837). Monographie des Braconides des Belgique. Nouveaux Mémoires de l'Academic Royale des Sciences et Belles-Lettres Bruxelles 10, 5-68.
Wharton, R. A., and Marsh, P. M. (Eds) (in press). Identification Manual of the New World Genera of the Family Braconidae (Hymenoptera). (International Society of Hymenoptera: Washington, D. C.).
Wharton, R. A., Shaw, S. R., Sharkey, M. J., Whal, D. B., Woolley, J. B., Whitfield, J. B., Marsh, P. M., and Johnson, W. (1992). Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea): A reassessment. Cladistics 8, 199-235.
Whitfield, J. B. (1985). The Nearctic species of Deuterixys Mason (Hymenoptera: Braconidae). Pan-Pacific Entomologist, 61, 60-7.
Whitfield, J. B. (1992). The polyphyletic origin of the endoparasitism in the cyclostome lineages of Braconidae (Hymenoptera). Systematic Entomology 17, 273-86.
Whitfield, J. B. (1995a). Annotated checklist of the Microgastrinae of North America North of Mexico (Hymenoptera: Braconidae). Journal of the Kansas Entomological Society 63, 245-262.
Whitfield, J. B. (1995b). Xanthapanteles, a new genus of Microgastrinae (Hymenoptera, Braconidae) from South America. Proceedings of Entomological Society of Washington 97, 879-83.
Whitfield, J. B. (in press). A revision of the Nearctic species of the genus Pholetesor Mason (Hymenoptera: Braconidae). University of California Publications in Entomology, 187.

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.
Whitfield, J. B., and Scaccia, B. (in press). A new species of Distatrix, (Hymenoptera: Braconidae) from California with biological notes. Proceedings of Entomological Society of Washington.
Wilbert, H. (1960). Apanteles pieridis (Bouche) (Hymenoptera, Braconidae), ein parasit von Aporia crataegi (L.) (Lepidoptera, Pieridae). Entomophaga 5, 183-211.
Wiley, E. O. (1981). Phylogenetics: The Theory and Practice of Phylogenetic Systematics. (John Wiley and Sons: New York) 439 pp.
Wiley, E. O., Siegel-Causey, D., Brooks, D. R. and Funk, V. A. (1991). The Compleat Cladist. A primer of phylogenetic procedures. (The Museum of Natural History, University of Arkansas: Arkansas) pp. 158.

Wilkinson, D. S. (1927). On the Indo-Malayan species of the genus Microgaster (Hymenoptera: Braconidae). Bulletin of Entomological Research 18, 171-8.
Wilkinson, D. S. (1928a). A revision of the Indo-Australian species of the genus Apanteles (Hym. Bracon.). Part I. Bulletin of Entomological Research 19, 79-105.
Wilkinson, D. S. (1928b). A revision of the Indo-Australian species of the genus Apanteles (Hym. Bracon.). Part II. Bulletin of Entomological Research 19, 109-46.
Wilkinson, D. S. (1929). A revision of the Indo-Australian and Ethiopian species of the genus Microgaster (Hym. Bracon.). Transactions of the Entomological Society of London 77, 99-123.
Wilkinson, D. S. (1930a). A revision of the Indo-Australian species of the genus Microplitis (Hym. Bracon.). Bulletin of Entomological Research 21, 23-7.
Wilkinson, D. S. (1930b). New Braconidae and other notes. Bulletin of Entomological Research 21, 275-85.
Wilkinson, D. S. (1932a). A revision of the Ethiopian species of the genus Apanteles (Hymenoptera, Braconidae). Transactions of the Entomological Society of London 80, 301-45.
Wilkinson, D. S. (1932b). Three new braconids (Hymenoptera). Stylops 1, 85-8.
Wilkinson, D. S. (1934a). On some Microgastrinae (Hymenoptera, Braconidae). Stylops 3, 118-20.
Wilkinson, D. S. (1934b). On some Apanteles (Hymenoptera, Braconidae). Stylops 3, 14556.

Wilkinson, D. S. (1935). Two new Apanteles (Hymenoptera, Braconidae). Stylops 4, 266-9.
Wilkinson, D. S. (1936a). Microgastrinae: notes and new species (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 5, 81-8.
Wilkinson, D. S. (1936b). A new Palaearctic species of Apanteles (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 5, 174-6.
Wilkinson, D. S. (1936c). On the identity of Apanteles pallipes Reinhard, with the description of a new, closely related, Palaearctic species (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 5, 220-4.
Wilkinson, D. S. (1937). On two new Palaearctic species of Apanteles (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 6, 65-72.
Wilkinson, D. S. (1938a). On the identity of Apanteles circumscriptus Nees (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 7, 41-51.
Wilkinson, D. S. (1938b). A new species of Apanteles (Hymenoptera, Braconidae) from South Africa. Proceedings of the Royal Entomological Society of London (B) 7, 131-3.
Wilkinson, D. S. (1938c). On a further two new Palaearctic species of Apanteles (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 7, 222-7.
Wilkinson, D. S. (1939). On the identity of Apanteles infimus Haliday and of Apanteles infimus Haliday of Marshall (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 8, 52-60.

Wilkinson, D. S. (1940a). New species of Apanteles (Hymenoptera, Braconidae).-1. Proceedings of the Royal Entomological Society of London (B) 9, 23-9.
Wilkinson, D. S. (1940b). On the identity of Apanteles carbonarius Wesmsel, with the description of a new, closely related, Palaearctic species (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 9, 157-63.
Wilkinson, D. S. (1941a). New species of Apanteles (Hymenoptera, Braconidae).-2. Proceedings of the Royal Entomological Society of London (B) 10, 28-34.
Wilkinson, D. S. (1941b). On the identity of Apanteles albipennis Haliday Non-Nees and of Apanteles albipennis Haliday of Marshall (Hymenoptera, Braconidae). Proceedings of the Royal Entomological Society of London (B) 10, 71-81.
Wilkinson, D. S. (1945). Description of palearctic species of Apanteles (Hymenoptera, Braconidae). Transactions of the Entomological Society of London 3, 35-226.
Williams, D. J. M. (1985). The new world genus Lathrapanteles n. gen.: Phylogeny and placement in the Microgastrinae (Hymenoptera: Braconidae: Cotesiini). Canadian Journal of Zoology 63, 1962-81.
Williams, D. J. M. (1988). Classification, phylogeny and zoogeographic studies of species of Sathon Mason (Hymenoptera: Braconidae). Quaestiones Entomologicae 24, 529-639.
Yeates, D. (1992). Why remove autapomorphies. Cladistics 8, 387-9.
Zetterstedt, J. W. (1840). Insecta Lapponica. Sectio secunda Hymenoptera. Lipsiae, Voss. pp. 1140 (Braconidae, 398-407).

