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ANT DIVERSITY IN ARID AUSTRALIA: A SYSTEMATIC OVERVIEW

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ABSTRACT

Australia is one of the world's hotspots for ant diversity, but diversity patterns within the Australian ant fauna remain poorly documented. The key to understanding patterns of ant diversity in Australia is an understanding of its arid fauna, as this is primarily where most of Australia's highly diverse genera have radiated. Based on the 3,750 Australian ant species held at the CSIRO Tropical Ecosystems Research Centre in Darwin, I estimate that the entire Australian fauna comprises about 6,500 species, only about one-fifth of which have been described. Species richness is heavily concentrated into 11 genera, each with over 100 Australian species. Most of these occur primarily in arid and semi-arid regions, and a systematic overview is presented for five of the most important: *Iridomyrmex*, *Melophorus*, *Camponotus*, *Monomorium* and *Rhytidoponera*. For each genus, a comprehensive species-group framework is proposed as a basis for documenting patterns of diversity and distribution. Many of the taxa are highly generalised morphologically, and much remains to be done to resolve difficult complexes at the species level, and to resolve relationships between species-groups. An answer to the fundamental question of why ant diversity is so remarkably high in arid Australia remains elusive, but may be related to unusually high ant productivity and behavioural dominance over evolutionary time.

Key words: ant diversity, arid, Australia, *Camponotus*, Formicidae, Hymenoptera, *Iridomyrmex*, *Melophorus*, *Monomorium*, *Rhytidoponera*

INTRODUCTION

Australia is one of the world's hotspots for ant diversity, but little systematic information is available on diversity patterns within the Australian ant fauna. The exceptional richness of *local* ant communities in Australia has been commonly reported (Andersen, 1995), but species richness within entire regional faunas have been poorly documented. Exactly how rich is the Australian ant fauna, and how is the richness distributed both from systematic and biogeographical perspectives? These questions can only be answered by a detailed understanding of diversity patterns within the major Australian ant genera, most of which have many more undescribed than described species, and lack comprehensive species-group frameworks.

It is clear that the key to understanding patterns of ant diversity in Australia is an understanding of the arid fauna. Most of Australia's 'megadiverse' (>100 species) ant genera have radiated primarily in the arid zone, and whichever way you look at it ant diversity in arid Australia is extraordinary by world standards (Table 1). Inland Australia routinely packs more than a hundred ant species per hectare, and in semi-arid regions one can find a hundred species within 0.1 ha (Andersen, 2003). These are the richest local ant communities on Earth. As many or more species can occur within a comparable area of lowland tropical rainforest, but here there is extreme vertical stratification of species (Brühl *et al.*, 1998), so that we are really dealing with multiple communities stacked on top of each other. Ironically, Australia's own lowland tropical rainforests are relatively poor in species, supporting a depauperate subset of the rich Indo-Malayan fauna (Taylor, 1972).

Table 1. Ant diversity at local and regional scales in arid Australia compared with arid North America and southern Africa. Data are maximum numbers of species recorded in local (within 1 ha) communities (see Andersen, 1997, 2003), and broad estimates of total arid faunas.

	Australia	North America	Southern Africa
Max no. species/ha	>100	35	30-40
Total no. species	4,500	300	400

Here I provide a systematic overview of diversity within the ant fauna of arid Australia. I use the term 'arid' very broadly to include semi-arid regions - up to about 350 mm annual rainfall in the southern semi-arid zone, and about 800 mm in the northern semi-arid tropics (where rain falls almost exclusively during a summer wet season). I begin by providing an overview of the diversity of the entire Australian fauna, before examining in detail the five major genera of the arid zone. For each genus, a comprehensive species-group framework is proposed as a basis for documenting patterns of diversity and distribution.

My analyses are based on specimens held at the CSIRO Tropical Ecosystems Research Centre (TERC) in Darwin that my collaborators and I have accumulated over the past 25 years. These holdings represent by far the largest collection of ants from arid Australia. As of January 2004 they comprise over 3,750 native Australian species, and have been accumulating at a relatively constant 200 additional species per year over the past decade, without any sign of levelling off (Fig. 1).

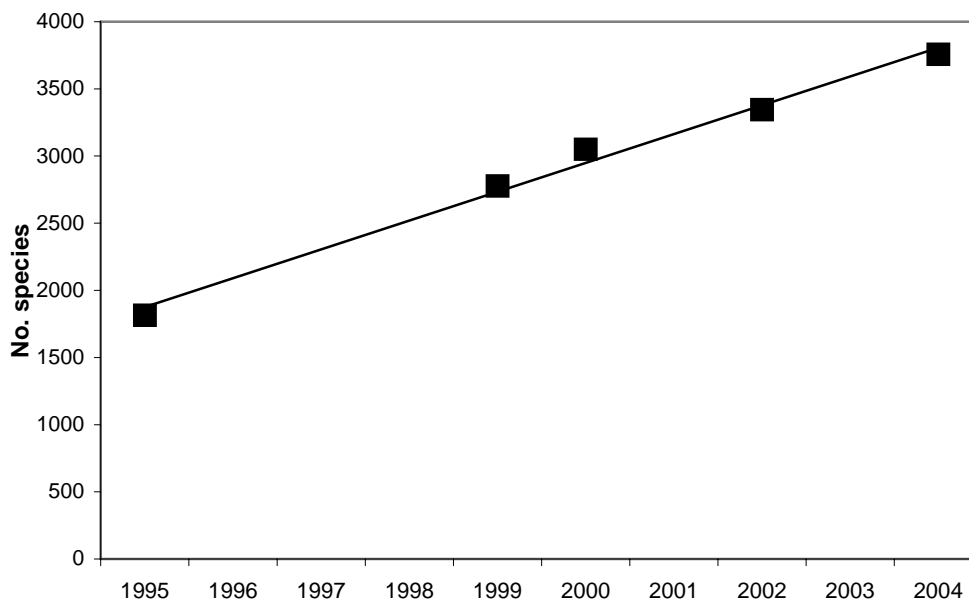


Fig. 1. Accumulation of Australian ant species in the CSIRO Tropical Ecosystems Research Centre collection over the past decade.

DIVERSITY OF THE AUSTRALIAN ANT FAUNA

Shattuck (1999) lists 1275 described species and subspecies of ants from Australia. Based on Taylor's (1991) opinion that "Only about a quarter of the Australian fauna has been named", this gives an estimated 5,000 Australian species. My own estimate based on the TERC collection is somewhat higher. About 40% (38 out of 103) of Australian genera contain twenty or more species, and I estimate that together they contribute about 6,000 species (Table 2). This would put the total Australian fauna at about 6,500 species.

