

Insects ‘Down Under’ – Diversity, endemism and evolution of the Australian insect fauna: examples from select orders

Andrew D Austin,^{1*} David K Yeates,² Gerasimos Cassis,³ Murray J Fletcher,⁴ John La Salle,² John F Lawrence,² Peter B McQuillan,⁵ Laurence A Mound,² Dan J Bickel,⁶ Penny J Gullan,⁷ Dinah F Hales⁸ and Gary S Taylor⁹

¹Centre for Evolutionary Biology & Biodiversity, School of Earth & Environmental Sciences, The University of Adelaide, SA 5005, Australia.

²CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia.

³Centre for Biodiversity & Conservation Research, Australian Museum, Sydney, NSW 2010, Australia.

⁴Orange Agricultural Institute, Orange, NSW 2800, Australia.

⁵School of Geography & Environmental Studies, University of Tasmania, Private Bag 78, Hobart, Tas 7001, Australia.

⁶Entomology Department, Australian Museum, Sydney, NSW 2010, Australia.

⁷Department of Entomology, University of California, Davis, CA 95616–8584, USA.

⁸Department of Biological Sciences, Macquarie University, NSW 2109, Australia.

⁹School of Agriculture & Wine, The University of Adelaide, PO Glen Osmond, SA 5064, Australia.

Abstract

The Australian insect fauna is highly endemic and characterised by numerous unique higher-level taxa. In addition, a number of groups are noticeably absent or depauperate on the continent. Many groups found in Australia show characteristic Gondwanan distribution patterns on the southern continents. There are extensive radiations on the plant families Myrtaceae and Mimosaceae, a specialised arid/semiarid fauna, and diverse taxa associated with rainforests and seasonally wet tropical regions. The fauna is also poorly studied, particularly when compared with the flora and vertebrate groups. However, studies in the last two decades have provided a more comprehensive picture of the size of the fauna, relationships, levels of endemism, origins and its evolution. Here we provide an overview of these and other aspects of Australian insect diversity, focusing on six groups, the Thysanoptera and the five megadiverse orders Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera.

INTRODUCTION

Australia is renowned for its diverse and unique biota and because of this, the continent has fascinated biologists from early times. The flagships of this biota have been the unique elements of its flora, such as *Eucalyptus* and *Banksia*, various groups of terrestrial vertebrates, particularly the marsupials (Strahan 1995) and, to a lesser degree, passerine (e.g. honey-eaters) and non-passerine birds (e.g. parrots) (Sibley & Ahlquist 1990), and its large reptile fauna dominated by elapid snakes and the skinks (Glasby *et al.* 1992). However, the unique status of the biota is just as obvious, if not more so, among the terrestrial arthropods, especially the insects.

Australia spans a latitudinal range of 35° from the tropics to the temperate zone, and has a geological history characterised by isolation that predisposes it to a high percentage of endemic taxa (Mummery & Hardy 1994). Occupying almost

6% of the land surface of the earth, it has a similar proportion of described species of higher plants, and some vertebrate and insect taxa (Gaston & Hudson 1994). In contrast to vertebrates and the flora, Australia's terrestrial arthropods are poorly documented (Nielsen & West 1994). Many diverse elements of this fauna have only recently been revealed and are often endemic to small geographical ranges (Harvey 2002).

There have been a number of previous attempts to estimate the species richness of Australian terrestrial arthropods over the last 70 years, and these have obviously been influenced by the state of collections and knowledge at the time. For insects, these have included recent estimates of between 84 000 and 140 000 species (e.g. CSIRO 1991; Nielsen & West 1994). Unfortunately, the methods used to derive these figures are either inconsistent or not stated. One thing is clear though: the estimates for Australian arthropod diversity are increasing with time as more comprehensive information becomes available. This is reflected in the most recent attempt to assess the size of the fauna. Using different approaches, Yeates *et al.* (2003) estimate the size of the Australian terrestrial arthropod fauna to be 253 000 species, of which 205 000

*Author to whom correspondence should be addressed (email: andy.austin@adelaide.edu.au).

species are insects. This is probably still on the conservative side, but means that at least 75% of the fauna has not been formally described or is yet to be discovered.

More difficult than estimating the size of the fauna is determining its origins and the factors involved in its evolution. Several source origins are usually postulated for terrestrial arthropods (Heatwole 1987). These include: (1) an ancient Pangean element of sedentary relictual lineages; (2) a Gondwanan element determined largely by southern continent vicariance events; (3) an Austral element of local and region radiations that occurred in association with post-Gondwana isolation of the continent; (4) a northern element comprising groups that migrated from Asia as the continent drifted into tropical latitudes; (5) a cosmopolitan element of highly mobile taxa; and (6) an introduced element brought onto the continent by Aboriginals and Europeans. Although most of these elements (or modifications of this scheme) can be easily identified in the insect fauna, the origins and makeup of specific higher level taxa (e.g. subfamily level and above) usually comprise a mosaic of several elements that have interacted in complex ways with long-term and short-term climate change (Frakes 1999), mediated through changes to the vegetation (Crisp *et al.* 1999). For example, most highly species-rich families of insects in Australia (e.g. Scarabaeidae, Tachinidae, Geometridae, Braconidae) have components that can be assigned to all the above elements, possibly with the exception of the Pangean element. However, the origins of most faunal components are obscured because of a lack of any detailed understanding of their phylogenetic relationships, or because interacting factors (e.g. vicariance events and subsequent endemic radiations) cannot be easily teased apart, or both. Evidence of the effect of aridification in the Miocene and Pliocene often can be seen in the evolution of the terrestrial arthropod fauna (e.g. Leys *et al.* 2003).

Our aim here is to overview the Australian insect fauna using six orders as examples to explore the general state of knowledge in regard to its species richness, levels of endemism, origins and evolution. The groups selected for this purpose are the Thysanoptera as they have recently come under intense scrutiny, and the five mega-diverse orders, Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera. Much of the information presented here updates the account for these groups in *Insects of Australia* (CSIRO 1991), which remains the best summary of the Australian insect fauna at family level, even though some sections of this compendium are now out of date. Also, of particular relevance to the study of Australian insects is the website for Australian Biodiversity Information Facility (ABIF 2004) that provides checklists, bibliographies and higher-level summaries of relationships, biology etc. for many groups.

THYSANOPTERA

Given that a large proportion of thrips species feed on green plants, it would be surprising if the diversity of Australian Thysanoptera was not correlated in some way with the diver-

sity of the Australian flora. However, these two are not directly related, with many of the highly species-rich plant genera such as *Eucalyptus* supporting very few species of thrips (Mound 2004b), whereas *Acacia* supports a great diversity (Crespi *et al.* 2004). Geographically, the thrips fauna, like the flora, comprises three major components, the Bassian in the south-east and south-west, the northern tropical, and between these the arid and semiarid Eyrean that extends across most of Australia. But these components are by no means discrete, being fragmented and overlapping seasonally to a considerable extent. Moreover, the northern, monsoonal part of the arid zone has a very different thrips fauna from the central and southern parts, with almost no *Acacia* thrips in the monsoonal region.

Southern Hemisphere relationships

The landmass of Australia was isolated from the rest of the world for much of the past 30 million years, but there is limited evidence for the presence in Australia of basal clades amongst the Thysanoptera. Thrips are considered to have shared a common ancestor with the Hemiptera and Psocodea, and their plesiotypic life style was as detritivores (Mound & Morris 2004). The thrips that retain the largest number of plesiomorphies are the litter-inhabiting species that are placed in the family Merothripidae. However, the only members of this family in Australia (Mound 1996) are introduced from the Neotropics.

Early in their evolution, thrips radiated onto plants, probably in association with the rich source of food available in plant reproductive organs. Two families with many Australian species, Melanthripidae and Aeolothripidae, possibly represent this early invasion of higher plants, the species in both groups retaining more plesiomorphies than do the majority of Thysanoptera. *Cycadothrips* Mound, a genus of equivocal systematic position within the Aeolothripidae (Mound & Morris 2004), is an Australian endemic that is associated only with the cones of *Macrozamia* cycads, of which these insects are important pollinators (Mound & Terry 2001; Terry 2001). This association of an apparently basal thrips clade with a basal clade of plants might suggest that thrips were amongst the earliest pollinators of higher plants (Terry 2002), although thrips are not known to be associated with cycad inflorescences in other parts of the world.

The family Melanthripidae comprises four genera, one largely restricted to the Palaearctic and the other three to the temperate areas of the southern hemisphere. *Cranothrips* Bagnall is represented in Australia by at least 10 species, with another known only from South Africa. Similarly, *Dorythrips* Hood, is known from two species in Western Australia and three from either Chile or Argentina. Again, the shared presence of these basal thrips genera across the southern hemisphere may be an indication that they shared a Gondwanan ancestor.

The worldwide family Thripidae includes two of the largest genera, *Thrips* L. with 280 species and *Frankliniella* Karny with 160 species (Mound 2002a). These two are not closely related, and they exhibit contrasting distribution patterns.

Thrips is a worldwide genus, with many species in south-east Asia, and a considerable number endemic to Australia, but with no species native to Central or South America. In contrast, *Frankliniella* is primarily a New World genus that is particularly species-rich in Central and South America, but with a few in the Palaearctic and none native to Africa or Australia (Mound 2002b). These distribution patterns suggest that both genera diversified after Africa and South America had moved apart, but whilst Europe and North America were still joined. The sister-genus to *Frankliniella* appears to be the Australian genus *Pseudanaphothrips* Karny, and also closely related is *Parabaliotrips* Karny, a genus distributed from eastern Australia to the Himalayas (Gillespie *et al.* 2002), and *Lomatotrips* Mound & Walker from New Zealand and Australia. These genera may have shared a common Gondwanan ancestor (Mound 2002b). Moreover, the only genus that has been considered likely to be sister-group to the *Thrips* genus-group is a New Zealand endemic, *Adelphithrips* Mound and Palmer (1981).

Trans-Tasman relationships are apparent in several Thysanoptera taxa, and although anthropogenic effects are possible, some of the relationships possibly predate human settlement. *Karphotrips dugdalei* Mound & Walker was described on a single specimen from near Auckland, but more recently has been found to be widespread across southern Australia in association with *Gahnia* (Poaceae) (Mound 2002a), a genus that occurs also in New Zealand. *Lomatotrips paryphis* Mound & Walker, described from several sites in New Zealand but without precise host information, has recently been found to breed in the buds of *Podocarpus totara* (Martin & Mound 2004), and a second but undescribed species of this genus is available in the Australian National Insect Collection taken from *Podocarpus lawrencei* in the mountains near Canberra. *Cartomothrips manukae* Stannard was described from New Zealand on *Kunzea ericoides*, a widespread shrub in eastern Australia, and the thrips was subsequently taken in Tasmania.