## Appendices A1-A3

Appendix A1: Means of quantitative characters
Appendix A1.1: Means of quantitative characters 36-39
Appendix A1.2: Means of quantitative characters 40-43
Appendix A2: Graphical representation of quantitative characters
Appendix A2.1: Graphical representation of character 36
Appendix A2.2: Graphical representation of character 37
Appendix A2.3: Graphical representation of character 38
Appendix A2.4: Graphical representation of character 39
Appendix A2.5: Graphical representation of character 40
Appendix A2.6: Graphical representation of character 41
Appendix A2.7: Graphical representation of character 42
Appendix A2.8: Graphical representation of character 43

Appendix A3: Data Matrix

Appendix A1. Means of quantitative characters (section 5.3.2.3) arranged in ascending order. Bold subheadings represent the character state coding. Refer to Appendices A2.1-A2.8 for the graphical representation of the data, Section 3.6.3 for the method of coding quantitative data, and Section 5.3.2.3 for discussion of characters used in analyses.

| 38. M+CU vs 1-M | Mean | 37.plical ve subbasal coll |  | 38. Hind coxa vs Ti |  | 39. IHTS vs OHTS | Moan |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Mean | 0.87 |  | 1.70 |  | 1.57 |  | 1.38 |
| S.D. | 0.15 |  | 0.28 |  | 0.36 |  | 0.25 |
| Coded 0 |  | Coded 0 |  | ${ }^{1} \mathrm{Coded} 0$ |  | Coded 0 |  |
| Diolcogaster whilfieldi | 0.57 | Epsilogaster panama | 0.80 | Microplitis murrayi | 0.86 | Coresia glomerata | 1.00 |
| Diolcogaster euterpus | 0.59 | Prasmodon sp. | 0.90 | iiMicroplitis denolitor | 0.89 | Deuterinys anica | . 00 |
| Diolcogaster nixani | 0.64 | Coded 1 |  | IDolichogenidea eucalypri | 0.93 | Deuterixys carbonaria | . 00 |
| Buluka straeleni | 0.65 | LDiolcogaster reates | 1.17 | Miropotes chookolis | 0.93 | Microoplitis denulitor | 1.00 |
| Parenion beelaronga | 0.67 | New genus | 1.27 | Deuterixys anica | 1.00 | \|MMicroplitis nuurrayi | 00 |
| Diolcagaster alkingara | 0.67 | Diolcogaster nixani | 1.29 | Deuterixys carbonaria | 1.00 | Miropotes chookolis | 1.00 |
| Diolcogaster dangerfieldi | 0.68 | Coded 2 |  | Xenogaster insolens | 1.00 | Xenogaster insolens | 1.00 |
| Diolcogaster merata | 0.70 | Wilkinsonellus striatus | 1.40 | Fornicia ceylonica | 1.10 | Apanteles ippeus | 05 |
| Buluka achiterbergi | 0.71 | Cardiocliles fuscipennis | 1.42 | Epsilogaster panama | 1.13 | Diolcogasier regularis | . 06 |
| Diotcogaster periander | 0.71 | Diolcogaster fascriipennis | 1.43 | Cardiochiles eremophilasturis | 1.13 | Protapanteles popularis | 07 |
| Microplitis nurrray | 0.72 | Diolcogaster nuzaffari | 1.43 | coded 1 |  | Diolcogaster oromes | 7 |
| Coded 1 |  | Diolcogaster rolersis | 1.43 | Apaureles inpeus | 1.25 | Ghyprapanueles deliasa | 1.10 |
| Diolcognster harrisi | 0.73 | Diolcogaster masoni | 1.43 | Diolcogaster rixosus | 1,30 | LDiolcogaster whitfreldi | 15 |
| Prasmodon sp. | 0.75 | Diolcogaster euterpus | 1.44 | Glypupaureles alticola | 1.31 | Glyptapanreles athicola | 1.15 |
| Miropotes chookolis | 0.76 | Microgaster kuchingensis | 1.45 | Diolcogaster regulanis | 1.36 | Diolcognster adiassola | 1.16 |
| Diolcogaster muzafari | 0.78 | Wikinsonellus amplus | 1.45 | Prasnodon sp. | 137 | Diolcogaster lucindae | 17 |
| Coresia glomerata | 0.79 | Cardiochiles eremophilasturit | 1.50 | Diolcogaster lucindae | 1.38 | Diolcogaster ippis | 1.20 |
| Cardiochites fuscipenmis | 0.80 | Diolcogaster arontes | 1.50 | Cotesia glomerata | 1.39 | Dolichogonidea eucatypti | 1.23 |
| Diolcogaster newguineaensis | 0.80 | Dioicogaster ippis | 1.51 | Diolcogaster whiffieldi | 1.40 | Epsilogaster panama | 1.23 |
| Diolcogaster reales | 0.80 | Diolcogaster astimeadi | 1.52 | Diolcogaster adiastola | 1.43 | Diolcogaster scatica | 1.23 |
| Diolcogaster vulpinus | 0.81 | Diolcogaster yousufis | 1.57 | Diolcogaster periander | 1.44 | Fornicia ceylonica | 1.24 |
| Diolcogaster adiassola | 0.81 | Diolcogaster alvearius | 1.60 | Diolcogaster masoni | 1.46 | Diolcogaster alvearius | 1.25 |
| Diolcogaster sons | 0.82 | Diolcogaster brevicaudus | 1.60 | Diolcogaster harrisi | 1.47 | Rasivalva stigmatica | 25 |
| Diolcogaster electes | 0.83 | Diolcogaster duris | 1.60 | Gyptapanteles deliasa | 1.47 | Coded 1 |  |
| Diolcogaster alvearius | 0.83 | Xenogaster insolens | 1.60 | Diolcogaster vulpinus | 1.48 | Diolcogaster sons | 1.28 |
| Diolcogaster lucindae | 0.83 | Microplitis demolitar | 1.63 | Diolcogaster pemiciosus | 1.50 | Diolcogaster periander | 1.28 |
| Xenogaster insolens | 0.83 | Diolcogaster learae | 1.63 | Diolcogaster reales | 1.52 | Diolcogaster iqbali | 1.29 |
| Diolcogaster ippis | 0.84 | Microplitis murrayi | 1.64 | Diolcogaster dichromus | 1.53 | Diolcogaster ashmeadi | 1.30 |
| Diolcogaster hadrommarus | 0.85 | Coded 3 |  | Fornicia muluensis | 1.54 | Diolcopaster rentes | 1.30 |
| Diolcogaster masoni | 0.85 | Diolcogaster ixosus | 1.66 | Protapanteles popularis | 154 | Diolcogaster rixosus | 1,30 |