A very large proportion (collectively about 80% of total species) of the fauna is contributed by 11 megadiverse (each with over 100 Australian species) genera (Table 2). Chief among these is *Melophorus*, with over 500 sorted species in the TERC collection and possibly as many more yet to be collected. Next is *Camponotus*, likely to have well over 500 Australian species. *Monomorium*, *Pheidole*, *Meranoplus*, *Rhytidoponera*, *Polyrhachis*, *Iridomyrmex* and *Tetramorium* each are likely to have more than 300 Australian species. *Cerapachys* and *Myrmecia* complete the 11 'centurion' Australian genera. Such an array of megadiverse genera is unparalleled anywhere in the world, with other continents having at most two or three genera containing one hundred or more local species. Interestingly, the frequency distribution of species richness in Australian ant genera is bimodal, with about twice as many genera containing more than a hundred species as those containing between 50 and 100 (Fig. 2).

The ratio of undescribed to described Australian species is very uneven among genera (Table 2). *Myrmecia* is by far the best known taxonomically of Australia's megadiverse genera in terms of proportion of species that are named (Ogata & Taylor, 1991), but even then a significant proportion remains undescribed. However, it is likely that most of these undescribed species are already represented in collections, awaiting the resolution of difficult species complexes, such that the total species count is unlikely to be boosted markedly by the collection

Table 2. Diversity within Australia's richest (those with 20 or more species) genera. Data are provided for the number of described species (including subspecies; following Shattuck, 1999 and Bolton, 2000), the number of sorted species in the CSIRO Tropical Ecosystems Research Centre (TERC) collection in Darwin (as of the end of 2004), and an estimate of total number of Australian species. The ratio of estimated total: number of described species is also provided.

	Described	TERC	Estimated Total	Total: Described
Myrmeciinae				
<i>Myrmecia</i>	89	90	130	1.5
Amblyoponinae				
<i>Amblyopone</i>	17	7	25	1.5
Ponerinae				
<i>Anochetus</i>	5	25	30	5.0
<i>Hypoponera</i>	10	24	35	3.5
<i>Leptogenys</i>	25	35	55	2.2
<i>Odontomachus</i>	3	25	35	11.7
<i>Bothroponera*</i>	20	42	60	3.0
Ectatomminae				
<i>Rhytidoponera</i>	76	247	350	3.25
Cerapachyinae				
<i>Cerapachys</i>	44	95	150	3.4
<i>Sphinctomyrmex</i>	15	15	25	1.7
Myrmicinae				
<i>Crematogaster</i>	34	60	80	2.4
<i>Colobostruma</i>	16	16	25	1.6
<i>Epopostruma</i>	18	12	30	1.7
<i>Meranoplus</i>	59	217	400	6.8
<i>Monomorium</i>	53	335	500	9.4
<i>Orectognathus</i>	18	3	20	1.1
<i>Pheidole</i>	53	297	500	9.4
<i>Podomyrma</i>	49	25	75	1.5
<i>Solenopsis</i>	7	26	40	5.7
<i>Strumigenys</i>	49	18	60	1.2
<i>Tetramorium</i>	24	192	350	14.6
Dolichoderinae				
<i>Anonychomyrma</i>	14	25	35	2.5
<i>Bothriomyrmex</i>	5	13	20	4.0
<i>Dolichoderus</i>	22	28	40	1.8
<i>Iridomyrmex</i>	63	223	350	5.6

Table 2. (continued)

	Described	TERC	Estimated Total	Total: Described
<i>Leptomymex</i>	27	16	30	1.1
<i>Ochetellus</i>	4	18	30	7.5
<i>Papyrius</i>	4	16	25	6.3
<i>Tapinoma</i>	5	22	30	6.0
Formicinae				
<i>Calomyrmex</i>	11	19	25	2.3
<i>Camponotus</i>	128	485	750	5.9
<i>Melophorus</i>	29	505	1000	34.5
<i>Notoncus</i>	6	30	40	6.7
<i>Opisthopsis</i>	15	19	25	1.7
<i>Paratrechina</i>	10	55	80	8.0
<i>Polyrhachis</i>	115	241	350	3.0
<i>Prolasius</i>	18	34	45	2.5
<i>Stigmacros</i>	48	58	80	1.7
TOTAL	1119	3606	5920	5.3

*The synonymy of *Bothroponera* with *Pachycondyla* listed in Bolton (1994) is not recognized here as it is based on an unpublished manuscript.

of significantly new material. Species of *Myrmecia* are very large and extremely conspicuous ants, and, like most Australians, occur primarily in the temperate south. In other words, the genus is unusually well collected. Indeed, Australia's four richest genera in terms of described species (*Camponotus*, *Polyrhachis*, *Myrmecia* and *Rhytidoponera*) are all among the country's largest and most conspicuous ants, and therefore have been subject to relatively high collecting effort.

Polyrhachis stands out as being in a far better taxonomic state than indicated by the relatively small proportion (about a third) of Australian species that are described, thanks to decades of work by Rudy Kohout from the Queensland Museum. All known Australian species outside the subgenera *Chariomyrma* and *Campomyrma* have been catalogued and assigned manuscript names. In each of the rich sub-genera *Hagiomyrma*, *Hedomyrma* and *Cyrtomyrma* there are more manuscript names than described species (R. Kohout, personal communication). All these subgenera have their centres of Australian distribution in relatively well-collected Queensland. In comparison, very large numbers of species of the far richer *Chariomyrma* and *Campomyrma* occur in poorly collected central and northwestern Australia; the proportion of undescribed species is far higher in these subgenera.

The most dramatic mismatch between described and actual species undoubtedly occurs in *Melophorus*, where only 29 of the possibly thousand or more species have been named. The majority of species are small, occur in remote regions, and forage during the hot parts of the day when most ants and ant collectors alike are inactive. The genus has never attracted serious attention by ant taxonomists. The true extent of their diversity has only been revealed during extensive pitfall trapping over the past decade, involving literally thousands of sites across central and northern Australia. The mismatch between described and actual species is also especially pronounced for *Tetramorium* (Table 2). As in *Melophorus*, most Australian species of *Tetramorium* are relatively small and inconspicuous, and occur in remote regions of the arid zone.