In general, thrips are not useful biogeographical indicators, partly because the systematics of the group is so insecurely based, with almost 50% of genera being monotypic (Mound & Morris 2004), and partly because the Southern Hemisphere faunas are so poorly known. Amongst the Thripidae, although there are many Australian endemic genera, relationships are largely equivocal with little evidence for a uniquely Southern Hemisphere fauna. The systematic situation amongst the large family, Phlaeothripidae, is even less resolved, with no effective classification between genus and subfamily levels in the Phlaeothripinae, the larger of the two accepted subfamilies (Mound & Morris 2004). Apart from several tropicopolitan genera, only one well-characterised genus, *Jacotia* Faure, is shared with southern Africa (Mound 1995), and none with South America.

Radiations amongst Australian thrips

The Aeolothripidae occurs worldwide and includes almost 200 species in 23 genera. Amongst these, the Australian endemic

genus *Desmothrips* Hood comprises 14 described species together with a considerable number that remain undescribed. These are the ecological equivalent of *Aeolothrips* species, an Holarctic genus that includes almost 50% of the species in the family. However, these two genera are not closely related, and the origin of this Australian aeolothripid radiation is not clear. Almost 60% of genera in the family are found only in the tropics, but there is no obvious sister-genus to *Desmothrips* amongst any of these.

Equally equivocal is the origin of the Australian Thripidae and radiation in the genus *Odontothripella* Bagnall. In addition to 17 described species, there remain many undescribed in this genus, and these are associated mainly with the flowers of Fabaceae. In structure, these species are similar to the members of the mainly Palaearctic genus *Odontotrips* Amyot & Serville, all of which live only in Fabaceae flowers. But whether or not these two genera are related requires molecular evidence. The most closely related genus to these two appears to be *Megalurothrips* Bagnall, with about six species living in Fabaceae flowers between northern Australia and Africa.

The Phlaeothripidae includes in Australia one lineage that is equal, in its range of body size and structural diversity, to that of the entire family of 3500 species. This lineage is restricted to the genus *Acacia*, and the radiation is known to include at least 250 species (Crespi *et al.* 2004; Mound 2004b). The range of biologies amongst these species includes gall induction, domicile creation, kleptoparasitism, and opportunistic invasion of small spaces such as old galls or abandoned leaf mines, but all of the species are phytophagous on the leaf tissues of *Acacia* species. It has not yet proved possible to suggest a sister-group to this diverse lineage (Crespi *et al.* 2004), no species that might be considered similar having been found on any plants in habitats surrounding the *Acacia* hosts.

Absences from the Australian thrips fauna

The most obvious absence from the Australian thrips fauna concerns taxa related to the genus *Chirothrips* Haliday in the Thripidae. These thrips all breed within the flowers of Poaceae, and they are found widely across the world. However, despite Australia's rich flora of grasses, no members of this group have been found on the continent apart from species that are clearly introduced from Europe, Africa or the Americas (Mound 1996). The apparent absence of some other major taxa is likely to be related to the lack of suitable host plants. Thus, the rich fauna of leaf-feeding Phlaeothripinae that is found in south-east Asia is only weakly represented in Australia (Mound 2004a). A further apparent absence may also have an ecological basis. In most parts of the world, there is a considerable diversity of fungus-feeding species related to the genera *Hoplothrips* Amyot & Serville and *Hoplandrothrips* Hood, but the rarity with which these are found in Australia may be due to the aridity and a highly diverse fauna of ant and spider predators. However, as with so many other aspects of thrips biology, firm conclusions on the nature of the fauna are not yet possible, due to the lack of studies particu-

larly in the northern tropical zone. Current work (Mound & Postle 2004) suggests that there are many more similarities to be discovered between the thrips fauna of northern Australia and that of south-east Asia.

HEMIPTERA

The Hemiptera of Australia are highly diverse with all four suborders represented; Sternorrhyncha, Auchenorrhyncha, Coleorrhyncha and Heteroptera. Five major components of the Australian Hemiptera fauna can be identified in terms of origins: (1) relict Gondwanan; (2) derived Gondwanan; (3) Indo-Pacific; (4) recent Oriental/Pacific influences; and (5) post-European incursions. Relict elements occur in most groups, including clades within the Sternorrhyncha (Aphidoidea), Auchenorrhyncha (Cicadellidae: Ulopinae: Sagmatiini, Fulgoromorpha, especially Cixiidae), Coleorrhyncha (Peloridiidae) and the Heteroptera (Enicocephalomorpha: Aenictopecheidae, Nepomorpha: Corixidae: Diapropocorinae, Pentatomomorpha: Idiostoloidea). The most impressive are the two hairy cicadas (Tettigarctidae) that are endemic and have morphological features that link them to Mesozoic and Tertiary fossils of the Northern Hemisphere.

The suborder Coleorrhyncha is monobasic, represented by the eastern Gondwanan family Peloridiidae. This family is presently known from Chile, Patagonia, New Zealand, eastern Australia and New Caledonia (Evans 1981; Cassis & Gross 1995), and comprises 13 genera and 25 species. Numerous new taxa exist, with the greatest species richness occurring in the Australian region. Peloridiids are commonly found in mosses and liverworts associated with *Nothofagus* forests. Of particular interest is the endemic genus *Howeria* Evans, which has three species restricted to the montane forests of Lord Howe Island; about 10% of the world peloridiid fauna.

Most aphids in Australia are of recent origin, but four genera are endemic and at least three others contain endemic species all of which can be considered relicts. *Neophyllaphis* Takahashi is associated with ancient Gondwanan gymnosperms. *Ceriferella* Carver and Martyn is known from Epacridaceae. *Taiwanaphis* (*Sensoriaphis*) Carver & Martyn is associated with *Nothofagus* but has acquired new host plants where this genus no longer occurs. Two species of *Anomalaphis* Baker are found on Myrtaceae. The host of the monotypic genus *Meringosiphon* Carver is *Oxylobium* (Fabaceae). *Casimira* Eastop contains a single species on *Epilobium* (Onagraceae). One endemic species of *Aphis* L. occurs on *Acaena* (Rosaceae) and the other on *Platylobium* and *Daviesia* (Fabaceae).

Following separation of the Australian continent from Antarctica, increasing aridity has generated a wealth of distinctively Australian Hemiptera associated with the radiation of eucalypt species (Myrtaceae) that dominate the Australian tree flora or with the speciose shrub genus *Acacia* (Fabaceae). The aphids are a notable exception. A significant hemipteran fauna is also associated with the she-oaks (Casuarinaceae) such as clades of the mirid tribe Austromirini. The het-

eropteran fauna also exhibits a wide association with many plant families belonging to the rosid and asterid angiosperms (Cassis & Gross 2002). In addition, many clades within heteropter families are specialised grass-feeders (e.g. Lygaeoidea: Blissidae, Cryptorhamphidae and Pachygronthidae). The mirid genus *Setocoris* China & Carvalho has radiated with the insectivorous plant genus *Drosera* (Droseraceae).

Typical of the eucalypt fauna are the gregarious and ant-attended gum treehoppers (Eurymelinae), particularly the tribes Eurymelini and Pogonoscopini. Other Auchenorrhyncha groups in Australia that are entirely or primarily endemic and associated with eucalypts include the leafhopper tribes Thymbrini, Trocnadini, Reuplemmelini and Dikraneurini, the subfamilies Austroagalloidinae and Tartessinae, the tube spittlebugs (Machaerotidae: Enderleiniinae) and many genera of Membracidae (Day 1999). There are two major heteropter radiations associated with *Eucalyptus*: the coreid genus *Amorbus* Dallas (Steinbauer *et al.* 2002) and the pentatomid genus *Poecilometis* Dallas (Gross 1972). The Heteroptera show great affinity with *Acacia*, with numerous independent derivations, particularly in the mirid subfamilies Phylinae and Orthotylineae, and many pentatomomorph groups (e.g. Coreidae: Agriopocorinae).

Many species of eucalypts shed their bark annually with the decortivating bark remaining on the tree for most of the year. Leafhoppers of the subfamily Ledrinae are flattened to live in this protective habitat. In addition, eucalypt leaves typically hang vertically to reduce the impact of the midday sun and the Australian dikraneurines are flattened to fit closely against these vertical surfaces. One species, *Kahaono montana* Evans, produces silk shelters under which it lives in small groups (Fletcher & Kent 2002).

Australian cicadas utilise a wide variety of plant species from trees to grass and from rainforest to desert. Australia has a rich and varied cicada fauna that is almost entirely endemic, even at the generic level, and those species that extend beyond Australia only reach New Guinea. The Australian cicada fauna has been reviewed recently by Moulds (1990).

Similarly, the Australian leafhopper fauna is more than 90% endemic at the species level and, in those groups in which endemicity is lower, the species are usually only shared with New Guinea or New Zealand (Fletcher 2002). Tartessinae and Eurymelinae extend into New Guinea and both also have representation in New Caledonia (Evans 1966). A similar distribution is found in the cixiid planthopper tribe Gelastocephalini (Birgit Löcker, pers. comm. 2004).

The Australian Psylloidea represents more than 10% of the world fauna. Eighty-five percent of the described species occur on Myrtaceae and of these 90% are associated with *Eucalyptus* (Hollis 2002). Endemism is high, particularly in the predominantly lerp-forming Spondylaspininae that have undergone a remarkable radiation on their myrtaceous hosts, mainly the 'eucalypts'. The nymphs of many Spondylaspininae produce characteristic lerps that minimise desiccation in arid habitats. Psylloid lerps and nymphs are an important food resource for many bird species. The bell miner is thought to 'farm' psyllid nymphs by removing lerps as a food source but leaving the

nymphs that then construct new lerps. The birds aggressively exclude other insectivorous birds from their territory (Loyn *et al.* 1983).

The second most prominent component of the Australian psyllid fauna occurs in the Acizziinae that includes up to 200 undescribed species of *Acizzia* on *Acacia* (Yen 2002), on *Amyema* (Loranthaceae) (Taylor 1999), *Dodonaea* (Sapindaceae) and other host genera. The Triozidae is represented in Australia by six genera of which *Aacanthocnema* Tuthill & Taylor and *Schedotrioza* Tuthill & Taylor are endemic. Species of *Aacanthocnema* (and numerous undescribed related forms) are free-living on Casuarinaceae and those of *Schedotrioza* are univoltine gall-formers on eucalypts (Taylor 1990).