| Diolcogaster notopeckios | 0.86 | "Diolcogaster regularis | 1.67 | Diolcogaster alvearius | 155 | Diolcogaster tearae | 1.30 |
| Diolcogaster walkerae | 0.86 | Diolcogaster whiffieldi | 1.67 | Diolcogaster walkerae | 1.57 | Diolcognster vulpinus | 1.30 |
| Apanteles ippeus | 0.86 | iProtomicroplitis callippera | 1.67 | Diolcognster tearae | 1.58 | Diolcos gaster walkerae | 130 |
| Diolcognaster ashmeadi | 0.87 | Ghyptapanteles deliasa | 1.69 | Diolcogaster muzaffari | 158 | Protomicroplitis calliptera | 1,31 |
| Coded 2 |  | Dioicogaster lucindae | 1.70 | Coded 2 |  | Diolcognster hadromminus | 1.32 |
| Diolcogaster coenonymphae | 0.88 | Distarix formosus | 1.71 | Cardiochiles fuscipemis | 1.60 | Fornicia nuluensis | 1,33 |
| Wilkinsonellus striatus | 0.88 | Diolcogaster coenonymphae | 1.71 | Diolcogaster dangerfiedi | 1.60 | Diolcogaster nusoni | 134 |
| Diolcogaster rixosus | 0.88 | Diolcogaster atrdominalis | 1.73 | Diolcogaster electes | 1.60 | Diolcogaster yousufi | 1,34 |
| Dialcogaster perniciosus | 0.88 | Diolcogaster newguineaensis | 1.75 | Diolcogaster hadrommatus | 1.61 | Prasmodon sp. | 1.38 |
| Diolcogaster robersi | 0.88 | Diolcopastrer scotica | 1.75 | Diolcogaster newguineriensis | 1.61 | 11 Diolcogaster robersi | 1,38 |
| Diolcogaster scotica | 0.89 | Parenion beelaronga | 1.75 | Diolcogaster duris | 1.62 | IDiolcogaster perniciosus | 1.40 |
| Diolcogaster tearae | 0.90 | Rasivalva stigmatica | 1.75 | Diolcogaster rohersi | 1.63 | Diolcogaster alkingara | 1,43 |
| Diolcogaster tepularis | 0.90 | Cotesin glomierata | 1.77 | Diolcogaster coenonymplay | 1.63 | Buluka sirreleni | 1.43 |
| Diolcogaster iquali | 0.90 | Grypapanueles alicoia | 1.79 | Protomicroplitis callipiera | 1.65 | Diolcogaster dangerfieldi | 1,48 |
| Glypatapanteles alticola | 0.91 | Buluka achterbergi | 1.80 | Diolcogaster notopecktos | 1.66 | Cardiochiles fuscipennis | 1.50 |
| Wikinsonellus anylus | 0.92 | Buluka stroeleni | 1.80 | Microgaster kuchingensis | 1.67 | Diolcogaster coenomymphas | 1.50 |
| Dolichogenidea euclaypri | 0.93 | Deuterixys anica | 1.80 | Diolcogaster naunumni | 1.68 | Dialcogaster diciramus | 1.50 |
| Fornicia ceylonica | 0.93 | Diolcogaster periander | 1.80 | Diolcogaster euterpus | 1.69 | Diotcogaster electes | 1.50 |
| Microplitis demolior | 0.94 | Deuterixys carbonaria | 1.82 | Diolcogaster sons | 1.70 | Diolcogaster fascripennis | 1.50 |
| New gcnus | 0.95 | $\\|$ Diolcogaster perniciosus | 1.84 | Buluka achtrerbergi | 1.71 | 1 Coded 2 |  |
| Diolcogaster yousufi | 0.95 | Dioicogaster sons | 1.84 | Rasivalua stigmatica | 1.71 | Distarix formosus | 1.51 |
| Protomicroplitis calliptera | 0.95 | lidiolcogaster electes | 1.84 | Diolcognsser iqbanli | 1.72 | Diolcogaster newguineaensis | 1.53 |
| Prolapanteles popularis | 0.96 | Fornicia ceylonica | 1.85 | Diolcogaster alkingara | 1.72 | Diolcogaster notopecktos | 1.59 |
| Deuterixys carbonaria | 0.98 | Fornicia muluensis | 1.90 | Diolcognster ashmeadi | 1.73 | Diolcogaster merata | 1.50 |
| Deuterinis anica | 1.00 | Diolcogaster adiastola | 1.91 | Diolcogaster nixomi | 1.80 | Microgaster kuchingensis | 1.60 |
| Diolcogaster brevicaudus | 1.00 | Coded 4 |  | Diolcogaster orontes | 1.80 | Wilkinsomellus striatus | 1.60 |
| Diolcogaster dichromus | 1.00 | Diolcogaster iqpati | 1.93 | Diolcogaster yousuf | 1.80 | Diolcogaster harrisi | 1.61 |
| Diolcogaster duris | 1.00 | Dolichagenidea eucalypti | 1.94 | Wilkinsonellus amplus | 1.82 | Cardiochiles eremaphilasturit | 1.67 |
| Diolcogaster fasciipennis | 1.00 | Protapameles popularis | 1.95 | Diolcogaster abdominalis | 1.83 | Buluka acilitrbergi | 1.67 |
| Diolcogaster naumunni | 1.00 | Diolcogasser dichromus | 2.00 | Diolcogaster brevicaudus | 1.83 | Diolcogaster duris | 1.67 |
| Diolcogastre orontes | 1.00 | Diolcogaster merata | 2 m | Diolcogaster scotica | 1.88 | Diolcogaster naunamni | 1.67 |
| Distatrix formosus | 1.00 | Diolcognster naumanni | 2.00 | Buluka straeleni | 1.93 | Diolcogaster brevicaudus | 1.70 |
| Fornicia muluensis | 1,90 | Diolcogaster vulpimus | 200 | Coded 3 |  | Diolcogaster muraffari | 1.70 |
| Rasivalva stigmatica | 1.00 | Apanteies ippeus | 2.01 | Diolcogaster merrata | 1.97 | New genus | 1.73 |
| Coded 3 |  | Miropotes chookolis | 2.02 | Diolcogaster ippis | 2.00 | 1 coded 3 |  |
| Glyptapanteles deliasa | 1.07 | Diolcogaster walkerne | 2.03 | Distarrix fomiosus | 2.09 | \| Diolcogaster abdominalis | 1.80 |
| Microgaster kuchingensis | 1,10 | Diolcogaster hadrommatus | 2.07 | Wikinsonellus striatus | 2.13 | Diolcogaster euterpus | 1.80 |
| Cardiochiles eremophilasturit | 1.11 | Diolcogaster dangerfieldr | 2.10 | Coded 4 |  | Diolcogastrer nixmi | 1.82 |
| Coded 4 |  | Diolcogaster harrisi | 2.15 | Diolcogaster faccinemin | 2.33 | Parenion beelaronga | 1.98 |
| Diolcogaster abdominalis | 1.22 | Dialcogasier atkingara | 2.17 | New genus | 2.38 | Wilkinsonellus amplus | 2.00 |
| Coded 5 |  | Coded 5 |  | Coded 5 |  |  |  |
| Ensilogaster panania | 1.43 | Diolcognster notopecktos | 12.33 | Parenion beelaronga | 2.80 |  |  |