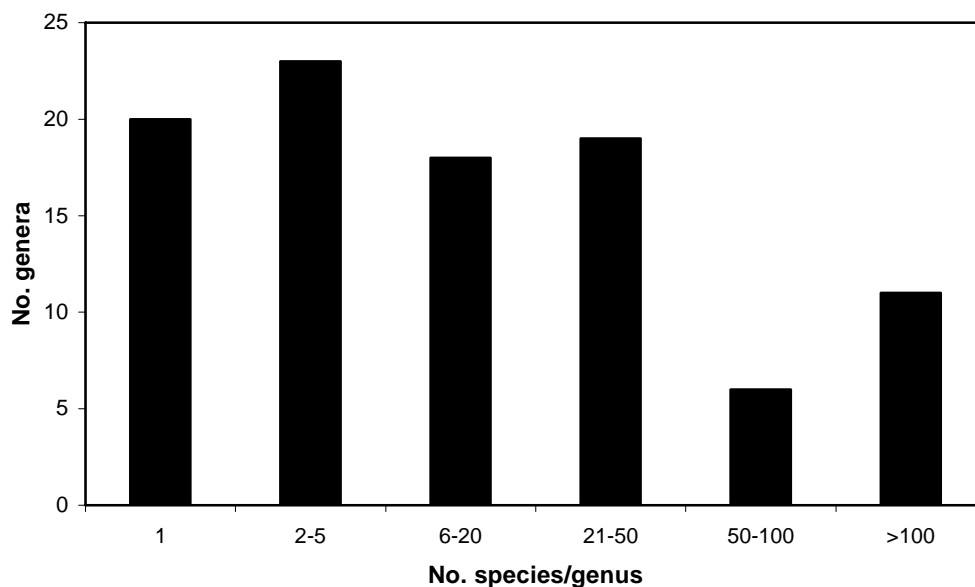


Fig. 2. Frequency distribution of species richness in Australian ant genera. Numbers of species per genus have been estimated based on Shattuck (1999) and holdings in the TERC collection.

DIVERSITY WITHIN MAJOR ARID GENERA

Of Australia's eleven megadiverse genera, all but *Polyrhachis* and *Myrmecia* have radiated primarily in the arid zone. In *Meranoplus*, *Tetramorium*, *Iridomyrmex*, *Cerapachys* and especially *Melophorus* the vast majority of species occur in arid habitats, whereas *Rhytidoponera*, *Monomorium*, and especially *Pheidole* and *Camponotus* have a greater proportion of species in mesic habitats. Here I examine in detail diversity within the five most important of these arid-adapted genera: *Iridomyrmex*, *Melophorus*, *Camponotus*, *Monomorium* and *Rhytidoponera*, building on preliminary species-group frameworks provided in Andersen (1991, 2000).

Iridomyrmex

Iridomyrmex might not be the richest ant genus in Australia, but is easily the most important ecologically, especially in the arid zone (Greenslade, 1979). Species of *Iridomyrmex* are highly abundant and aggressive ants that exert a level of behavioural dominance over other ants that is unparalleled in arid regions elsewhere in the world (Andersen, 2003). All species of *Iridomyrmex* are sun-loving ants, with the vast majority occurring in arid and semi-arid habitats. The genus can be reasonably well-represented in more humid regions, but tends to be restricted to open habitats, or to open patches within more forested habitats.

A comprehensive species-group framework for *Iridomyrmex* is presented in Table 3. It needs to be noted that the species- and even higher-level taxonomy of the genus is extremely challenging, given that morphology is highly generalised and conservative throughout the genus. There are many complexes of unresolved sibling species, and in many cases morphological similarity between species might well be a result of convergence. The species-group framework proposed here is therefore very preliminary.

Table 3. Classification, distribution and diversity of major species-groups and complexes of *Iridomyrmex* in Australia. Figures are numbers of sorted species in the TERC collection as of the end of 2004. Distribution is described as predominantly northern (N; occurring primarily within the northern arid zone), southern (S; occurring primarily in the southern arid zone), monsoonal (M; occurring primarily in the monsoonal tropics), widespread (W; well-represented throughout arid Australia), or Bassian (B; occurring primarily in humid habitats of southern Australia).

***calvus* radiation**

calvus group (3, B)
rufoinclinus group (6, N)
viridigaster group (3, S)

***agilis* radiation**

agilis group (9, S)
anceps group (14, M)
bicknelli group (10, S)
gracilis group (25, W)
pallidus group (41, W)
purpureus group (12, W)
 discors complex (1, S)
 purpureus complex (11, W)

***rufoniger* radiation**

conifer group (7, B)
mattiroloi group (44, W)
rufoniger group (21, W)
suchieri group (15, W)
vicinus group (10, B)
Group A (3, M)

calvus radiation

This is a relatively small but clearly defined radiation, characterised by a uniformly curved configuration of the frontal carinae, and anteriorly inclined and asymmetrical (anterior face markedly shorter than posterior face) petiolar node. The frontal carinae are sinuate in all other groups of *Iridomyrmex*, suggesting a basis for a primary higher-level classification of the genus. Species of the *calvus* radiation have been revised by Shattuck (1993a), who referred to them as a single species-group. However, he recognised three distinct complexes, which I have elevated to species-group status because of their diversity and morphological and biogeographical distinctiveness.

The *calvus* group (*ss*) comprises eight smallish species from moister habitats of southern Australia, Norfolk Island and New Caledonia. They superficially resemble many other small and robust species of *Iridomyrmex* from unrelated groups. All species have restricted distributions, with the notable exception of *I. notialis*, which occurs throughout subhumid and semi-arid southeastern and southwestern Australia, as well in the McDonnell Ranges of central Australia.

The *viridigaster* and *rufoinclinus* groups contain larger, reddish or red and black species, all of which are uncommon. Species of the *viridigaster* group have a prominently rounded promesonotum, and scale-like petiole, and are restricted to the southern arid zone. In the *rufoinclinus* group the mesosoma is more gracile, and the petiolar node is relatively long, low and broadly rounded dorsally. *Iridomyrmex cappoinclinus* occurs in the central arid zone, *I. cephaloinclinus* throughout the northern arid zone, *I. rufoinclinus* throughout the monsoonal

tropics, and *I. anteroinclinus* is restricted to the northern Kimberley region of far northern Western Australia (WA). There are at least two additional, undescribed species in the group, including a uniformly blackish species from Cape York Peninsula.

agilis radiation

This is an extremely rich radiation of arid-adapted groups of long-legged, often extremely gracile species. In all cases, the antennal scapes exceed the vertexal margin by at least one-fifth their length, and usually much more. The *agilis* group comprises relatively large, extremely gracile and exceptionally fast-moving species. *Iridomyrmex agilis* is a red species with contrasting black legs and gaster that occurs throughout arid Australia. *Iridomyrmex rubriceps* is an unusual member of the group in that it occurs in humid coastal eastern Australia, where it is patchily distributed in open habitats. The *bicknelli* group seems to be closely related to the *agilis* group, with both occurring primarily in the southern arid zone. Species of the *bicknelli* group are smaller and uniformly blackish, often with feeble iridescence, and have a convex vertexal margin. *Iridomyrmex bicknelli* occurs throughout southern Australia, most abundantly in the arid zone, but also in open habitats of mesic regions. An undescribed species has a similarly wide distribution across northern Australia. Species of both the *agilis* and *bicknelli* groups do not appear to be as aggressive as other species of *Iridomyrmex*.