In the Australian Coccoidea just five families contain most of the species richness and display high endemism. These are the Margarodidae (margarodids), Coccidae (soft scales), Eriococcidae (felt scales), Pseudococcidae (mealybugs) and Diaspididae (armoured scales). The Eriococcidae and Margarodidae are of special interest due to the unique biology and morphology of many taxa. Several Australian eriococcid genera have radiated in association with members of the Myrtaceae, especially *Eucalyptus* s.l. Surprisingly, eriococcids rarely occur on *Acacia*. A distinctive feature of the Australian eriococcid fauna is the diversity of gall-inducing taxa and the complex and distinctive morphology of their galls (Gullan *et al.* 2004). Species of two of the largest genera, *Apiomorpha* Rübsaamen and *Opisthoscelis* Schrader, induce sexually dimorphic galls on eucalypt species, with galls of females also highly species-specific in shape. The largest galls, induced by females of *A. duplex* (Schrader), sometimes reach 20 cm in length and carry two apical leaf-life projections, perhaps functioning to camouflage the gall from cockatoos and parrots that relish the giant coccoid inside. In six other eriococcid genera, the male nymphs develop to adulthood feeding on nutritive tissue within their mother's gall, rather than inducing their own galls. In one of these genera, *Cystococcus* Fuller, the mother gives birth to her sons before her daughters (sexual dichronism) and, when adult, sons carry their tiny first-instar sisters out of the gall on their bodies (intersexual phoresy). Galls of *Cystococcus*, which may be up to 9 cm in diameter, grow only on bloodwood 'eucalypts' (*Corymbia*). They are called bloodwood apples or bush coconuts because the enclosed insects and the nutritive tissue are a favoured Aboriginal food.

Among Australian margarodids, four groups are especially distinctive elements of the fauna. One is the tribe Iceryini that includes the cottony-cushion scale, *Icerya purchasi* Maskell, a worldwide pest native to Australia. Another is the endemic tribe Monophlebini with large orange-coloured females that mostly feed on *Eucalyptus*. The third is the endemic genus *Callipappus* Guérin-Méneville in which adult females lay their eggs into a marsupium formed from their invaginated abdomen and adult males are known as 'bird-of-paradise flies' because of their beautiful purple-red colour and long white tail filaments (Gullan & Brookes 1998). The fourth noteworthy group feeds on native conifers (Araucariaceae) and includes

two gall-inducing species from Queensland (Gullan *et al.* 2004).

Australian planthoppers (Fulgoromorpha) display a wide range of plant associations and have clearly responded to changes in the Australian climate in many ways. Species of *Platybrachys* Stål (Eurybrachyidae) are usually found on eucalypt trunks while those of *Olonia* Stål are found on *Acacia*. Some Meenoplidae have associations with native Chenopodiaceae. Adaptation for inhabiting arid regions of the continent are found by Issidae, Caliscelidae, Flatidae and Acanaloniidae. These adaptations include development of a squat shape to minimise surface area and extreme modification of the forewings to form elytriform covers that wrap around the body, presumably to reduce water loss.

Of more recent tropical origins are the spittlebugs (Aphrophoridae) which are primarily in Pacific or Oriental genera (Liang & Fletcher 2003), the froghoppers (Cercopidae), the microleafhopper tribes Emposcini and Erythroneurini (that has numerous undescribed taxa in northern Australia), the planthopper families Delphacidae, Dictyopharidae, Ricaniidae and Lophopidae, many of which are grassfeeding, and most of the remaining leafhopper subfamilies.

Some tropical aphids of interest include *Schoutedenia* Rübsaamen, which produces sexual and parthenogenetic forms throughout the summer, *Cerataphis* Lichtenstein species on palms and orchids, and *Pseudoregma* Doncaster, a soldier-producing aphid. Work on New Zealand endemic Aphidinae has suggested that they form a clade basal to the rest of the world fauna (von Dohlen & Teulon 2003) and, despite the vast preponderance of north-temperate aphidines, it seems that their origins may be Australasian.

The suborder Heteroptera is represented in Australia by 64 families, 791 genera and 2088 species (Cassis & Gross 1995, 2002). The basal Enicocephalomorpha are depauperate in continental Australia. The plesiomorphic Dipsocoromorpha are represented by three of the five families, with the Schizopteridae comprising more than 35% of the world's described fauna (Hill 1984). The semiaquatic Gerromorpha are not particularly diverse in Australia, aside from the Veliidae that is represented by 67 species, mostly within the *Microvelia* Westwood complex (Andersen & Weir 2004). The truly aquatic Nepomorpha is represented in Australia by eight families, with only the Gelastocoridae (Cassis & Silveira 2001, 2002), Corixidae and Notonectidae (Andersen & Weir 2004) exhibiting significant species richness. The landbugs (Cimicomorpha and Pentatomomorpha) are the most diverse group of heteropterans globally and in Australia. The Cimicomorpha is represented by two major groups, the predacious group of superfamilies Reduvidioidea, Naboidae and Cimicoidea, and the primarily phytophagous Thaumastocoridae, Tingidae and Miridae. The Pentatomomorpha of Australia comprise all the described superfamilies with the Aradidae, Coreidae, Lygaeidae, Rhyparochromidae, Acanthosomatidae, Cydnidae and Pentatomidae having significant diversity in Australia.

Overall, the Australian Heteroptera exhibit moderate species richness (about 5% of global species richness) and very

high endemism. They are, however, significantly more diverse than currently indicated by described taxa. Existing collections, coupled with species taxonomic accumulation curves (Cassis & Gross 1995, 2002), suggest that the Australian true bug fauna is roughly 50% described. Not surprisingly, the fauna of true bugs for Australia is highly autochthonous, with about 50% of genera and 80% of species being endemic. In addition, Australia has four endemic families (Henicocoridae, Hyocephalidae, Aphyllidae and Lestoniidae) and numerous endemic tribes (e.g. Agriopocorini), or suprageneric groups that are chiefly Australian in nature.

The distribution patterns of the true bug fauna exhibit the following significant area relationships: (1) eastern component of Gondwana (e.g. Peloridiidae, Idiostolidae, Aradidae: Iso-derminae, Rhyarochromidae: Udeocorini), or more regional components (Australia + New Caledonia + New Caledonia) (e.g. Aradidae: Mezirinae, Rhyarochromidae: Targaremini); (2) Indo-Pacific (e.g. Miridae: Ecritotarsini); (3) Indo-Malayan (e.g. Pentatomidae: *Catacanthus* Spinola); and (4) Eastern Hemisphere (e.g. Corixidae: Micronectinae: *Micronecta* Kirkalby). Catalogues of the described species (Cassis & Gross 1995, 2002) suggest that the tropical heteropteran fauna is the most diverse, particularly for tropical north-eastern Queensland. However, recent collections indicate that the true bugs of temperate Australia, particularly in arid and semiarid regions, are hyperdiverse, and are supportive of the notion that, for some groups, diversity does not increase towards the tropics. Areas of endemism identified for vertebrates (Cracraft 1991) and higher plants (Crisp *et al.* 1995) are not informative for many true bug distributions, with many taxa found more broadly across temperate Australia (Cassis & Silveira 2001; Cassis & Moulds 2002) and eastern Australia (Cassis & Silveira 2002).

COLEOPTERA

The Australian beetle fauna includes about 23 000 described species in 3265 genera and 121 families (Yeates *et al.* 2003). These totals are all slightly less than those recently recorded for the Nearctic region (Arnett & Thomas 2001, 2002; Marske & Ivie 2003), a megadiverse area of comparable size but one with a very different geological history and a fauna that has been much more thoroughly sampled and described. While Marske and Ivie predicted that the total number of Nearctic beetle species might be as high as 28 000 species, an increase of 13.6%, similar estimates for poorly studied regions such as Australia are much higher. Prior to a recent generic revision by Chandler (2001), the Australian pselaphine Staphylinidae included 65 genera and 483 species; the fauna now consists of 163 genera and 578 described species, but the total number of species recognised by him was 1537 species. This represents a 150% increase in genera with an expected 200% increase in species. Yeates *et al.* (2003) predicted that the number of Australian beetle species might reach 80 000–100 000, and even higher estimates have been given by Hammond (1992, 1994) and Oberprieler (in press).

Australian endemic taxa include five families (Rhinorhipidae, Acanthocnemidae, Lamingtoniidae, Tasmosalpingidae and Myrabioliidae), five subfamilies (Ommatidae: Ommatinae, Heteroceridae: Elythomerinae, Corylophidae: Periptyctinae, Boridae: Synerctinae and Brentidae: Eurhynchinae), at least five tribes (Nitidulidae: Nitidulinae: Cychramptodini and Lawrenceosini, Tenebrionidae: Diaperinae: Ectychini, Chrysomelidae: Sagrinae: Carpophagini and Curculionidae: Cyclominae: Amycterini) and numerous genera. A few taxa, which are relatively common in most parts of the world, are either absent from Australia or represented by a small number of native species; these include geotrupine Geotrupidae (0), Dryopidae (0), Lampyridae (25 spp. in 4 genera, all Luciolinae), dasytine Melyridae (20 spp. misplaced in '*Dasytes*'), meligethine Nitidulidae (one species in *Pria* Stephens) Tetratomidae (0), pimeliine Tenebrionidae (7 spp. in 3 genera and 2 tribes), Meloidae (60 spp. in 3 genera, all Nemognathinae), bruchine Chrysomelidae (20 spp. in *Bruchidius* Schilsky) and lepturine Cerambycidae (0). Dominant groups that have radiated extensively during the latter part of the Tertiary in association with *Eucalyptus* and *Acacia* communities include the paussine, carenine and pseudomorphine Carabidae, chlamydopsine Histeridae, bolboceratine Geotrupidae, heteronychine, liparetrine and scitaline Melolonthinae and anoplognathine Rutelinae (Scarabaeidae), stigmoderine Buprestidae, metriorrhynchine Lycidae, malachiine Melyridae, adeliine and heleine Tenebrionidae, phoracanthine Cerambycidae, cryptocrephaline, eumolpine and chrysomeline Chrysomelidae, beline Belidae and cyclomine Curculionidae.

The Australian flora is often grouped into three or four major components based on age and origin (Crisp *et al.* 1999), and the continent has been divided into three (Torresian, Bassian and Eyrean) to as many as 17 (Allsopp 1995) faunal subregions. Matthews (2000) referred to four elements: (1) Indo-Malayan, composed of a relatively recent influx of northern species across an archipelago of Gondwanan fragments; (2) Austral Gondwanan or Southern, with sister taxa in southern South America, New Zealand and New Caledonia; (3) Tethyan or Pangean, an older assemblage with connections to India, the Mediterranean region, Africa and the New World; and (4) Amphitropical or Amphipolar, consisting of groups occurring in temperate regions of both Northern and Southern Hemispheres.