Appendix A2.1. Graphical representation of the means of hind wing vein $\mathrm{M}+\mathrm{CU}$ versus $1-\mathrm{M}$ length (character 36) arranged in ascending order. The taxa are in the order represented in
Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6.3 for the method of coding quantitative characters.


Appendix A2.2. Graphical representation of the means of hind wing plical cell versus sub-basal cell length (character 37) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6.3 for the method of coding quantitative characters.


Appendix A2.3. Graphical representation of the means of hind coxa versus first metasomal tergite (T1) length (character 38) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6.3 for the method of coding quantitative characters.


Appendix A2.4. Graphical representation of the means of inner hind tibial spur versus outer hind tibial spur length (character 39) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6 .3 for the method of coding quantitative characters.


Appendix A2.5. Graphical representation of the means of inner hind tibial spur versus hind basitarsus length (character 40) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6.3 for the method of coding quantitative characters.


Appendix A2.6. Graphical representation of the means of hypopygium versus hind tibia length (character 41) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6 .3 for the method of coding quantitative characters.


Appendix A2.7. Graphical representation of the means of ovipositor sheaths versus hind tibia length (character 42) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6 .3 for the method of coding quantitative characters.


Appendix A2.8. Graphical representation of the means of first metasomal tergite (T1) maximum length versus maximum width (character 43) arranged in ascending order. The taxa are in the order represented in Appendix A1, and the bold numbers on the right of the graph represent the character state codes derived from one standard deviation from the mean. See Section 3.6.3 for the method of coding quantitative characters.


Appendix A3. The data matrix of characters and states for 64 in -group and four out-group taxa. The outgroups are: Epsilogaster panama, Cardiochiles fuscipennis, Cardiochiles eremophilasturtiae, and the hypothetical ancestor. The characters, their state assignments, and the corresponding codes are given in Section 5.3.2 and the taxa are listed in more detail in Table 5.1. The characters are as follows:

1. Arrangement of placodes on flagellomeres
2. Distribution of placodes on flagellomeres
3. Fluted bent-tipped sensilla on ventro-lateral surface of medio-apical flagellomeres
4. Presence of grooves on lateral pronotum
5. Sculpturing of ventral area of lateral pronotum
6. Propleural flange
7. Epicnemial carina
8. Presence of notauli
9. Shape of scutellum
10. Carina on posterior margin of scutellum
11. Sculpturing of medial posterior band of scutellum
12. Phragma of scutellum
13. Median spine on metanotum
14. Shape of propodeum
15. Medial longitudinal carina of propodeum
16. Areola of propodeum
17. Lateral carinae of propodeum
18. Anal cross vein of forewing (1a)
19. 4th Radius Sector (4-RS) of fore wing
20. Fore wing areolet
21. Vein 2-RS of hind wing
22. Vein $2 \mathrm{r}-\mathrm{m}$ of hind wing
23. Vein $2-1 \mathrm{~A}$ of hind wing
24. Vein cu-a of hind wing
25. Shape of hind wing vannal lobe margin
26. Pilosity of hind wing vannal lobe margin
27. Shape of first metasomal tergite (T1)
28. Medial groove of T1
29. Suture between T2 and T3
30. Median field of T2
31. Median field of T3
32. Carapace
33. Sclerotisation of hypopygium
34. Pilosity of ovipositor sheaths
35. Specialised sensilla on ovipositor sheaths
36. Length of $\mathrm{M}+\mathrm{CU}$ vs length of $1-\mathrm{M}$ of hind wing.
37. Length of plical cell (vannal lobe) vs length of sub-basal cell of hind wing
38. Size of hind coxa