As the name suggests, species of the *gracilis* group are also extremely gracile. They can have particularly long scapes, exceeding the vertexal margin by up to half their length. They are hairier than species of the *agilis* and *bicknelli* groups, and are more aggressive. *Iridomyrmex fusciventris* is a relatively small species with hairy scapes that occurs throughout the southern semi-arid zone. A more robust species with glabrous scapes has a similar distribution, but extends into the central arid zone. Several particularly gracile species are locally dominant ants throughout the northern arid zone and semi-arid tropics. The group includes a small number of larger, reddish species (*I. mayri* and close allies), one of which is extremely abundant and widespread in the northern arid zone. The group (apparently) also includes a very distinctive mid-sized blackish species with bicolored black and brown head, which occurs in association with salt lakes throughout the southern arid zone. *Iridomyrmex gracilis* itself is a medium-sized blackish species with hairy scapes that is atypically distributed in coastal and subcoastal eastern Australia. There are several similar-looking species, but with shorter antennal scapes, that also occur in subcoastal southeastern Australia; it is possible that these (including *I. gracilis*) are actually related to species of the temperate *vicinus* group discussed below, rather than to the arid and northern species described above.

The tropical *anceps* group seems to be very closely related to the *gracilis* group, and indeed it is difficult to find clear characters that separate them. Compared to the *gracilis* group, species of the *anceps* group tend to be less gracile and less hairy, without, for example, erect hairs on the scape or hind femur. One species of the *anceps* group (possibly *I. anceps* itself) is one of the most abundant ants throughout the semi-arid tropics and northern monsoonal zone. It (or possibly a sibling species) also occurs extensively in South-East Asia.

I have included the *purpureus* group in this radiation, with the yet-to-be-substantiated proposition that it is most closely allied to the *gracilis* group. The group is most distinctive, with very broad heads, relatively short scapes, and densely hairy scapes and legs. It includes the famous meat ants of the *purpureus* group in the more narrow sense, which have been comprehensively revised by Shattuck (1993b) following extensive ecological and molecular work by John Greenslade and Bruce Halliday (e.g. Greenslade & Halliday, 1982). However, I also include in the group as a small complex of species described by Shattuck (1996) as belonging to the *discors* group (*Iridomyrmex discors* and *I. obscurior*).

The final group that I have included in the *agilis* radiation is the *pallidus* group of pale, large-eyed, nocturnal species, which is represented throughout arid Australia. It would not be surprising if this group proved to be polyphyletic. *Iridomyrmex pallidus* (originally described as

a subspecies of *I. rufoniger*, which belongs to an unrelated group; see below) is extremely abundant throughout tropical Australia. Like most other species in the group, its mesosoma has numerous short, silvery hairs. However, the group includes several glabrous species. One of these is *I. hartmeyer*, a relatively large species with a prominently rounded propodeum, which occurs throughout most of arid Australia.

rufoniger radiation

This radiation comprises relatively small and stout brownish or blackish species with short antennal scapes (only slightly exceeding the vertexal margin). *Iridomyrmex rufoniger* and allies represent the most distinctive group within this radiation. The head is cordate, with a conspicuously concave vertexal margin, and the mesosoma features a steeply rising, prominently rounded pronotum and short propodeum. The pronotum sports a distinctive tuft of long hairs. The group includes a complex of small, uniformly blackish species with a flattened propodeum. One such species with a mostly glabrous gaster occurs throughout most of arid Australia. There are several similar species with hairy gasters, mostly in the northern arid zone and semi-arid tropics. A closely related complex contains larger reddish species. One of these, possibly *I. rufoniger* itself, occurs throughout the southern arid zone. A similar species, but with hairy hind tibiae, occurs in central WA. A third complex consists of slightly larger species with a prominently rounded propodeum. I have included *I. septentrionalis*, a uniformly brownish species that is extremely common throughout subcoastal eastern Australia, in the *rufoniger* group, but it may actually be related to *I. gracilis* and close allies described above.

Species of the *mattiroloi* group superficially resemble those of the *rufoniger* group, sharing a stout mesosoma with steeply rising pronotum and short propodeum. However, they lack the cordate head and tuft of long hairs on the pronotum, and I suspect the two groups are not so closely related. Whereas species of the *rufoniger* group occur almost exclusively in the arid zone, the *mattiroloi* group occurs in a wide range of habitats. In many species the mesosoma is hairy throughout, and in one of these from the northern arid zone the scapes are also hairy. In other species the mesosoma is glabrous except for several hairs on the pronotum. One such species is extremely common throughout the semi-arid tropics and northern monsoonal zone, and the same or a similar species occurs throughout eastern Indonesia. Numerous other species are entirely glabrous. A complex of glabrous species has a particularly deep metanotal groove, and one such species from the southern arid zone has striking pink and blue iridescence. *Iridomyrmex mattiroloi* itself is a relatively hairy species from southeastern forests, and recent molecular analysis (Rod Eastwood, personal communication) suggests that it might in fact be quite unrelated to the arid species with similar morphology.

The *suchieri* group is closely related to the *mattiroloi* group (at least to the arid species), and indeed the boundary between them is not so clear cut. Species of the *suchieri* group tend to be larger, the pronotum is not so steeply rising and prominently rounded, and the propodeum is longer. Some species are densely hairy. Two of these, one with hairy and the other with glabrous scapes, occur from central northern Queensland to central western New South Wales. A more sparsely hairy species is the dominant species of *Iridomyrmex* in a range of relatively moist and shady habitats throughout the semi-arid tropics and northern monsoonal zone. An entirely glabrous species is distributed throughout most of the arid zone.

Species of the *vicinus* group resemble those of the *suchieri* group, but have longer scapes (exceeding the vertexal margin by about one-fifth of their length) and a prominently rounded propodeum. The group has a Bassian distribution, occurring primarily in mesic and sub-humid habitats of southern Australia. *Iridomyrmex vicinus* is restricted to mesic southern Victoria and northern Tasmania, and a similar species occurs in high rainfall areas of far southwestern Australia. Several other species extend into the southern semi-arid zone. One particularly distinctive species (possibly *I. emeryi*) occurs in montane and alpine areas from southeastern New South Wales to central Tasmania. It is a conspicuous ant of alpine grasslands, building

nests of fragmented plant material around the bases of tussock grasses, presumably to avoid waterlogged soils. The *conifer* group comprises relatively large species from southwestern Australia that have a distinctively conical propodeum (Shattuck, 1998). Despite their distinctive appearance, I consider them to be closely related to species of the *vicinus* group (especially the alpine species discussed above).

Species of the final group (referred to as Group A in Table 3) in the *rufoniger* radiation also resemble those of the *suchieri* group, with which they are presumably allied, but have larger eyes and blue iridescence. The group is referred to as the *cynaesus* group in Andersen (2000), but I am now not so sure that *I. cyaneus* in fact belongs to this group. One species is common throughout most of tropical Australia.