Included in the first group are genera such as *Tricondyla* L. (Carabidae: Cicindelinae), *Clidicus* Laporte (Scydmaenidae), *Priochirus* Sharp (Staphylinidae), *Niponius* Lewis (Histeridae), *Onthophagus* L. (Scarabaeidae: Scarabaeinae), *Haploscapanes* Arrow (Scarabaeidae: Dynastinae), *Chalcotaenia* Deyrolle (Buprestidae), *Galbites* Fleutiaux (Eucnemidae), *Melanotus* Eschscholtz (Elateridae), *Pteroptyx* Olivier (Lampyridae), *Encaustes* Lacordaire (Erotylidae), *Horia* F. (Meloidae), *Batocera* Castelnau (Cerambycidae), *Sagra* F. (Chrysomelidae), *Ithystenus* Pascoe (Brentidae), and *Mecopus* Schoenherr (Curculionidae), and groups such as the Melolonthini (Scarabaeidae: Melolonthinae), Coelometopinae (Tenebrionidae) and Galerucinae (Chrysomelidae).

Within the southern Gondwanan element, there are three main groups of Australian taxa: (1) those shared with southern South America; (2) those shared with New Zealand and/or New Caledonia but not South America; and (3) those found in both areas. The first includes the following genera: *Plagiotelem* Solier (Carabidae), *Neopelatops* Jeannel (Leiodidae), *Glypholoma* Jeannel (Staphylinidae), *Syndesus* Macleay and *Sphaenognathus* Buquet (Lucanidae), *Lemidia* Spinola (Cleridae), *Ericmodes* Reitter (Protocucujidae), *Rhopalobrachium* Boheman (Phloeostichidae), *Hobartius* Sen Gupta & Crowson (Hobartiidae) and *Archeophthora* Kaszab (Tenebrionidae), the following generic pairs: *Ptomaphila* Hope – *Oxelytrum* Gistel (Silphidae), *Austrorhysus* Steel – *Megarhroides* Steel (Staphylinidae), *Cacostomus* Newman – *Casignetis* Macleay (Lucanidae), *Sclerocyphon* Blackburn – *Tychepephus* Waterhouse (Psephenidae), *Egolia* Erichson – *Acalanthis* Erichson (Trogossitidae), and some family group taxa like Ommatinae (Ommatidae), Eunemadina (Leiodidae), Aclopininae (Scarabaeidae), Anoplognathini (Scarabaeidae: Rutelinae), Stigmoderini (Buprestidae), Perimyopidae, Palophaginae (Megalopodidae) and Caridae.

Taxa shared by Australia and New Zealand and/or New Caledonia include the genera *Hyphalus* Britton (Limnichidae), *Phycosecis* Pascoe (Phycosecidae) and *Dryocora* Pascoe (Prostomidae), the generic pairs *Pamborus* L. – *Maoripamborus* Brookes (Carabidae), *Anepius* Blackburn – *Eupsorus* Broun (Staphylinidae), *Trichelodes* Carter – *Hexanodes* Blair (Dermestidae), and *Tanylypa* Pascoe – *Zolodinus* Blanchard (Tenebrionidae), plus the tenebrionid tribes Choerodini, Heleini and Titaenini. *Hyphalus*, comprised of intertidal species, has a broader distribution, including the Aldabra and the Ryukyu Archipelago (Hernando & Ribera 2000), while the littoral genus *Phycosecis* has also been seen from Vanuatu.

Taxa occurring in all three southern regions include the genera *Metacoroneolabium* Steel and *Microsilpha* Broun (Staphylinidae), *Sphaerotherax* Endrödy-Younga (Clambidae), *Rhipicera* L. (Rhipiceridae), *Hydora* (Elmidae), *Nothoderodontus* Crowson (Derodontidae), *Archeocrypticus* Kaszab (Archeocrypticidae) and *Lagrioida* Fairmaire & Germain (Anthicidae) and higher taxa such as Migadopini and Zolini (Carabidae), Lampriminae (Lucanidae), Rentoniinae (Trogossitidae), Priasilphidae, Cavognathidae, Ulodidae, Adeliini (Tenebrionidae), Spilopyrinae (Chrysomelidae), Belinae (Belidae) and Eugnomini (Curculionidae). The so-called Amphipolar or Amphitropical element includes taxa with a similar southern pattern but also with relatives in the Northern Hemisphere. Examples include the Broscini (Carabidae), Scirtidae, Nicaginae (Lucanidae), Byrrhidae and Nemonychidae.

Matthews (2000) characterised the members of his Tethyan element as: (1) inhabiting deserts and coastal dunes; (2) lacking forest-inhabiting relatives; (3) having no areas of endemism east of the Great Dividing Range; and (4) lacking relatives in southern South America; included were the tenebrionid tribes Belopini, Cnemeplatiini, Vacronini, Hyociini, Ectychini and Trachescelini. Possible examples from other families are *Oxyptus* Newton (Staphylinidae: Oxytelinae) a Western Australian genus whose sister taxon (*Euphantias*

Fairmaire & Laboulbène) occurs in the western Palearctic and Brazil (Newton 1985), and *Sphaericus* Wollaston, with two species from North-west Cape and Barrow Island, Western Australia, and the remainder endemic to the Mediterranean and Macaronesian regions (Bellés 1998). A link between Australia and southern Africa may be seen in the pollenivorous Boganiidae, with the Australian and South African sister taxa *Paracucujus* Sen Gupta & Crowson and *Metacucujus* Endrödy-Younga & Crowson associated with cycads, and *Boganium* Sen Gupta & Crowson and *Afroboganium* Endrödy-Younga & Crowson associated with angiosperms.

Taxa that do not fit well into the above groups are members of old Gondwanan or Pangean lineages with relatives in Africa or tropical America but with at least some centres of diversity in eastern rainforest patches. The most obvious example involves dung beetles in the tribes Canthonini and Dichotomini, whose closest relatives appear to be Afrotropical, with *Lepanus* Balthazar, *Demarziella* Balthazar and *Amphistomus* van Lansberge possible sister taxa to the Madagascar *Arachnodes* Westwood and the African *Pedaria* Castelnau and *Anachalcos* Hope, respectively (Davis *et al.* 2002; Philips *et al.* 2004). Basal scarabaeines are widely distributed in Australia, but several lineages have radiated in montane rainforests along the east coast and in New Guinea. Insights into the evolution and historical biogeography of these and other rainforest Coleoptera have been made possible by intensive studies conducted in the Australian Wet Tropics, an area of high regional endemism between Townsville and Cooktown (Yeates *et al.* 2002; Bouchard *et al.* in press). Cladistic and biogeographical studies on the scarabaeinae genera *Aptenocanthon* Matthews, *Temnoplectron* Westwood and *Coptodactyla* Burmeister (Reid 2000a; Reid & Storey 2000; Storey & Monteith 2000; Bell *et al.* 2004) and coelometopine Tenebrionidae (Bouchard & Yeates 2001) have done much to clarify areas of endemism in this region.

General references relevant to this section are: Alonso-Zarazaga and Lyal (1999); Britton (1957, 1978, 1987); Cassis and Weir (1992); Gardner (1989); Kolibáč (1998); Lawrence and Britton (1994); Newton (1985, 1998); Reid (2000b); O'Keefe and Monteith (2001).

DIPTERA

The Australian continent is home to a species-rich and diverse component of the world fly fauna that is largely endemic at species level (Evenhuis 1989 and website for checklist of described species; Colless & McAlpine 1991 and Bugledich 1999 for catalogue of Diptera: 'Nematocera'), and displays a wide range of anatomical and biological specialisations (Merritt *et al.* 2003). Of a total Australian fly fauna estimated at 30 000 species, just over 6400 have been described (Yeates *et al.* 2003) in 104 families. Estimating the total size of the fauna is difficult given the size of the continent. Most collecting and sampling has been undertaken along the eastern coast and ranges where moist forests, especially rainforests, harbour a rich fauna. By contrast, the arid interior has been more

poorly surveyed, but recent studies suggest that some arid adapted families have undergone extensive radiation. By comparison, the described Nearctic fauna is estimated at 20 000 species (Thompson 2002), while the European fauna is estimated to have 17 000 described species (Pape *et al.* 2000).

The Australian fauna includes most major fly families, and notable absences include the Ptychopteridae, Vermileonidae (worm lions), the Diopsidae (stalk-eyed flies), the acalyptrate family Opomyzidae, and the Scathophagidae. Only one dipteran family is entirely endemic to Australia, the Ironomyiidae, a lower cyclorrhaphan family containing a handful of species restricted to south-eastern Australia (McAlpine in press) and also with species known from Cretaceous amber fossils in North America. Two other families are largely restricted to Australia. The recently described Axiniidae (Colless 1994) is found in Australia and New Guinea and are probably related to Tachinidae. Fergusoninidae are also largely restricted to Australia and form galls on *Eucllyptus* and other Myrtaceae. The fly larvae have an intricate symbiotic relationship with nematodes of the genus *Fergusobia* Currie, where nematodes travel between host plants in the bodies of the flies (Giblin-Davis *et al.* 2001).

Current knowledge suggests that the largest fly families in Australia are in the Tipulidae (*s.l.*), Mycetophilidae (*s.l.*), Sciaridae, Cecidomyiidae, Chironomidae, Asilidae, Bombyliidae, Therevidae, Empididae, Dolichopodidae, Phoridae, Lauxaniidae, Platystomatidae, Chloropidae, Muscidae, and Tachinidae. Some of these families may have more than 1000 species in Australia, and most are also diverse in other regions of the world. A recent estimate of the Australian tachinid fauna suggests there may be 3500–4000 species based on data from intensive surveys in central Queensland (O'Hara *et al.* 2004). The Australian fauna is also unusually rich in Pyrgotidae, although few species have been described, and Coelopidae (McAlpine 1991). By comparison, some families that are species-rich in other continents, such as the Anisopodidae and Syrphidae, are depauperate in Australia.