## 39. Length of hind tibial spurs

40. Length of inner hind tibial spur vs length of hind basitarsus
41. Length of hypopygium
42. Length of ovipositor sheaths
43. Size of T1 (Maximum length of T 1 vs maximum width of T1)

|  | Matrix |  |  |  |  |  |  |  |  |  |  |  | 12：13｜1 |  | 14｜15｜c｜ |  |  |  |  |  |  |  |  | ｜ 2312423 |  |  |  |  |  |  | 129 30 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1 | Emitamertemana |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | － | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ |  |  |  |  |  | － | ${ }^{\circ}$ |  |  |  |  | 0 |  |  | ， | $\bigcirc$ |  |  |  | 3 | 2 | $\div$ | 2 | 2 | 2 | $\frac{3}{3}$ |  |
| 2 |  | $\frac{3}{3}$ | ！ | 2 | $\bigcirc$ | $\frac{\square}{1}$ | $\stackrel{0}{0}$ | $\bigcirc$ | $\frac{1}{0}$ | ： | \％ | i | $\div$ | － | $\div$ | 3 | $\bigcirc$ | 0 | 2 | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | － |  |  |  |  | 0 | 0 | ， |  | ， | － |  |  | $\bigcirc$ | 1 |  |  | 0 |  |  |  |  |
|  | Corcerbirfomipmat | 3 |  | 2 | $\bigcirc$ | $\bigcirc$ | － | ． | 0 | 0 | O |  | $\bigcirc$ | 0 | $\cdots$ | 3 | 0 | 0 | － |  |  |  |  |  |  |  |  |  |  | 0 |  |  |  |  |  |  | $\bigcirc$ | $\stackrel{1}{1}$ | $\stackrel{2}{4}$ |  |  |  |  |  |  |
| 5 | Apmenetrer ipocar | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | $\bigcirc$ | 0 |  | $\bigcirc$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | $\frac{1}{1}$ | 2 | 3 | 2 | 2 |  |  | 1 | $\bigcirc$ |  | 2 | 2 | 2 | 0 | － | 0 |
| 6 | Biduen materterxi | 1 | $\bigcirc$ | ！ |  |  | 1 | $\bigcirc$ | 3 | $\bigcirc$ | － |  | － | $\bigcirc$ |  | － | 2 | 2 | $\stackrel{1}{2}$ | ！ | ＋ |  | － | \％ |  |  |  |  | － | ！ | ${ }^{2}$ | 3 | ${ }^{2}$ | i | $\bigcirc$ | 1 | 1 | $\bigcirc$ | 3 | $\frac{2}{2}$ | 1 | 2 | 0 |  |  |
| 7 | Eutaturnimi |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 5 |  |  | 0 | 0 |  |  |  | 0 | ． |  |  | 2 | 0 | 0 | 2 | 0 | 1 | 3 | 1 | 0 | 1 |  |  |  |
| 8 | Corrtag ${ }^{\text {dimementa }}$ | $\bigcirc$ | $\bigcirc$ | 2 | 2 |  |  |  |  |  |  |  |  |  |  |  |  | 2 | 2 | ＋ | 5 | － |  | － | ． | 0 | 0 | $\bigcirc$ | 0 | 2 | $\square$ | 1 |  |  |  |  | $\bigcirc$ | 2 |  |  |  | 0 |  |  |  |
|  | Bxatring outemmia | $\bigcirc$ | $\frac{1}{1}$ | $\stackrel{1}{0}$ | $\frac{1}{2}$ | I | $\bigcirc$ | 0 | ${ }^{3}$ | $\bigcirc$ | 0 | 0 | $\bigcirc$ |  |  |  | 2 | 2 | 2 | ！ | 5 | － |  | 0 |  |  | 0 | 0 | 0 | 2 | 0 | － |  | 1 | $\bigcirc$ | － | $\bigcirc$ | ？ | $\frac{3}{3}$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | 1 | $\bigcirc$ | $\div$ |
| 10 |  | 0 | 1 |  |  | ！ | 1 | $\bigcirc$ | ， 3 | $\bigcirc$ |  |  | $\bigcirc$ | － | ， | － | 2 | 1 | 0 | 1 | 2 |  |  |  | － |  |  |  |  | 1 | ？ | 1 |  |  |  |  | 0 |  | 3 | \％ | 0 | i | 1 | 0 | $\bigcirc$ |
| 12 |  | 0 |  |  |  |  |  |  |  |  |  |  |  | － | ！ | 。 | 2 | 1 | $\frac{2}{2}$ | ！ | 4 | 0 |  | － | ！ |  |  | 2 | 0 | 1 | ？ | 。 | 0 |  | － | 1 | 1 | － | 4 | 2 | 1 | 3 | $\bigcirc$ | $\bigcirc$ | 0 |
|  |  |  |  |  | 2 | $\frac{1}{0}$ | － | \％ |  | $\bigcirc$ |  |  |  | $\bigcirc$ | 1 | － | 2 | 2 | 2 | 1 | 2 | － |  | － | 0. | － | － | 1 | 3 | $\bigcirc$ | 0 | 1 |  | $\bigcirc$ | $\bigcirc$ | － | $\bigcirc$ | 1 | $\frac{2}{2}$ | $\frac{1}{2}$ | $\bigcirc$ |  | $\bigcirc$ | $\bigcirc$ | 1 |
| $\frac{14}{15}$ | Didur | i | $\bigcirc$ | 1 | $\bigcirc$ | 1 | 1 | 0 | 3 | 0 | － | I | $\stackrel{\square}{0}$ | 0 | ， | － | 2 |  | 2 | 1 |  | － |  |  | 0 | － |  |  |  | 1 | 1 |  |  |  | $\bigcirc$ |  |  | $\frac{1}{2}$ | 2 | 2 | $\frac{1}{2}$ | $\stackrel{0}{2}$ | 0 | $\bigcirc$ | － |
|  | Didenpuier triximene | 1 | 1 |  | 2 |  |  | 0 |  | － | $\bigcirc$ | 1 | $\bigcirc$ | $\bigcirc$ | I | $\bigcirc$ | 2 | 1 | $\frac{1}{2}$ | ＋ | $\frac{1}{2}$ | － |  |  |  |  |  |  | 0 | 2 |  |  | 1 | － | － | $\bigcirc$ | $\bigcirc$ | 2 | 3 | 2 | 1 | 1 | 1 | 0 | 0 |