Melophorus

Species of *Melophorus* are highly thermophilic and polymorphic formicines, and therefore parallel (but are not related to) species of *Myrmecocystus* in the New World and *Cataglyphis* in the Old World. Their foraging activity is typically restricted to hot parts of the day, where they can tolerate temperatures that are lethal to most other ants (Fig. 3). As for *Iridomyrmex*, the overwhelming impression for such a speciose genus is one of morphological generalisation and conservatism, with many species-groups appearing superficially similar to each other. However, such morphological conservatism belies remarkable biological diversity. Although the vast majority of species seem to be generalist predators and scavengers, the genus includes specialist predators of ant brood and termites, specialist granivores, and at least one 'honeypot' with specialized repletes (*M. bagoti*). A comprehensive key to provisional species-groups is provided as Appendix 1. A number of distinct radiations can be recognised within the genus (Table 4), as outlined below.

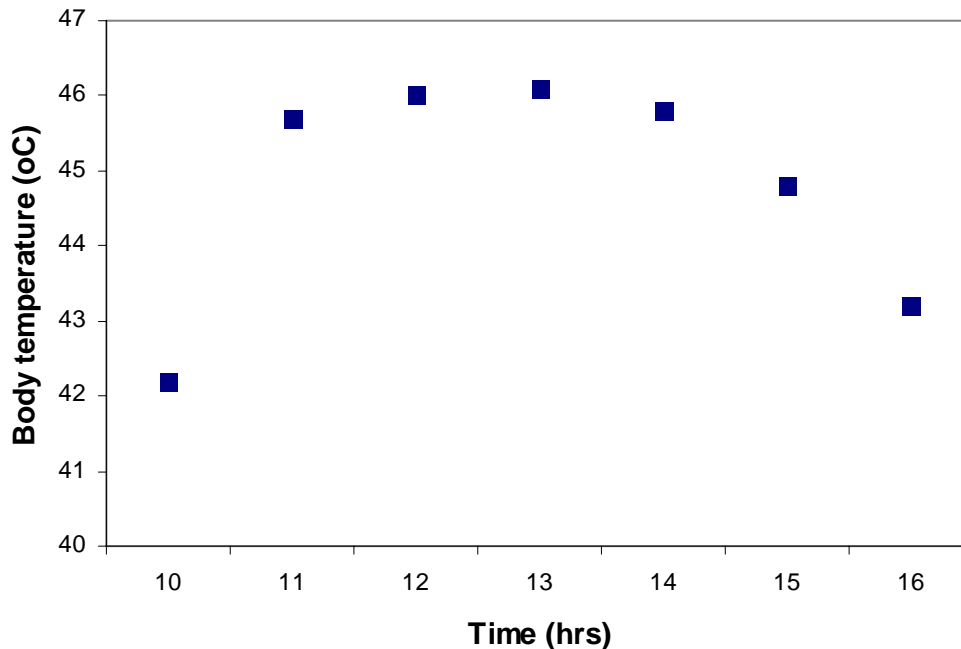


Fig. 3. Diel patterns of body temperature of foraging *Melophorus bagoti*, one of the most thermally tolerant insects known. Above-ground activity commences only when soil surface temperature exceeds 50°C, and continues with temperatures exceeding 70°C. Data from Christian & Morton (1992).

Table 4. Classification, distribution and diversity of species-groups of *Melophorus*. Figures are numbers of sorted species in the TERC collection. Distribution is described as predominantly northern (N; occurring primarily within the northern arid zone), southern (S; occurring primarily in the southern arid zone) or widespread (W; well-represented throughout arid Australia).

***fulvihirtus* radiation**

anderseni group (6, N)
fulvihurtis group (2, S)
 Group G (2, N)
 Group I (3, W)

***majeri* radiation**

majeri group (1, S)

***potteri* radiation**

potteri group (12, S)

***aeneovirens* radiation**

aeneovirens group (16, N)
froggatti group (42, W)
 Group A (24, N)
 Group B (10, N)
 Group L (4, N)

***wheeleri* radiation**

wheeleri group (43, W)
 Group F (17, N)
 Group H (2, N)
 Group K (1, N)

***mjobergi* radiation**

hirsutus group (2, mesic SE)
mjobergi group (91, W)
 Group C (18, W)
 Group D (14, W)
 Group J (9, N)

***fieldi* radiation**

fieldi group (110, W)
perthensis group (5, W)
pillipes group (16, N)

Unclear affinities

iridescens group (9, W)
bruneus group (37, S)
 Group E (9, N)

fulvihurtis radiation.

These relatively few species lack tibial spurs, and characteristically have a thick and sculptured integument. Species of the *fulvihirtus* (southern arid zone) and *anderseni* (northern arid zone and seasonal tropics) groups raid brood from the nests of highly aggressive species of *Iridomyrmex*, without apparent interference from their unwitting hosts (Clark, 1941; Agosti, 1997). Species of Groups G and I are presumably also specialist brood-raiders. Species of the *fulvihirtus* group, *anderseni* group and Group I all have reduced maxillary palps, with the final segment peculiarly pointed apically. The *majeri* group, represented by a single (and rare) known species from southwestern WA. (Agosti, 1997) also lacks tibial spurs and its integument is densely sculptured. However, it is otherwise so morphologically distinct that I have considered it to represent a separate radiation (indeed, it is arguably distinctive enough to warrant generic rank).

potteri radiation

The bulldozer ants of the *potteri* group from the southern arid zone are characterised by stout bodies, short legs, and massive mandibles, all adaptations for hunting their termite prey (McAreevey, 1947). Two major complexes can be recognized. In one, the anterior clypeus is acutely angled and projects over the base of the mandibles, and the mandibles have five or six distinct teeth. In the other, the anterior clypeus is not acutely angled, and the mandibles are particularly large and blade-like, with just a single apical tooth (Fig. 15f in Greenslade, 1979).

aneovirens radiation

This comprises long-legged species with an acutely angled clypeus that projects over the base of the mandibles, and a dome-shaped occiput. The *froggatti* group, characterised by its short and high propodeum, occurs throughout inland Australia and is particularly rich in species. The closely related *aneovirens* group and Group A consist of relatively large and gracile species that occur primarily in the northern arid zone; they are strongly reminiscent of species of *Myrmecocystus* and *Cataglyphis*. Groups B and L also occur primarily in the northern arid zone. The latter appears closely allied to Group A, whereas the former is very distinctive, with a thick and often conspicuously sculptured integument, short funicular segments, and is hairy throughout. In one complex the hairs are particularly long and abundant, and the head of minor workers is peculiarly hour glass-shaped (Fig. 15d in Greenslade, 1979).

wheeleri radiation

These species have characteristically short maxillary palps, and often a bulging clypeus. The radiation features the seed harvesters of the extremely rich *wheeleri* group, the only formicines known to be specialist granivores (Andersen, 1991). The major workers have very large heads, strangely reminiscent of those of the myrmicine genus *Messor*. Several distinct complexes can be recognised within the group. One comprises relatively large and gracile, reddish species in which the two posterior clypeal setae are located slightly behind the anterior margin of the antennal sockets, rather than slightly in front as is typical for *Melophorus*. Another comprises relatively large and gracile, blackish species with conspicuously sculptured heads, and mandibles with six or seven (rather than five) teeth.