As a result of recent revisionary work, some taxa are now shown to be highly diverse. For example, the dolichopodid subfamily Sciapodinae has 253 Australian species, compared with 45 previously valid species (Bickel 1994). The Bombyliidae and Therevidae have come under intense scrutiny recently (e.g. Yeates 1991; Yeates & Lambkin 1998; Winterton *et al.* 1999, 2000; Lambkin *et al.* 2003), including extensive fieldwork in remote areas of the continent. This has revealed a surprisingly diverse fauna in semiarid Australia, with high alpha and beta diversity unexpected in these relatively uniform landscapes. These faunas include a number of large, apparently recent radiations consisting of hundreds of species each, and extensive cryptic diversity at species level masked behind a few old species names.

Our knowledge of species is relatively complete in a number of families, especially those with economic or evolutionary importance, such as Ceratopogonidae, Culicidae, Tabanidae, Drosophilidae, Tephritidae, Calliphoridae, and Platystomatidae. By contrast, many Australian families are 'orphan taxa', in that they have been neglected or are without

current taxonomic 'guardians.' Quite simply, keys do not exist and old descriptions are unusable, meaning that some of the most abundant taxa cannot be identified much beyond family level. For example, the Sciaridae can be extraordinarily abundant in Australian forests. The larvae feed variously on detritus, rotten wood, fungi, and are important in nutrient cycles. In the Australian fauna, some 65 species have been described, mostly by Frederick Skuse between 1888 and 1890, who placed them in the then vaguely defined type genus, *Sciara* Meigen. There has been little work since and there are no keys to the Australian fauna. By comparison, some 728 species are described for the Palaearctic region, keys are available, and there are several active researchers, who estimate the Palaearctic fauna to be 1100 species. In the Australian fauna the following major families are orphaned: Mycetophilidae, Sciaridae, Cecidomyiidae, Phoridae, Chloropidae, Muscidae and Tachinidae.

Biogeography

Many families, subfamilies and genera found in Australia have disjunct distributions around the world, suggesting they are either ancient relicts or components of the Gondwanan biota. The Australian genera of Thaumaleidae are all found in South America and New Zealand. The Perissomatidae are winter swarming relatives of the bibionoids, and are also only found in Australia and South America. The Pelecorhynchidae occur in Australia and South America, with a single genus in North America. The Austroleptidae were recently removed from the Rhagionidae (Stuckenberg 2001) and are a small family endemic to temperate Australia and South America. The Apioceridae are most species rich in Australia and western North America, but a few species of the only genus *Apiocera* Westwood are known from South Africa and southern South America; members of the closely related megasceline Mydidae have a similar distribution (Yeates & Irwin 1996). The fauna of Australian Nemestrinidae is dominated by *Trichophthalma* Westwood, also found in South America. The Apsilocephalidae is a small family recently removed from the Therevidae (Nagatomi *et al.* 1991), with species in western North America and Australia. The Xylophagidae have a relictual distribution with a few species on each continent, and with the enigmatic *Exeretonevra* Macquart in Australia (Palmer & Yeates 2000). Lomatiine Bombyliidae, extremely diverse in Australia with large genera such as *Comptosia* Macquart and *Aleucosia* Edwards, have close relatives in South America and Africa (Yeates 1990). The empidid subfamily Ceratomerinae displays a classical Gondwanan distribution and occurs on river rocks in southern rainforests (Sinclair 2003). While extant species of the primitive cyclorrhaphan Sciadoceridae are known only from Australia, New Zealand and Chile, fossil taxa occur in Baltic amber.

Some Australian tropical taxa (e.g. Dolichopodidae, Drosophilidae) display strong links with the Oriental-Papuan fauna, and many are relatively recent arrivals, having reached Australia as the continental plate moved progressively north. These northern elements often have penetrated southward in

Australia along the eastern ranges, but mostly in association with tropical and subtropical rainforests.

Ecological and economic importance

Flies are ubiquitous and often abundant in Australian terrestrial ecosystems, and perform such important ecological functions as nutrient recycling, predation, pollination, and parasitoidism of other insects. Some are a significant nuisance, such as the bush fly (*Musca vetustissima* Walker), and various species of blood sucking mosquitoes, sandflies and blackflies (Culicidae, Ceratopogonidae: mostly *Culicoides* L.; and Simuliidae: mostly *Simulium* L., respectively). Flies outrank other orders in terms of medical and veterinary significance, being responsible for the transmission of a wide variety of pathogens in humans and animals. These diseases are mostly absent from Australia, with exceptions such as dengue (transmitted by *Aedes aegypti* L.) and various encephalitides (transmitted by several species). Malaria has been eradicated from Australia, but was transmitted by species of the *Anopheles farauti* Laveran complex. Phlebotomine sandflies (Psychodidae) are known from Australia, but do not appear to transmit diseases of humans or domestic animals on the continent, as they do in other parts of the world. The sheep blowfly (*Lucilia cuprina* Wiedemann: Calliphoridae) causes extensive economic losses in sheep when the larvae infest the host tissues causing myiasis. Probably the most important pests of Australian horticulture belong to the Tephritidae, most notably the Queensland fruit fly (*Bactrocera tryoni* Froggatt) in the east, and the introduced Mediterranean fruit fly (*Ceratitis capitata* Wiedemann) in Western Australia. Mosquitoes were used as vectors of myxoma virus, which dramatically reduced Australia's rabbit plague (Fenner & Ratcliffe 1965), and some leaf-mining Agromyzidae have been introduced for biological control of weeds such as lantana. Of quarantine concern are pest flies that are currently absent from Australia such as the Old World screw worm fly (*Chrysomya bezziana* Villeneuve: Calliphoridae), and various invasive fruit flies in south-east Asia of the genus *Bactrocera* Macquart such as the oriental fruit fly *B. dorsalis* Hendel. A close relative, *B. papayae* Drew & Hancock, was recently eradicated from north Queensland after invading from the north (Cantrell *et al.* 2002).

Morphology and behaviour

Some Australian fly taxa have unusual behaviours, morphology or life histories that are worthy of note. Larval *Arachnocampa* Edwards (Keroplastidae) are known as 'glow worms' and have light producing organs associated with the malpighian tubules. The larvae can be found in caves and rainforests along the east coast, where they produce light at night and attract insect prey to sticky threads that they spin. *Planarivora* Hickman (Mycetophilidae) larvae parasitise land planarians (Hickman 1965). Male flies of the genus *Mycomya* Rondani (Mycetophilidae) and some Sciaridae and Cecidomyiidae pollinate ground orchids. Evidence for *Mycomya* suggests the pollination strategy is probably sexual deception, much better known in wasp-orchid systems (Hamilton *et al.* 2002). Larvae

of the endemic, wingless micropezid fly *Badisis* McAlpine live in pitchers of the endemic western Australian pitcher plant *Cephalotus* (Yeates 1992). They can survive the plant digestive enzymes, and feed on the insect prey of the pitcher, much as other insects do in association with pitcher forming carnivorous plants in Queensland and other parts of the world. Male *Achias* F. (Platystomatidae) may have eyes on stalks similar to Diopsidae (McAlpine 1994). Males of the Australasian fruit fly genus *Phyrtalmia* Gerstaecker (Tephritidae) defend oviposition sites on fallen logs in rainforest from conspecific males using bizarre antler-like head projections (Dodson 1997). Adult upside-down flies of the genus *Neurochaeta* McAlpine (Neurochaetidae) rest with their head facing downwards on native lilly stems in rainforest. The adult morphology is highly modified, and they can run as quickly backwards as forwards (McAlpine 1988). Larvae of *Batrachomyia* Krefft (Chloropidae) live beneath the skin of frogs, feeding on blood. Hill-topping is also a common phenomenon in Australia, with males of species in the Bombyliidae, Pipunculidae and Tachinidae commonly found aggregating on prominent hilltops (e.g. Yeates & Dodson 1990; Skevington 2001).

Future directions

The taxonomically orphaned groups mentioned above are in greatest need of systematic research. Another important challenge is to make identification of the Australian fly fauna more accessible for non-taxonomists. For example, Chironomidae are important indicators of the health of aquatic ecosystems, and an identification guide to the larvae is now available on the Web (Cranston 2000). Currently being developed is a computer-based interactive key, image gallery, and information guide to Australian fly families (Hamilton *et al.* 2004). The evolutionary relationships of flies have been reviewed recently (Yeates & Wiegmann 1999), and are the subject of ongoing investigation.

LEPIDOPTERA

Australia supports a typical continental fauna of Lepidoptera with some 81 families represented; while 43 mostly small families are absent or undiscovered. The recent checklist of Australian Lepidoptera catalogues 10 583 valid species, about half the estimated fauna (Nielsen *et al.* 1996) that approximates in richness with the 20 000+ species of vascular plants. The proportional contribution of the higher taxa broadly reflects the global profile (Kristensen 2003), with a few exceptions: there are relatively more Gelechioidea due to the extraordinary dominance of Oecophorinae (5500 spp.), more Geometridae relative to Noctuidae (especially in arboreal groups) and fewer butterflies.

Australian moths span the full size range of the order, from the nepticulid *Stigmella* Schrank to the saturniid *Coscinocera* Butler and massive *Endoxyla* Herrich-Schäffer cossids. However, Australia is notably rich in micromoths whose concealed feeding habits and small size may be an advantage in the

generally dry, low nutrient and unpredictable environment. The Lepidoptera of Australia have been moulded by a history of long isolation in the Tertiary and exposure to a unique and largely sclerophyllous flora. The following account broadly outlines this fauna, draws attention to some significant taxa and provides an overview of evolutionary trends in relation to the environment. Comprehensive views of the fauna are those of Common (1990) and Nielsen and Common (1991), and the butterflies are recently monographed by Braby (2000). Family classification follows appendix 1 in Kristensen (2003).

Noteworthy taxa and endemics

Australia is rich in ancient taxa such as Micropterigidae (*Sabatinca* Walker) and Agathiphagidae, the two most basal members of the order (Kristensen 1999; Wiegmann *et al.* 2002), and Lophocoronidae (*Lophocorona* Common, 6 species in dry woodland). At least 126 species of Hepialidae *s.str.* are present, about 20% of the world fauna, while the primitive Bassian genus *Fraus* Walker comprises 25 species. Most hepialids have soil-dwelling larvae but the attractive *Aenetus* Herrich-Schäffer (15 species) and monotypic *Zelotypia* Scott bore in tree trunks. Australia also has the largest regional diversity of Incurvariidae (100+ species in 5 genera) (Nielsen *et al.* 1996), detritivorous Erechthiinae (50+ species) (Robinson & Nielsen 1993) and Xyloryctidae (250 species in 46 genera).