|  | Dinkegaut raxmomph |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 2 | 1 | 2 | 1 | 4 | ${ }^{4}$ |  |  |  |  |  |  | 0 |  | 2 |  |  |  |  |  |  |  |  |  |  |  |  | $0$ |  |
| 18 |  | 1 | $\bigcirc$ | 1 | 2 | ！ | $\frac{1}{0}$ | $\bigcirc$ | ， | \％ |  |  |  | ． |  |  | $\frac{2}{2}$ | － | $\frac{2}{2}$ | － | 1 | 1. | － | $\bigcirc$ | ， | ． | 0 | $\frac{2}{2}$ | 4 |  |  |  |  | 。 | － |  | － | 2 | 4 |  |  |  |  |  |  |
| 19 | Diderepatir dichomer | $\bigcirc$ | 1 | $\stackrel{1}{2}$ | 1 | 1 |  | － |  | 0 | 0 | 1 | $\bigcirc$ | $\bigcirc$ | 1 | 0 | 2 | ， | 1 | 1 | 3 |  |  |  |  | 1 | 0 |  | 3 | ， | 0 | 1 |  | 0 | 0 | 0 | 0 |  | 2 | 2 | 2 |  |  | 0 | $\bigcirc$ |
| 21 | Didecorateremintar | 1 | $\bigcirc$ | 1 | 2 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | $\bigcirc$ | 0 | 1 | 0 | 2 | 2 | 2 | 1 |  | ． |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | － |  |
| 22 | Didobymirnempur |  | 1 | 0 | 0 | 0 |  |  |  | $\bigcirc$ |  | $\bigcirc$ |  |  |  | $\bigcirc$ | 2 | 2 | $\frac{2}{2}$ | ！ | 3 | $\frac{4}{3}$－ | － | － | $\bigcirc$ | 2 | $\bigcirc$ |  | $\bigcirc$ |  | $\frac{0}{0}$ | $\frac{2}{3}$ |  | － | $\div$ |  |  |  | $\frac{2}{2}$ | $\frac{2}{4}$ | $\frac{1}{1}$ | 3 |  | $\bigcirc$ |  |
| 23 |  | 1 | 0 | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 | 2 | 1 |  | 1. | 0 | ， | 0 | ， | 0 |  | 3 | ， |  |  |  |  | 0 | 1 | 1 | 1 | 4 | 2 | 1 | 2 |  | 0 |  |
| $\frac{24}{24}$ |  | － | $\bigcirc$ | 2 | ： | ＋ | 1 | 0 | 3 | 0 | 0 | ， | － | 0 | 1 | － | ${ }^{2}$ |  |  | 1 |  |  |  |  |  |  | 0 | 0 | 3 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | $\bigcirc$ | 1 | 4 | 1 | 2 | 3 |  | $\bigcirc$ |  |
| 26 | Dintronater imia | ！ | $\bigcirc$ | 2 | 2 | $\pm$ | 1 | 0 | － | $\bigcirc$ | $\bigcirc$ | $!$ | $\bigcirc$ | $\bigcirc$ | $\pm$ | $\bigcirc$ | 2 | ， | $\bigcirc$ | ． 1 | 1 | 1 | O |  |  |  | $\frac{1}{0}$ | $\frac{2}{0}$ | $\frac{1}{3}$ | ${ }_{1}$ | － | ！ | 2 | $\bigcirc$ | $\frac{0}{0}$ | $\frac{1}{1}$ | $\bigcirc$ | $\frac{1}{2}$ | $\frac{2}{4}$ | $\frac{3}{2}$ | $\stackrel{1}{1}$ | 3 | $\div$ | $\bigcirc$ | $\bigcirc$ |
|  | Diatotater mera |  |  |  |  |  |  |  | 3 | $\bigcirc$ |  | － | $\bigcirc$ | $\bigcirc$ | ＋ | － | ${ }^{2}$ | 2 | 2 | ， |  |  |  |  |  |  | 0 |  | 3 | ！ | $\bigcirc$ | 2 | 2 |  | 0 | ， | 0 |  | 3 | 1 | $\bigcirc$ | 4 | 1 | 1 |  |
| 28 | Dashoswerlmadr |  |  |  | 2 |  |  |  |  |  |  |  |  |  | ＋ |  | 2 | 2 | 2 | 2 | 3 | 3 |  |  |  |  | 0 |  | 4 | 1 | 0 | 3 |  |  | 0 | 2 | 0 |  |  |  |  |  |  |  |  |
| 29 | Diok patier miven |  |  | 1 | 2 | 1 | 1 | ${ }_{0}$ | 3 |  | － | 1 | $\bigcirc$ | $\bigcirc$ | － | 0 | 2 | 1 | 0 | ， |  | 4 | 0 |  | 0 | 0 | 1 | 2 | 0 | I | － | 0 | ？ | 0 | 0 | 1 | 1 | $\bigcirc$ | 4 | 3 | 2 | 1 | $\bigcirc$ | $\bigcirc$ | － |
| $\frac{30}{31}$ |  |  | － | 0 | 1 | 1 | 1 | 。 | 3 | $\bigcirc$ |  | 1 | $\bigcirc$ | － | i | 0 | 0 | 2 | 2 | 2 |  |  |  |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 32 | Diskeramer numami | 。 | $\bigcirc$ | 0 | 1 | 1 | 0 | － | ${ }^{3}$ | － | 0 | ${ }^{1}$ | $\bigcirc$ | 0 | 1 | 10 | － 2 | 1 | 2 | 2 |  |  |  |  |  |  |  |  |  |  |  | 2 |  | 0 |  |  |  |  | $\frac{4}{3}$ | 2 |  |  |  | ！ |  |
| 33 |  |  |  |  |  |  |  | － | ， | $\bigcirc$ |  |  |  | $\bigcirc$ |  | ， | 2 | 2 | 2 |  |  |  |  |  |  |  |  | 0 |  | $\bigcirc$ | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 3 | 2 | $i$ | 1 | 0 |
| $\frac{34}{35}$ | Diokosgutr nital | 1 | 1 | 2 | 1 | $\bigcirc$ |  | $\bigcirc$ | $\frac{3}{3}$ | － |  | $\bigcirc$ | $\bigcirc$ | － | 1 | i | $\bigcirc$ | 1 | 2 | ${ }_{2}$ |  |  | \％ |  | $\stackrel{\square}{0}$ | ${ }^{\circ}$ | 0 | 2 | － | i | 1 | 3 | 2 | 0 | － | 2 | 0 | 1 | 5 |  |  |  |  |  |  |
| $\frac{35}{36}$ | Diokroputerenwes | $\bigcirc$ | － | ${ }_{2}$ | 1 | ！ | 0 | 。 | $\frac{3}{3}$ | － | － | ． | 。 | O | 1 | 10 | ${ }^{-}$ | 2 | 1 |  |  |  |  |  |  |  |  |  |  |  | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 4 | 0 | 0 | 0 |