Species of Group F look very similar to those from a complex of less gracile species within the *wheeleri* group, but major workers do not have such massive heads, and the species are apparently not granivorous. Group K is represented by a single known species from the Northern Territory's (NT) Victoria River District. It is large, black, and heavily sculptured, with mandibles that are remarkably armed with very numerous (15 or more), long, sharp teeth. It presumably has a specialist diet unrelated to granivory. Group H is represented by two known species (one from the northern Top End of the NT, and the other from the nearby Victoria River

District) that appear to be associated with nests of species of the *rothsteini* group of *Monomorium*, which are of similar size and color (reddish head and mesosoma, with contrasting black gaster). Is this another group of specialist brood-raiders?

mjobergi radiation

These relatively stout-bodied species have a short and high propodeum, head that is slightly-to-markedly compressed dorso-ventrally, and typically a short, scale-like petiole. Species of the *mjobergi* group are the smallest (total length of minor workers about 1.5 mm) of the genus, and resemble plagiolopidines. The group is exceptionally rich, with an estimated 200 species. It includes several very distinctive complexes. One of these has very long and flattened heads, and is characteristic of clay soils across the semi-arid north. Another, more widespread, complex is very gracile compared with typical species, with antennal scapes exceeding the vertexal margin by half or more their length. In the vast majority of species the mesosoma is entirely glabrous, but a complex of hairy species with very large eyes occurs in the eastern arid zone. Representing another complex, two species from southern Western Australia have a bulbous metanotal process, strongly reminiscent of the *enormis* group of *Notoncus*.

Group C appears to be closely allied to the *mjobergi* group, but its species tend to be larger and more conspicuously sculptured, and are covered with adpressed pubescence in addition to erect hairs. The group contains two distinct complexes: smaller, more robust, darkly colored species with hairy scapes; and larger, more gracile and usually yellowish species with glabrous scapes.

In Group D, the mesosoma is very stout, with a particularly short and high propodeum. The group appears to be restricted to higher rainfall areas, being absent from the central arid zone and penetrating wetter habitats where no other *Melophorus* occurs. For example, one species is restricted to sub-coastal Top End of the NT and the far northern Kimberley region of WA, where it occurs in relatively shady habitats, and another species occurs in mesic habitats of southeastern Australia. I suspect that Group D is allied to the highly distinctive *hirsutus* group, whose dark reddish, heavily sculptured and densely hairy mesosoma is remarkably barrel-shaped, with dorsally protruding metanotal spiracles. The group is represented by a small number of species restricted to relatively mesic habitats of southeastern Australia. The final group that I place in this radiation, Group J, consists of densely hairy species with a biconvex mesosoma, and a relatively long and narrow, rather than scale-like, petiolar node. The group occurs primarily in central Queensland (Qld) and semi-arid NT.

fieldi radiation

This comprises morphologically generalised taxa that are among the most common ants throughout arid Australia. The radiation includes two very distinctive groups, with complimentary distributions in semi-arid Australia. One of these, the Bottle-brush ants of the *pillipes* group, is characterised by a dense covering of long, erect hairs on the tibiae. The group occurs throughout semi-arid Australia, but is best represented in central Qld. The other, the *perthensis* group, is characterised by a short, low and prominently rounded propodeum. It is found primarily in the southwestern semi-arid zone, but one species occurs from the southern Top End of the NT to the Gulf region of northwestern Qld. Both groups appear to be absent from the central arid zone.

I have placed all other species in the radiation into the *fieldi* group (Plate 17, Andersen, 2000), which, as constituted, is a grab-bag of very morphologically generalised species that may prove to represent several distinct species-groups. In the strict sense, species of the *fieldi* group are largely glabrous (minors at most with a pair of pronotal hairs), gracile ants. In some, antennal scapes are entirely glabrous, whereas in others the scapes have a single row of sparse erect hairs. In one complex the glabrous scapes are particularly long, exceeding the vertexal margin by about half their total length, and the species are often yellow. In the broader sense, the group

includes relatively hairy species, as well as the *turneri* complex of relatively stout species (scapes exceeding vertexal margin by only about one-third their total length) that are very similar in appearance to species of Group F within the *wheeleri* radiation.

Other species-groups

There are some additional species-groups whose relationships to other species-groups are unclear. The most important of these is the *bruneus* group, whose dozens of species occur primarily in the southern arid zone. One radiation (including *M. bruneus* itself) is very distinctive, with short funicular segments and a relatively thick and sculptured integument. The scapes and mesosoma are covered with short, erect hairs, and the head is conspicuously bicolored (dark brown posteriorly, yellowish anteriorly). One species is very widely distributed, occurring in all mainland States and the NT. In other species of the group, antennal scapes are more sparsely hairy and funicular segments are not so short. Some of these species otherwise look similar to those described above, but sometimes with longer and stouter setae. Others are clothed with long silvery hairs, often also with dense silvery pubescence. In another radiation the mesosoma is very sparsely hairy, and the ants closely resemble species of the *fieldi* group.

Another group with unclear affinities is the extremely gracile *iridescens* group, consisting of two distinct complexes. The *iridescens* complex consists of medium-sized species that are reminiscent of species from Group A within the *aeneovirens* radiation. Major workers are orange-red with contrasting black gaster, but minor workers are often uniformly brownish. The species appear to be restricted to the southern semi-arid zone, except for one known from far northwestern Australia. One species with a peculiarly flattened head (Fig. 15a in Greenslade, 1979) occurs in mallee habitats throughout the southern semi-arid zone. The *bagoti* complex consists of at least three very large species that are reminiscent of species from the *aeneovirens* group. *Melophorus bagoti* is the largest species of the genus, and has specialised repletes. It is uniformly orange, and occurs throughout the central and northern arid zones. A closely related but beautifully shiny species with iridescent black gaster occurs in the Great Sandy Desert of northern WA. Another species with orange foreparts and contrasting black gaster occurs in central WA. The very strong similarities with species from the *aeneovirens* radiation would suggest that the *iridescens* group belongs there; however the latter lacks the projecting clypeus that is so characteristic of the *aeneovirens* radiation.

The final group with unclear affinities is Group E, comprising densely hairy species with a thick and heavily sculptured integument. All species have orange or red foreparts with contrasting black gaster, and occur primarily in the northern arid zone.