Most notable of many intrafamily radiations is the estimated 5000 species of Oecophorinae, comprising 20% of Australia's moth fauna (Common 1994). They are largely associated with Myrtaceae in the southern half of the continent and consume dead leaves of low nutritive value, although *Barea* Walker (94+ species) is associated with decaying wood (Common 2000). In the Tortricidae, tribe Archipini (e.g. *Merophyas* Common, *Epiphyas* Turner) is a diverse and largely Bassian group associated with many plant families (McQuillan 1992), while the *Arotrophora* group (e.g. *Arotrophora* Meyrick, *Peraglyphis* Common and *Syllomatia* Common) is restricted to Proteaceae.

Australia has a high percentage of endemic taxa, approaching 100% at species level in many families. Endemic, or largely endemic, higher taxa include the Lophocoronidae (Common 1973) and the hepialoid families Palaeosetidae (2 species) and monobasic Anomosetidae. Pectinivalvinae (2 genera), the sister group to the worldwide Nepticulinae, are restricted to Australia. The endemic Hypertrophidae (11 genera) are associated with Myrtaceae while zygaenoid Cyclotornidae are predatory on leafhoppers and ant brood. Carthaeidae, Anthelidae and Eupterotidae: Panacelinae are bombycoid endemics. The Australian Oenosandridae (4 genera, 8 species) display the most 'primitive' type of noctuid tympanal organ (Minet & Surlykke 2003).

Endemism at genus level ranges from zero in Immidae to almost complete in Oecophoridae. All *Synemon* Doubleday (Castniidae, 45 species) are endemic. Tineidae are intermediate with 12 of 44 genera Australian (Robinson & Nielsen 1993). Although Australia is relatively poor in butterflies,

almost half of the genera are endemic (96 of 207), while the hesperiid subfamily Trapezitinae (about 70 species) is characteristic of the region (de Jong 2003). There is relatively poor representation of Sesiidae (19 species, Kallies 2001), Eriocottidae (1 species), Coleophoridae (11 species) and Saturniidae (14 species), and only one endemic genus of Bombycidae.

Absences

Of the three most basal clades only the Heterobathmioidea is absent from Australia, although a potential host (deciduous *Nothofagus*) occurs in Tasmania. Also lacking are Eriocraniidae (basal in the clade Glossata), the exoporian Mnesarchaeidae and two of the five families of Hepialoidea, viz. Prototheoridae and Neotheoridae. Of the four superfamilies of monotrystian Heteroneura (10 families), only Tischerioidea is missing. The incurvarioid Prodoxidae, Cecidosidae (South Africa, South America, New Zealand) and Crinopterygidae are also absent, although a cecidosid is recently reported from New Zealand (Hoare & Dugdale 2003). Australia is also devoid of the primitive Acanthopteroctidae and Neopseustidae, a few yponomeutoid groups, seven small zygaenoid families and several bombycoid families such as Brahmaeidae and Lemoniidae.

Associations with the flora

Patterns of diversity in the highly distinctive Australian flora are variously reflected in the Lepidoptera (Common 1990). Two megadiverse plant genera, *Eucalyptus* and allies (800+ species) and *Acacia* (950+ species), dominate the vegetation continent-wide. At this scale, the most speciose plant families (e.g. Myrtaceae, Mimosaceae, Poaceae) display rich moth associations; at more local scales, climate, site productivity and vegetation community type modify the patterns strongly. For example, south-western Australia, a global floristic hotspot, is not correspondingly enriched with Lepidoptera. New Caledonia is similar, suggesting substrate poverty is not conducive to high moth diversity (Holloway 1993).

Eucalyptus forms extensive forests and woodlands with a monogeneric, flammable, nutrient-poor canopy, usually infested with ants. Eucalypt pollen first appears in the Eocene and today *Eucalyptus* supports at least 21 families and several hundred lepidopteran species on living foliage, and several thousand species on dead leaves (Common 1990). The incurvarioid *Perthida* Common, nepticulid *Pectinivalva* Scoble, gelechiid *Ardozyga* Lower (200+ species), various oecophorid genera and the limacodid *Doratifera* Duncan are typical micromoths of the canopy, while a large range of macromoths including Geometridae, Anthelidae, Lasiocampidae, Notodontidae and the nolid *Uraba lugens* Walker can be common.

Australian phyllokinous *Acacia* are recently diversified but related to the mimosaceae tribe Ingeae rather than acacias elsewhere (Miller & Bayer 2001). At least 18 families, including Cosmopterigidae (*Macrobathra* Meyrick 100+ spp.), various catocaline noctuids and numerous Geometridae (Ennominae and Geometrinae) rely on *Acacia*.

Native grasslands (e.g. *Triodia*, *Astrebla*, *Austrodanthonia*, *Poa*), expanding with seasonal aridity since the Miocene, cover 30% of the continent and support a characteristic fauna. At least 11 families utilise Poaceae as food. Noteworthy are some pyraloid groups, especially the phycitine Anerastiini (Horak 2003) and *Hednota* Meyrick, the largest genus (60+ species) of the Crambidae. Hadenine and amphipyrene Noctuidae include many grass dependent taxa of which *Proteuxoa* Hampson (77+ species) is pre-eminent in species, while *Persectania* Hampson and *Mythimna* Ochseneheimer include familiar pests. Hepialids (*Fraus*, *Oncopera* Walker, *Oxycanus* Walker) can also achieve pest status in pastures, while the psychid *Lomera* Walker is significant in alpine grasslands. Also associated with grass (and other monocots) are some *Synemon* (Castniidae 45 species) and anthelids such as *Pterolocera* Walker (8+ species) and certain *Anthela* Walker. Nine genera of Satyrinae feed on grasses along with many Hesperiiidae, Glyphipterygidae and Elachistidae.

Plant families with a long fossil record may host distinctive endemic moths including some with Gondwanan affinities. Proteaceae supports about 40 moth genera, such as the palaephatid *Ptysoptera* Turner, the tortricine *Arotrophora* group, the geometrid *Oenochroma* Guenée and its allies, *Carthaea* Walker, and the giant sphingid *Coequosa* Walker. Monimiaceae hosts *Graphium* Scopoli, *Euschemon* Doubleday, *Aenetus*, *Panacula* Walker, and *Opodiphthera* Wallengren. Winteraceae supports the geometrid *Archephanes* Turner and an archipine tortricid.

Nothofagus and the austral conifers are now largely relict and confined to mesic refuges, but insights into their insect associates might be gleaned from their limited contemporary fauna. *Nothofagus* has a *Stigmella* and the roeslerstammiid *Chalcoteuches* Turner. *Agathiphaga* Dumbleton is on *Agathis*; among geometrids, *Milionia* Walker (2 species) is also on Araucariaceae, while *Acalyphes* Turner (2 species) and the plutellid *Chrysorthenches* Dugdale (2 species) feed on Podocarpaceae and Cupressaceae.

The pectinivalvine *Roscidotoga* (3 species) mines foliage of the austral rainforest families Cunoniaceae, Eucryphiaceae and Elaeocarpaceae (Hoare 2000). The butterflies *Delias* (8 species) and *Ogyris* Angas (10 of 13 species) exploit Loranthaceae. Casuarinaceae feeders include Xyloryctidae, *Rhynchopsota* Lower (Geometridae), Anthelidae: Munychryiinae, Lasiocampidae and Noctuidae. The driest and most saline landscapes have limited Lepidoptera and the highly apparent Chenopodiaceae seem under-exploited.

Leaf litter is widely exploited by moth larvae in Australia (Common 1990) as well as in New Zealand and New Caledonia (Dugdale 1996a). Seven families exploit the unusually persistent dead leaves of eucalypts, most notably Oecophoridae but the tortricine tribe Epitymbiini (100+ species) is also significant. Marsupial droppings are eaten by the lithosine *Prinasura* Hampson (Common 1990) and the oecophorid *Telanepsia* Turner (Common & Horak 1994).

Australia may contain the highest proportion of obligately ant-associated lycaenid butterflies of any zoogeographical

region (about 40%, Eastwood & Fraser 1999), mostly involving the ecologically dominant Dolichoderinae. Ant nests are inhabited by the scavenging psychids *Iphiherga* and *Ardios-teres* while some Cyclotornidae and Lycaenidae feed on ant brood.

Distributions

Present day distributions may largely reflect climate changes since the late Pleistocene imposed on earlier patterns resulting from gradual drying of the continent since the Tertiary and the retreat of mesic adapted groups to the continental margins in the south and east. Some of the most remarkable disjunctions (e.g. the *Hypsidia* group of Drepanidae (Scoble & Edwards 1988) and pyrgine hesperiids) between the mesic south-western corner and the tropical north-east of the continent, may hint at the early Tertiary rainforests which spanned Australia prior to the Miocene.

The large size (7.7 million km²) and wide latitudinal range of Australia encompass a wide variety of environments summarised in three broad biomes: Bassian (southern, winter rainfall), Torresian (northern, summer rainfall) and Eyrean (centre, arid), or 80 bioregions. There are very limited areas above 1000 m and <0.1% of Australia carries winter snow. Annual rainfall ranges almost fifty-fold, from 100 mm to 4600 mm. The unpredictable climate and high variability of rainfall associated with the El Niño-Southern Oscillation strongly influence the size of insect populations. Windborne migration may shift populations into agricultural regions, and low winter temperatures in the south limit the distribution of tropical species. Species with the widest distribution often tend to be migratory or nomadic, e.g. *Agrotis infusa* (Boisduval), *Hippotion scrofa* (Boisduval) (Gregg et al. 1993).

Regular summer drought in the southern half promotes pupal aestivation in many Hepialidae, Geometridae and Noctuidae whose autumn emergence is synchronised by rainfall or temperature. Migratory noctuids, including species of *Mythimna*, *Persectania*, *Dasygaster* Guenée, *Helicoverpa* Hardwick, and *Agrotis* Ochseneheimer, regularly exploit ephemeral grasslands and herbfields.

Some taxa are distributed across several southern hemisphere landmasses and are generally considered Gondwanan in origin. Examples include the 'Australian' *Sabatinca* s.l. (Australia, New Caledonia, New Zealand) in the Micropterigidae (Gibbs 1983), Palaephatidae (2 genera) (Australia, South America), Castniidae, and the geometrid tribe Trichopterygini (south-east Asia, Australia, New Zealand, South America). Few of the butterflies appear to be Gondwanan, with *Cressida* Swainson (related to the neotropical *Euryades* Felder) perhaps the best candidate (de Jong 2003), but almost no well-resolved phylogenies are available.

Biotic interchange with Asia since the late Tertiary has embellished the autochthonous fauna, notably in Olethreutinae, Pyralidae, Geometrinae, bombycoids and catocaline noctuids among others. The noctuid fauna of the dry tropics includes many widespread Asian taxa (ED Edwards pers. comm. 2004). The majority of butterfly genera seem related

to Oriental taxa (de Jong 2003), and it may be noteworthy that very few butterflies (a few polyphagous Lycaenidae) feed on *Eucalyptus* or Proteaceae (Braby 2000).