| 37 | Didozogrereparimder |  |  |  | － | 0 | 0 | 0 | 3 | 0 | 1 | ， | 0 | 0 | 1 | 1. | 0 | 2 |  |  |  |  | 0 |  | － | － | － |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 38 | Diokezater creibinur | $\div$ | 1 | 2 | 1 | $!$ | $\square$ | $\bigcirc$ | 3 | $\bigcirc$ | － | － | $\bigcirc$ | － | 1 | － | $\bigcirc$ | 1 | ${ }_{2}$ |  |  |  | $\bigcirc$ |  | $\bigcirc$ | ！ | $\div$ | $\bigcirc$ | $\frac{1}{2}$ | 2 | $\bigcirc$ | ！ | $\frac{2}{2}$ | $\bigcirc$ | 0 | $\frac{1}{0}$ | $\div$ | $\stackrel{2}{1}$ | $\frac{1}{1}$ | 1 | $\bigcirc$ | $\frac{2}{2}$ | $\frac{2}{0}$ | $\bigcirc$ | $!$ |
| 30 |  | $!$ | 1 | － | 2 | $!$ | 0 | ， | 0 | ． | ， | ， | 。 | ， |  | 1. | 。 | 2 | ${ }^{\circ}$ |  |  |  |  |  | $\bigcirc$ | ． | $\bigcirc$ | － | ， | － | － | 1 | 2 | 0 | － | 2 | － | 2 | 3 |  |  | 2 | 1 | 1 | 1 |
| 41 | Diohepgaster mbensi | － | 0 | 2 | 1 | I | 1 | 。 | 0 | 0 | 0 | 0 | ． | 0 |  | 1. | 0 | 1 |  |  |  |  |  |  | 。 |  |  |  | 3 | 2 | 0 |  | 2 | 0 | 0 |  | 0 | 2 | 2 |  |  |  |  |  |  |
| 42 | Diotogasarer sotica | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 3 | － | $\bigcirc$ | － | $\bigcirc$ | － 1 | $\bigcirc$ | 0 | 1 | ${ }^{2}$ | 2 |  | 2 | $\bigcirc$ |  | $\div$ | $\bigcirc$ | $\bigcirc$ | 2 | 0 | $\frac{1}{1}$ | 2 | $\frac{2}{0}$ | 0 | － | 0 |  | $\bigcirc$ | $\frac{2}{1}$ |  |  |  |  |  | $\frac{2}{0}$ |  |
| $\frac{43}{34}$ | Dindozater tast | ！ | $\bigcirc$ | $\frac{1}{0}$ | 2 | ！ | 1 | － | $\bigcirc$ | 0 | － | $\frac{1}{0}$ | $\stackrel{0}{0}$ | 0 |  |  | $\bigcirc$ | 2 |  |  |  | $\stackrel{1}{2}$ | － |  | $\bigcirc$ | $i$ | 0 | 1 | 3 | 1 | ${ }^{\circ}$ | 1 | 2 | \％ | $\bigcirc$ |  | 1 | 2 | 2 | i | ＋ | － | 3 | 1 | ！ |
| $\frac{89}{45}$ <br> 8 | Ditheneacricare | 1 | $\bigcirc$ | $\bigcirc$ | 2 | $\bigcirc$ | 0 | 0 | 0 | ${ }^{\circ}$ | － | － | － | 0 | － | i． | 0 |  |  |  |  |  | － |  | 0 | － | 0 | 1 | 3 | 1 | 0 | 1 |  | 0 | － |  | 0 |  | 4 |  |  |  |  |  |  |
| 46 | Diockoguter wateme | 1 | $\bigcirc$ | 1 | 2 | 1 | $\bigcirc$ | 0. | $0 \cdot 3$ | 30 | － | $\bigcirc$ | $\bigcirc$ | － | － | 1. | － | 2 | － | 0 |  | 2 | － |  | $\bigcirc$ | － | $\bigcirc$ | $\bigcirc$ | 3 | 1 | $a$ | 1 | 2 | $\bigcirc$ | $\bigcirc$ | ， | － |  | 4 | $\frac{1}{2}$ | 1 | $\frac{2}{2}$ | $\bigcirc$ | － | 1 |
| 48 | Diukegater y musui |  |  |  |  |  |  |  | 0 3 | ， |  |  |  | 0 |  |  | 。 | 2 |  |  |  |  |  |  |  |  |  | $\bigcirc$ | 3 |  | 0 | 1 | 2 | $\bigcirc$ | 0 | 1 |  | 2 |  |  |  |  |  |  |  |
|  | Dium | 1 |  | 2 | 1 | 0 |  | 0 | 0 | 0 |  | 0 |  |  |  |  |  | 2 |  |  |  |  | $\bigcirc$ |  | $\bigcirc$ | $\stackrel{\square}{2}$ |  | $1$ | $\bigcirc$ |  | $\bigcirc$ |  |  | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | 2 | 3 |  | 2 |  |  | $\bigcirc$ |  |
| $\frac{49}{50}$ |  | $\stackrel{1}{1}$ | $\bigcirc$ | $\stackrel{1}{2}$ | $\stackrel{2}{1}$ | i | $\stackrel{1}{2}$ | ${ }^{2} 1$ | 3 | ${ }^{3}$－ |  | $\stackrel{1}{2}$ | 1 | － | 1 |  | \％ |  |  |  |  | 5 | $\bigcirc$ |  | $\bigcirc$ | $\frac{2}{3}$ | 1 | 2 | 0 | 2 | $\stackrel{1}{2}$ | i | 2 | 2 | 0 | 2 | $\bigcirc$ | 2 |  |  | 0 | － | 2 | $\bigcirc$ |  |
| 31 | Fonniciamiownix | 1 | $\bigcirc$ | 2 | 1 | 1 | 2 | 2.1 | $1{ }^{3}$ | ， |  | i | 0 | 0 | 1 | 1. | 2 | 1 |  | ${ }_{0}$ |  | 5 | $\bigcirc$ |  | $\bigcirc$ | ， |  | $\frac{2}{2}$ | $\bigcirc$ |  | 2 |  |  |  | － |  |  |  |  |  |  |  |  |  |  |
| 5 5 |  |  | 0 |  |  |  |  | 0 | 0 | ， 0 |  | － | 。 | ． |  |  | 。 | 2 | 2 | 2 |  | 5 | － |  | $\bigcirc$ | 1 | $\bigcirc$ | $\bigcirc$ | 2 |  | 0 | 2 | 2 |  | $\bigcirc$ |  |  |  |  |  | $\bigcirc$ |  |  |  |  |
| 53 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | $\bigcirc$ | 1 |  |  |  |  | $\bigcirc$ |  |  |  |  |  |  |  |  |