Although the species richness of *Melophorus* in arid Australia is remarkable, it is not unique among the Australian biota. Arid Australia supports many hundreds of species of the plant genus *Acacia* (Maslin & Hopper, 1982). *Acacia* is absent from many habitats in the region, and at most a handful of species co-occur at any particular site. In comparison, *Melophorus* is ubiquitous, more than ten species frequently co-occur, and spatial turnover is particularly high, much more so than in other ant genera. For example, ant surveys of two nearby stations in the Victoria River District of the NT (Fisher *et al.*, 2004) yielded a total of 32 species of *Melophorus*, only four (13%) of which were shared; this compares with 44% shared species among the remaining 90 ant species collected. These observations suggest that the total number of *Melophorus* species in arid Australia might be truly staggering.

Camponotus

As previously mentioned, *Camponotus* is well-represented in all Australian biomes, but is particularly rich in the arid zone. The arid fauna includes several radiations that occur primarily or exclusively in arid regions (Table 5), as well as representatives of virtually all other Australian species-groups within the genus. The major exceptions are the groups of arboreal,

phragmotic species that are restricted to wetter forests (Andersen, 2000; McArthur & Shattuck, 2001).

Table 5. Classification, distribution and diversity of major species-groups and complexes of *Camponotus* that occur primarily or exclusively in arid or seasonally arid Australia. Figures are numbers of species in the TERC collection. Distribution is described as predominantly northern (N; occurring primarily within the northern arid zone), southern (S; occurring primarily in the southern arid zone), monsoonal (M; occurring primarily in the monsoonal tropics) or widespread (W; well-represented throughout arid Australia).

***aurocinctus* radiation**

aurocinctus group (5, S)
ceriseipes group (8, S)
denticulatus group (24, W)
 denticulatus complex (13, N)
 terebrans complex (10, S)
 postcornutus complex (1, S)
perjurus group (2, S)
setosus group (4, M)

***subnitidus* radiation**

subnitidus group (19, W)
 rufus complex (1, S)
 subnitidus complex (7, N)
 tricoloratus complex (11, S)
Group A (10, W)
Group B (2, S)

***whitei* radiation**

intrepidus group (3 arid species, S)
 intrepidus complex (mesic habitats only)
 suffusus complex (3, S)
whitei group (9, S)
 leae complex (7, S)
 whitei complex (2, S)
Group C (3, S)
Group D (3, M)

***discors* radiation**

discors group (40, W)
evae group (9, S)
minimus group (18, S)
sponsorum group (13, S)
Group E (10, S)

***maculatus* radiation**

ephippium group (46, W)
 capito complex (11, S)
 ephippium complex (19, W)
 tasmani complex (16, S)
nigriceps group (27, S)

- consobrinus* complex (14, S)
- nigriceps* complex (13, S)
- nigroaeneus* group (32, W)
- pellax* group (30, M)
 - bigenus* complex (19, M)
 - pellax* complex (11, M)

aurocinctus radiation

The most conspicuous species of *Camponotus* in arid Australia belong to a radiation of fast-moving, diurnal, reddish and/or black species that have a characteristic cluster of long, J-shaped hairs on the base of the mentum (leading to the description ‘Bearded sugar ants’; Andersen, 2002). This is referred to as the *wiederkehri* group by Shattuck & McArthur (2002), but I consider it to include a number of distinct species-groups (see *aurocinctus* radiation in Table 5), all of which occur exclusively (or nearly so) in the arid zone or seasonal tropics. The most common of these is the *denticulatus* group, whose minor workers have an undifferentiated propodeum such that the mesosomal profile is a simple curve. The group includes the *denticulatus* complex of the central and northern arid zones, and the *terebrans* complex of the southern arid zone.

The *denticulatus* complex is considered a single species by Shattuck & McArthur (2002), but I recognise at least 13 species in the TERC collection. The complex occurs throughout central and inland northern Australia, building distinctive nests that have conspicuous mounds and often slit-shaped entrances. *Camponotus denticulatus* itself is a bicolored black and red species occurring throughout central Australia. Most other species are uniformly reddish, and occur in the northern arid zone or monsoonal tropics. In the field, minor workers strongly resemble meat ants (highly aggressive species of the *purpureus* group of *Iridomyrmex*, as outlined above). Interestingly, *C. denticulatus* is primarily black, as is the dominant meat ant (*I. viridiaeneus*) where it occurs, whereas most species in northern Australia are uniformly reddish, as is the locally dominant meat ant (*I. sanguineus*). This suggests that species of the complex might be meat ant mimics.

Unlike McArthur *et al.* (1998), I similarly recognise a number of species in the *terebrans* complex. One of these (possibly the species described by Santschi as *C. latrunculus victoriensis*) is restricted to mesic habitats of southern Victoria and Tasmania. In contrast, an undescribed pale species with large, bulbous eyes extends into the central arid zone. It is sympatric with *C. terebrans s.s.* in semi-arid northwestern Victoria. The complex seems to be particularly speciose in southwestern WA. In one such species, the vertexal corners of major workers form angular projections as in *C. postcornutus*, which I consider belongs to a monospecific complex within the *denticulatus* group (Table 5). I also include *C. gouldianus*, occurring throughout the southern semi-arid zone, in the *terebrans* complex.

Other groups within the *aurocinctus* radiation have a saddle-shaped mesosoma. In the *aurocinctus* group, the mesosoma has a conspicuous metanotal groove and the petiolar node is very long and low. Four species have been described in this group: *C. arenatus*, *C. aurocinctus*, *C. owensae* and *C. versicolor* (Shattuck & McArthur, 2002), but I consider *C. ‘aurocinctus’* to represent a complex of at least three species. In *C. aurocinctus ss*, the propodeum has a concave anterior face that forms an obtuse angle with the dorsal surface, and the gaster has conspicuous golden pubescence. The species is widely distributed in arid Australia, occurring in most mainland States and in the NT. It is morphologically uniform from southern South Australia (SA), through central Australia, to its northern limit in northern central WA. In what I consider to be an undescribed sibling species from the southeastern arid zone, the propodeum is variably rounded (never obtusely angled), the gaster totally lacks golden pubescence, and the petiole is

shorter and higher. Another apparent sibling species without gastric pubescence occurs in WA; it has a very broad and unusually hairy head.