Australia and New Zealand have been separated by the Tasman Sea for about 80 million years. Vicariance is seen in the arctiid *Phaos* Walker (McQuillan 1986) with possible additional connections to arctiines in austral South America, some Scopariinae (Munroe & Solis 1999), the plutellid *Proditrix* Dugdale, the tortricine *Ericodesma* Dugdale, the larentiine *Austrocidaria* Dugdale and the choreutid *Asterivora* Dugdale in the highlands. *Chrysoteuches* Dugdale (Plutellidae) on conifers is presumed to predate spreading of the Tasman Sea floor (Dugdale 1996b). Some migrant species reach Macquarie Island (55°S), Norfolk Island and New Zealand.

Tasmania has been an intermittent island and mesic refuge since the Miocene, separated from the mainland by the 150 km wide Bass Strait. Its 68 000 km² of mountainous terrain, maritime climate and strong longitudinal rainfall gradient result in very diverse habitats from temperate rainforest to heathland. Novelty in the fauna increases with elevation. Noteworthy are alpine taxa such as the symmocine *Nemotyla* Nielsen, McQuillan & Common, the 'archiearine' *Dirce* Prout, and diversification in the geometrid tribe Xanthorhoini. Some endemic plant genera have unusual moths, e.g. *Athrotaxivora* McQuillan on *Athrotaxis*; there is an endemic *Sabatinca* and butterfly genus *Nesoxenica* Waterhouse & Lyell. The lowlands have an attenuation of the mainland fauna, e.g. a single Saturniidae and Papilionidae, and no Lophocoronidae, Castniidae, Brachodidae, Cyclotornidae, native Pieridae or Sesiidae. Sister species are commonly separated by Bass Strait (*Aenetus*, *Argyninma* Butler) or by elevation (*Phaos*, *Plesanemma* McQuillan). Clinal variation in phenotype is unusually well developed in some Tasmanian butterflies.

Despite recent interest in the higher-level classification of the Australian fauna there is much more work required to describe the fauna and its biology. Less than 10% of the known nepticulid fauna of several hundred species is described and about two-thirds of the oecophorids are unnamed. Australian Lepidoptera are increasingly threatened with local or complete extinction from landuse change especially in the south and east, but conservation planning to secure their future is only just beginning.

HYMENOPTERA

The Hymenoptera are more biologically diverse than any other hexapod order (Naumann 1991) and are renowned for their diversity of predators and parasitoids that develop at the expense of other arthropods, pollinating species, gall-forming taxa, and highly evolved social groups. Among other features, they are characterised by having a haplo-diploid sex determining mechanism (arrhenotokous parthenogenesis) and a modified ovipositor that is used as a specialised egg-laying device and/or as a hypodermic system for the injection of venom (Naumann 1991).

Like the other megadiverse orders of insects, the Australian hymenopteran fauna is an incredibly rich one containing a very high proportion of endemic species and genera, and numerous unique elements at higher levels. However, after several decades of study, the fauna still remains poorly known, although intensive surveys of the more remote parts of the continent, coupled with broad-scale revisionary studies and phylogenetic work on the order as a whole over the last 20 years, provide a framework for examining the make-up of the Australian Hymenoptera, its origins, and importance biogeographically in a world context.

Conservatively, the Hymenoptera fauna for the continent has been estimated at about 44 000 species, of which about 8000 have been described, more-or-less evenly divided between the aculeate wasps (Chrysoidea, Vespoidea, Apoidea) and the parasitoid superfamilies. However, the huge species diversity within the order exists disproportionately among the parasitoid groups; it is just that these have been vastly understudied, largely because of the tiny size of many groups (0.5–2 mm). In reality, the true size of the Australian fauna is difficult if not impossible to estimate with any accuracy given the current state of knowledge, although it is worth noting that several studies of other regions of the world have demonstrated a species richness for the Hymenoptera close to or in excess of the Coleoptera (La Salle & Gauld 1993).

Symphytans

The Symphyta or 'sawflies' as they are commonly called, are a predominantly phytophagous group with often large, 'lepidopteran-like' larvae. Previously treated as a suborder, this group is demonstrably paraphyletic and represents a basal grade of separate lineages (Vilhelmsen 2001). In Australia, the symphytans represent a missing component of the hymenopteran fauna compared with the Northern Hemisphere. Several families and superfamilies are absent from the continent, while the Siricidae is represented only by the introduced *Sirex noctilio* F. a pest of *Pinus* in southern Australia. The Tenthredinidae and Argidae, with about 5000 and 800 species, respectively, worldwide, are represented in Australia by about 20 species combined, including the introduced pest *Caliroa cerasi* L. The Xiphidriidae are strongly endemic and have putative Gondwanan connections, but again are represented by few species (20 species, mostly undescribed). The Orussidae, which are parasitic on wood-boring coleopteran larvae, have recently been examined in detail (Vilhelmsen 2004) and comprise 12 species. Only the Pergidae are well represented in the fauna and account for about 80%+ of the estimated 250–300 species of Australian sawflies. This family is most diverse in South America and Australia, and undoubtedly has Gondwanan relations, although the strict phylogenetic evidence to demonstrate this is lacking. The most commonly encountered pergids are the large, gregarious *Eucalyptus*-feeding *Perga* Leach that regurgitate eucalypt oil as a defensive mechanism, and the more specialised eucalypt leaf-mining genus *Phylac-teophaga* Froggatt (Mayo *et al.* 1997).

Parasitoid superfamilies

Although the fauna is dominated by the very diverse Ichneumonoidea, Chalcidoidea and Platygastroidea, the smaller and some relictual families are well represented in the Australian fauna. These include the Stephanidae, Trigonalidae and Megalynidae, all of which have been recently well-studied (Shaw 1990; Weinstein & Austin 1991; Aguiar 2001) and parasitise sawfly or lepidopteran larvae, in the case of Trigonalidae, or beetle larvae in wood in the case of the others. The proctotrupoid families Monomachidae, Heloridae, Peradeniidae, and Austroniidae (Naumann & Masner 1985) are also represented by few species, the last two being endemic to Australia but with unknown biologies and the Monomachidae by a distribution (southern Australia, South America) likely determined by Gondwanan vicariance events. The Proctotrupidae, associated with coleopteran larvae, are represented by a mixture of cosmopolitan and endemic genera, for example the highly distinctive *Austroserphus* Dodd. The Diapriidae are particularly diverse, highly endemic and contain numerous unusual forms. The fauna is largely undescribed except for the Ambositriinae (Naumann 1982) that show strong Gondwanan relations. Diapriids are most diverse in the moist regions of the continent, are parasitoids of late-stage dipteran larvae and pupae, and can be extremely abundant in leaf-litter at particular times of the year.

The Ceraphronoidea (Ceraphronidae and Megaspilidae) of Australia mostly belong to cosmopolitan genera, are moderately diverse, and are common as parasitoids in leaf-litter assemblages and as hyperparasitoids of leaf-mining and some gall-forming Hymenoptera. The Evanioidae have recently come under intensive study and are far more species rich than previously thought. The Evaniidae, which parasitise cockroach oothecae, are represented by two species rich genera, *Szepligetella* Bradley and *Acanthinevania* Bradley, of about 40–50 species each but the vast majority of species are currently misclassified in *Evania* F. (A. Deans pers. comm. 2004). The Gasteruptiidae and Aulacidae, which parasitise solitary bee and coleopteran larvae, respectively, are highly diverse in Australia and may represent as much as 25% of the world fauna. Combined, they comprise only five genera, with gasteruptiids being particularly diverse in arid or seasonally dry regions while aulacids are more diverse in higher rainfall forested areas (Jennings & Austin 2002, 2004).

Compared with other regions, the Cynipoidea are very depauperate in Australia, mostly because of the virtual absence of gall wasps (Cynipinae), although most subfamilies are represented by at least a few species. The exception is the Eucoilinae that parasitise cyclophorid Diptera and are reasonably diverse and common in litter. Austrocynipidae is known from a single species reared from hoop-pine (*Araucaria*), is endemic to Australia, and is the most basal member of the Cynipoidea (Ronquist 1999). The Ibalidae is not a natural part of the fauna and is only represented by two species introduced against *S. noctilio*.

The Platygastroidea includes two families, the Scelionidae and Platygastriidae. Both are extremely diverse in Australia

and, together, contain in excess of 2000 species, with >80% undescribed. The superfamily has been examined at generic level (Galloway & Austin 1984; Masner & Huggert 1989). Although these studies are now out of date, they do serve to indicate numerous endemic elements. The group comprises endoparasitoids of eggs (all Scelionidae) or postembryonic stages of Auchenorrhyncha, Sternorrhyncha and Cecidomyiidae (many Platygastriidae), and has effectively exploited most insect orders as hosts (Austin *et al.* 2005). However, in Australia the Baeini appears to represent one of the most diverse groups and parasitises the eggs of spiders in foliage, leaf-litter and under bark (Iqbal & Austin 2000).

The Ichneumonoidea is a huge assemblage of small to large parasitoids that attack a great range of insect hosts. Of the two families, the Ichneumonidae has been well-studied for Australia at least at generic level (Gauld 1984), while knowledge on the Braconidae is more patchy. Interestingly, the Ichneumonidae is less diverse in Australia relative to the Braconidae, a situation not found in at least the well-studied Northern Hemisphere regions. Ichneumonid diversity is centred on the permanent or seasonal wet forests of the north-eastern and south-eastern parts of the continent, including Tasmania, and is low in the drier regions, although there are some specialist forms, mostly nocturnal, that inhabit these regions. The total fauna is thought to be about 2000 species (Gauld 1984), which is significantly less than most regions, e.g. Nearctic – 8000 species, Afrotropical – 11 000 species. Groups that are well represented in the fauna mostly include lepidopteran parasitoids such as the Phygadeuontinae, Ichneumoninae, Bachinae, Cremastinae, and the Gondwanan Labeninae.