| $\frac{54}{55}$ | Micmeater bextincentil | $\bigcirc$ | ！ | ${ }_{2}^{2}$ | ？ | ！ |  | $\bigcirc$ | $0_{0}^{0} \frac{3}{2}$ | － |  |  | $\bigcirc$ | － |  |  | － |  |  |  |  |  |  |  | $\bigcirc$ | $\bigcirc$ | 。 | $\begin{aligned} & 1 \\ & 0 \end{aligned}$ | 3 | 0 | $\bigcirc$ | 3 | 2 | $\bigcirc$ | $\bigcirc$ | 2 | － | 2 |  |  |  |  |  | － |  |
| 56 | Msorepdiar mumeni | 1 | 1 | ${ }^{2}$ | 1 | 1 | 0 | 0 | 0 | 2. |  | － | 0 | 0 | 0 | 1 | 0 | 2 |  | 0 |  | 1 | $\bigcirc$ | 1 | 0 | $\bigcirc$ |  | 0 | 3 |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 57 | Mimporea choosdis |  |  |  | 1 |  |  | 0 | 0 3 | 3. |  |  |  | 0 |  | 1 | 1 | 0 |  | 0 |  | 2 |  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |  |  |  |  |  |  |  |  |  |  | 2 |  |
|  |  | $\bigcirc$ | 1 | ${ }^{2}$ | 1 | ！ |  | $\bigcirc$ | $\bigcirc 3$ | 3 － |  |  |  | － |  |  | $\frac{3}{3}$ | 2 |  |  |  | 1 |  |  | $\bigcirc$ |  |  | $\bigcirc$ | $\frac{2}{2}$ |  | $\div$ |  | 2 | $\bigcirc$ | $\div$ |  |  |  |  |  |  |  |  | $\frac{1}{0}$ |  |
| 59 | Neadioloputur mivicht |  |  |  |  | － |  | $\bigcirc$ | $\bigcirc$ | 20 |  | \％ |  | － | 0 | ＋ | 3 | 2 | ， | ${ }^{2}$ |  | $\frac{1}{5}$ | ！ | 1 | $\bigcirc$ | ${ }_{1}$ | $\stackrel{1}{1}$ | $\stackrel{1}{1}$ | 2 | $\bigcirc$ | 1 | 1 | 2 | 0 | $\bigcirc$ |  | － | ， |  | 4 | 2 | ． | 2 | $\bigcirc$ | 1 |
| 6. | Pamioin becharnea | 1 | 1 | 2 | I | 0 |  | 0. | $0 \cdot 3$ | 30 |  | － | 0 | 0 | 0 | ， | － | 2 |  | 2 |  | 4 | $\bigcirc$ |  | a |  | 0 | 0 | 3 | 1 | 1 | 3 | ， | 0 | 0 |  | 0 | 0 | 3 | 5 | 3 | $\pm$ | 0 | $\bigcirc$ |  |
| 62 | Pramodon 9 P． | 1 | 1 | 2 | 1 | － |  | 0 | $\bigcirc$ | t |  | $\bigcirc$ |  |  |  |  |  |  |  |  |  |  | $\bigcirc$ |  | $\frac{1}{6}$ |  | ！ | $\frac{2}{2}$ | 2 |  | $\bigcirc$ | 3 | 2 | $\stackrel{\square}{0}$ |  |  |  |  |  |  |  |  |  | $\frac{2}{0}$ |  |
| $6{ }_{6} 6$ |  | 3 | 1 | ${ }^{2}$ |  | － |  | ． | $\div$ | 30 |  | \％ | ！ | ！ | － |  | $\frac{5}{0}$ | 2 | 1 | ${ }^{2}$ |  | $\frac{2}{2}$ | 0 | I | $\bigcirc$ |  | 0 | － | ， | － | 0 |  |  | 0 | 0 |  | 0 | $\stackrel{2}{2}$ | 3 | 2 | 1 | 3 | $\bigcirc$ | 0 | 4 |
| $\underline{6.5}$ | Rastiotios silignuica |  | 0 |  | 1 |  |  | 0 | 0 | 30 |  | $\bigcirc$ |  | 0 |  |  |  |  |  | － |  |  |  |  | 0 |  |  | $\bigcirc$ | 2 | 1 | － | 2 | 2 | 0 | 0 |  | 0 |  |  |  | 0 |  |  |  |  |
|  | Whiteorthe aryfur |  |  |  |  |  |  |  | 0 |  |  |  |  | $\bigcirc$ | $\bigcirc$ | 1 | $\bigcirc$ |  |  |  |  | 5 | $\bigcirc$ |  | $\bigcirc$ | $\stackrel{0}{2}$ | $\bigcirc$ | $\stackrel{\square}{0}$ |  |  | 1 | 1 | 2 |  |  |  | $\frac{\square}{0}$ |  |  |  |  |  |  | $\stackrel{\square}{\square}$ |  |
| $\frac{61}{68}$ |  |  |  |  |  |  |  | 0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

## CORRIGENDA

page x , line 18
page 4
page 15
page 16 , last sent.
Table 2.7
page 43
page 59
page 60-61
page 63, 1st para
page 200, 2nd para
"Margaret Schneider" - misspelling.
"Cassava" - misspelling.
"'restricted lateral shape of the ovipositor" refers to the preapical restriction when viewed laterally.
should read "scutellar phragma".
The totalal new species should read "68".
The probable reason why malaise traps were not successful in collecting Diolcogaster was because wasps were not present in the area traps were run at that particular time, not because they avoid this type of trap.
should read "equilateral" not "more equilateral".
The terms "mesosoma" and "metasoma" are now almost universally adopted by hymenopteran taxonomists, but their exact definition can be found in Gauld and Bolton (1988) or Naumann (1991).
page 241
page 245
page 246
page 247-8
page 249
page 251
page 253
should read "typically does not show an infuscate pattern". should read Annette K. Walker.
"New World" should start with capitals.
"Microplitis croceipes" - misspelling.
"Apanteles" - misspelling.
"Förster" - misspelling.
"Krombein" - misspelling.
"Bouché" - misspelling.
"Apanteles" - misspelling.