It is difficult to estimate the size of the braconid fauna but it is probably at least two times that of the Ichneumonidae. If the braconids have a centre of diversity it will be along the eastern seaboard and in the south-west. There are fewer species in the drier regions but many more than for the Ichneumonidae. Australia has two endemic subfamilies, the cecidogenic Mesostoinae (Austin & Dangerfield 1998) and the ichneumonid-like Trachypetinae (Austin *et al.* 1993) that is possibly the most basal extant group of Braconidae. The microgastroid subfamilies Cheloninae and Microgastriinae, that parasitise lepidopteran eggs and larvae, respectively, are particularly diverse comprising 600+ species, as are the cyclostome subfamilies Braconinae and Doryctinae; all of which contain numerous endemic genera and/or species groups. Other groups are also well-represented in the Australian fauna and are often seasonally abundant, viz. Alysiinae, Hormiinae and Rogadinae. The aphid-parasitising Aphidiinae are mostly represented by introduced species except for a few such as *Paraephedrus relictus* Carver & Stary associated with *Taiwanaphis* on *Nothofagus*. The putatively relict subfamily Sigalphinae that parasitises lepidopteran larvae is represented by two endemic genera (van Achterberg & Austin 1992). Numerous species have been introduced as biological control agents (Waterhouse & Sands 2001), with some genera such as the highly species rich *Cotesia* Cameron being better known for its introduced beneficial taxa, than its large number of undescribed endemic species.

The Chalcidoidea is the most diverse parasitoid superfamily worldwide, and this is no exception in Australia where they are numerous in all habitats. There are 19 families of Chalcidoidea, of which all but one occurs in Australia. The Eulophidae, Pteromalidae and Encyrtidae are the most diverse families and, as with other groups, there are many unique elements in the Australian fauna. For example, the family Pteromalidae is huge and cosmopolitan in distribution, yet six of the 31 subfamilies are endemic to Australia. Another subfamily, Leptofoeninae, shows a Gondwanan distribution, and is found in Australia and South America. The Eulophidae has one tribe, Ophelimini, which is endemic to Australia where it is associated with gall on eucalypts (see below). Another endemic tribe, Platytetracampini, contains parasitoids of whiteflies, and the Australasian Anselmellini contains seed infesters and gall associates. The vast majority of the 3400 Australian chalcidoid species were described by A.A. Girault in the early part of the 20th century (Dahms 1978); however, it is the monumental work of Bouček (1988) that created order from the chaos left by Girault and made this group accessible to contemporary researchers. The Chalcidoidea exhibits a remarkable range of biologies. The majority of species are parasitoids, and attack insects in 13 orders, as well as ticks and spider eggs. Phytophagy has arisen secondarily in several groups, and comprises species that are seed infesters, gall formers orinquilines, or stem borers (see below). The Chalcidoidea has been responsible for more biological control successes than any other group of insects, and many species have been introduced into Australia for this purpose (Waterhouse & Sands 2001).

'Phytophagous parasitoids'

One of the more interesting radiations among Australian parasitoids is that of gall induction in the Chalcidoidea. Although relatively uncommon among chalcidoids more generally, gall induction has evolved several times and is known to occur in six families (La Salle 2004). The Cynipinae, well known as oak gall wasps in the Northern Hemisphere, are largely absent and this niche in Australia is largely filled by gall inducers mainly from the chalcid families Eulophidae and Pteromalidae. Within both these groups, it is assumed that gall induction evolved from forms that were parasitoids of other gall inducing arthropods (La Salle 2004), but the phylogenetic evidence is not available to demonstrate this conclusively.

Within the Eulophidae, gall inducers are found in the Ophelimini and Tetrastichinae. The genus *Ophelimus* Haliday (Ophelimini) contains 50+ described species, with many more that are undescribed; this may very well be the largest single genus of chalcidoid gall inducers, and it is almost exclusively restricted to *Eucalyptus*. Several species have been recorded anecdotally as gall associates, but only *O. eucalypti* (Gahan) is well-documented as a gall inducer (Withers *et al.* 2000). Bouček (1988) regarded all species as gall inducers, however, this may not always hold true (La Salle 2004), and some species are apparently parasitoids or inquilines in galls of other chalcidoids or other gall inducers. There are several instances

of gall induction in the Tetrastichinae, and these almost certainly represent more than a single lineage (La Salle 2004). Australian genera of Tetrastichinae, where gall induction is known to occur, include *Quadrastichodella* Girault, *Oncastichus* La Salle, *Epichrysocharis* Girault and *Leptocybe* Fisher & La Salle. Although other host plants are known, the majority of eulophid gall inducers are associated with eucalypts, and it only requires a few minutes of searching to find eulophid galls on eucalypts in most natural situations. Several species of Australian eulophid gall inducers have become invasive pests in other regions, and these include *Quadrastichodella nova* Girault, *Oncastichus goughi* Headrick & La Salle, *Epichrysocharis burwelli* Schauff, *Leptocybe invasa* Fisher & La Salle and *Ophelimus* species (La Salle 2004; Mendel *et al.* 2004).

In the Pteromalidae, gall inducers are restricted to the tribe Melanosomellini (Ormocerinae), which is richest in the Australasian region. Species in this tribe have varied biologies that include gall inducers, parasitoids, inquilines and seed infesters, as well as a variety of host plants. The genus *Trichilogaster* Mayr is associated with *Acacia*, and one species is being used as a biological control agent of invasive *Acacia* in South Africa (Dennill 1987, 1988).

Aculeates

The largest families of Chrysoidea, the Dryinidae, Bethyloidea and Chrysididae, are all well represented in Australia, but are not well-studied, and there are large numbers of undescribed species. Bethyloids, which parasitise coleopteran and lepidopteran larvae, are often extremely abundant in leaf-litter. While most of the minor chrysidoid families are represented in the Australian fauna, with the exception of the Plumariidae, several of the smaller vespoid families are missing from the region, i.e. Sapygidae, Sierolomorphidae and Bradynobaenidae. The Rhopalosomatidae, that parasitise gryllid crickets, are recorded from Australia by two rare species of *Olixon* Cameron described from north Queensland. However, this brachypterous genus is now known to occur widely across the continent and comprises at least 15 species, several of which occur in arid regions and apparently mimic ants.

The large vespoid families are all well-represented in Australia and contain numerous endemic Austral elements. The Pompilidae (spider wasps) are particularly diverse and ubiquitous, but poorly studied. *Epipompilus* Kohl has a Gondwanan distribution (Australia, New Zealand, South America), is possibly basal to all other extant pomilids and has an atypical biology in that the larvae feed on spider eggs. The Pompilinae are substantially more diverse than the Pepsinae, and include several genera that form a mimicry complex of black and orange or black and white wasps, that make casual identification difficult. The Mutillidae comprise several hundred species, apparently have major endemic and gondwanan elements, but are largely unstudied and comprise mostly undescribed species.

The tiphiid fauna is dominated by the Gondwanan Thynninae (mostly Australia and South American), a group that represents 90%+ of the estimated 1200 species. Males of sev-

eral genera occur in large numbers at eucalypt flowers in summer and are often seen carrying the smaller wingless females in copula. The biology of very few species is known; all are parasites of beetle larvae in soil, except for *Diamma* Westwood that is a parasite of mole crickets. Several species act as pollinators of some orchids (e.g. *Caladenia* spp.) that apparently mimic tiphiid sex pheromones and attract naïve male wasps which pseudocopulate with the flower (Adams & Lawson 1993).

The Vespidae are well represented in the fauna and again are dominated by a single subfamily, the mostly solitary Eumeninae, comprising some 30 genera and about 75%+ of the estimated 700 species. Their mud nests are common in drier regions although many utilise existing holes and are less obvious. The paper wasp (Polistinae) genera *Polistes* L. and *Ropalidia* Guérin-Méneville are common in urban environments along the east coast, while the only members of the Vespinae, the introduced *Vespula germanica* (F.) and *V. vulgaris* L., are urban pests in southern Australia but have potential as viticultural pests and as competitive invaders of native vegetation (Matthew et al. 2000).

Both taxonomically and ecologically, the most important group of aculeates in Australia are the Formicidae. With nearly 1300 described species and an estimated fauna of 5000 species, virtually all of which are endemic, this is a huge group that act as predators regulating abundance of other insects, seed-dispersers, and soil 'engineers' (Shattuck 1999; Andersen 2003). The fauna is well-known for its endemic, plesiomorphic genera such as *Myrmecia* Fabricius and *Nothomyrmecia* Clark, its hot climate specialists such as *Melophorus* Lubbock, and its ubiquitous members, particularly *Iridomyrmex* Mayr and *Camponotus* Mayr. More so than in any habitat, ants dominate in the Australian arid zone, where they achieve local species diversities and abundances not recorded in other arid regions worldwide. The reason for this are complex but are postulated to be driven by very high levels of available carbohydrates from homopteran exudates and extrafloral nectaries especially on *Acacia* spp. (Andersen 2003). Several introduced species are pests, but the recent introduction of the red fire ant, *Solenopsis invicta* Buren, in the Brisbane area is of particular concern and the target of a major eradication program (Vanderwoude et al. 2003).

The Australian fauna of Apoidea is huge and, like other groups, is highly endemic at several taxonomic levels. Here we use the family classification of Brothers (1999) to discuss the fauna. This recognises five families of Apoidea on phylogenetic grounds, viz. Heterogynidae, Ampulicidae, Sphecidae s. str., Crabronidae and Apidae s. l., of which the Heterogynidae is absent from the continent. Larvae of the Ampulicidae develop on cockroaches, after they are paralysed. The fauna is small and represented by about 20 species. The Sphecidae comprise the mud-dauber and digger wasps, a group in Australia comprising some 100+ species, and provision their nests with spider, lepidopteran or orthopteran prey. Although most species are endemic, most genera appear to have wider distributions. The Crabronidae are a huge group with more than

1000 species displaying a diverse array of prey preferences (Bohart & Menke 1976). Several genera such as *Tachysphex* Kohl, *Sericophorus* F. Smith, *Bembix* F. and *Cerceris* L. are rich in species (60+ species) particularly in open and/or sandy areas.

The Apidae of Australia comprise some 1500 species but the fauna is highly skewed towards the more primitive short-tongued bees (Michener 2000). Indeed, compared with other regions the fauna is disproportionately represented by two subfamilies, the Colletinae and Halictinae, that account for about 90% of species and are thought to have radiated as pollinators with the explosion of Myrtaceae over the last 20 million years. Major components of this endemic radiation include the hylaeine and euryglossine bees (Colletinae), the latter being restricted to Australia, and the nomiine and halictine bees (Halictinae), particularly *Lasioglossum* (*Chilalictus*) Michener, an endemic subgenus with some 160+ species. Of the small subfamilies, Andreninae and Melittinae do not occur in Australia, the Stenotritinae (20+ species) is endemic to the continent, while the long-tongue Apinae is represented mostly by the anthophorine bees, best known for the black and blue-banded *Amegilla* Friese.

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