In the remaining three groups of the *aurocinctus* radiation, a metanotal groove is more weakly developed (often absent), and the petiolar node is relatively short, high and rounded dorsally. The *ceriseipes* group consists of about ten species from the southern arid zone, four of which are described (*C. cerseipes*, *C. donnellani*, *C. prosseri* and *C. rufonigrus*; Shattuck & McArthur, 2002). The *setosus* group comprises at least four species from the northwestern monsoonal zone, only one of which is described (as a member of the *aurocinctus* complex; Shattuck & McArthur, 2002). Most species of the *setosus* group are covered with whitish pubescence (more golden on the gaster) and are densely clothed with long hairs. *Camponotus setosus* is a red and black species distributed from the Kimberley to the southern Top End of the NT, occurring on sandy soils associated with sandstone outcrops. The three other species are uniformly black; one of these from the Top End is unusual in that it is very sparsely hairy. Finally, the *perjurus* group consists of two known species in which the head is peculiarly attached well below the occipital margin (Shattuck & McArthur, 2002). In *C. perjurus* the foreparts are red and only weakly iridescent. An undescribed species from SA is uniformly blackish, with strong blue-green iridescence throughout.

subnitidus radiation

A second arid-adapted radiation of *Camponotus* comprises species of the *subnitidus* and related groups, which have extremely long and glabrous antennal scapes (hence the name Aerial sugar ants; Andersen, 2002). The clypeus of major workers projects as a simple, rectangular lobe, distinguishing these ants from superficially similar species belonging to the *maculatus* radiation (see below). The clypeal region of major workers is often heavily pitted and somewhat flattened, suggestive of partial phragmosis. The ants are primarily nocturnal, so are somewhat inconspicuous despite including some of the largest species of Australian *Camponotus*.

The *subnitidus* group comprises very large species in which the sides of the heads of minor workers are markedly divergent anteriorly. Two major complexes can be recognised: the *subnitidus* complex of northern Australia, in which the petiolar node is very long and low, with a nipple-like projection dorsally, and the *tricoloratus* complex of the southern arid zone, where the node is short and erect. A second group (Group A in Table 5) comprises smaller, often pale species that look superficially like members of the *claripes* group from the *maculatus* radiation. They occur throughout inland Australia, but are not commonly collected. The final group (Group B in Table 5) consists of a small number of dark reddish brown species from the southern semi-arid zone, in which the mesonotum of minor workers has a posterior hump.

whitei radiation

A third major arid-adapted radiation of Australian *Camponotus*, comprising the *whitei* and related groups, consists of mostly dark-colored, diurnal species with thick and often coarsely sculptured integuments. The *whitei* group consists of medium-sized species that occur primarily in southern semi-arid regions. Two complexes can be recognised, one in which the mesosoma is biconvex (*whitei* complex) and the other in which the mesosoma is saddle-shaped (*leae* complex). *Camponotus whitei* is by far the most common and widespread species of the group, occurring from central northern Qld, through western NSW to northwestern Victoria, and across to southern WA. All other species of the group have been rarely collected. A related group (Group C in Table 5) consists of small, robust and brownish species in which the mesosoma is straight and uninterrupted in profile, with the propodeum often projecting backwards over the petiole. The group appears to be endemic to central and southern WA. In another, possibly closely-related group from northwestern Australia (Group D in Table 5) the mesosoma is likewise straight and uninterrupted in profile, but the species are larger and more gracile. All species of Groups C and D appear to be rare. Finally, the *intrepidus* group seems to belong to the

whitei radiation. Most species of this group occur in mesic habitats, but at least two species of the *suffusus* complex occur in semi-arid southeastern Australia.

discors radiation

I have perhaps artificially clustered together a range of morphologically generalised species-groups from arid Australia as the *discors* radiation, a fourth major radiation of arid-adapted Australian *Camponotus*. Some of these species-groups closely resemble species-groups from the *maculatus* radiation (see below), and very possibly belong there. However, in all cases major workers lack the conspicuously notched or otherwise indented anterior clypeal margin that is so characteristic of Australian groups within the *maculatus* radiation (except for the *novehollandiae* group). It is very possible that this clypeal character has been secondarily lost in some or all of these species-groups, rather than them belonging to a separate radiation.

In the *discors*, *minimus* and *evae* groups the mesosoma is disc-shaped and laterally compressed posteriorly. I suspect that such morphology is convergent, given that it occurs in unrelated species-groups both in Australia and overseas. The *discors* group is particularly rich in species, and occurs throughout inland Australia. Minor workers of all species are yellowish, either uniformly so or with infuscated patches on the mesosoma and head. Species of the apparently closely related *minimus* group, which are restricted to the southern arid zone, are among the smallest of all terrestrial *Camponotus*, with minor workers only 3-4 mm in total length. They are either blackish with pale legs (as in *C. minimus*) or uniformly yellowish (e.g. *C. scratius*), and strongly resemble miniature species from the *claripes* group (*C. minimus* was in fact described as a subspecies of *C. claripes*). In the *evae* group the mesosoma is especially strongly compressed (the propodeal dorsum is ridge-like), and the pronotum is markedly flattened dorsally. All species are black, often with pale legs, and the integument is rather conspicuously sculptured and dull. Two complexes can be recognised, one in which the anterior clypeal margin is a simple convexity, and the other in which the margin is concave medially. It is possible that the Australian honeypot ant *Camponotus inflatus* also belongs here as a third complex, rather than where it has been traditionally placed as a member of the *nigroaeneus* group of the *maculatus* radiation.

I have also included the *sponsorum* group and apparently closely related Group E in the *discors* radiation. Both groups comprise relatively small, diurnal species from the southern arid zone. The petiole is relatively long and broadly rounded, and the gaster is covered with silvery pubescence. Species of the *sponsorum* group have a saddle-shaped mesosoma where the propodeum is markedly concave in profile. Most species are bicolored yellowish and black. One such species (possibly *C. sponsorum* itself) is extremely widely distributed, occurring throughout the southern arid zone and extending into central Qld. Species from Group E have longer and narrower heads and longer scapes (exceeding vertexal margin by at least half their total length), and the mesosoma has a simple profile (propodeum at most feeble concave in profile). They have the appearance of small species of the *nigroaeneus* group, to which they are in fact possibly related.

maculatus radiation

In addition to the four major arid-adapted radiations outlined above, several arid-adapted species-groups occur within the cosmopolitan *maculatus* radiation, which is ubiquitous in Australia (Table 5). As previously mentioned, this radiation comprises a range of species-groups in which the anterior clypeal margin of major workers is conspicuously notched or otherwise indented medially (see Greenslade, 1979). The *nigriceps* group consists of large, yellowish (head and often also gaster contrasting black) nocturnal species from southern Australia, in which the anterior clypeal margin of all workers projects as a pair of moustache-shaped angular lobes (McArthur and Adams, 1996). Two complexes can be recognised, one (*nigriceps* complex) in which the gula has numerous erect hairs, and the other (*consobrinus* complex) where the gula is

glabrous. Most species of the *consobrinus* complex have a bicolored gaster, with the first segment yellowish anteriorly; exceptions include *C. loweryi* from eastern semi-arid Australia (gaster uniformly yellowish) and an undescribed species with a uniformly black gaster from northern NSW and southeastern Qld. *Camponotus consobrinus* itself is restricted to mesic habitats of southeastern Australia (including Tasmania), but most other species occur in semi-arid regions. The *nigriceps* complex extends deeper into the central arid zone.

The remaining arid-adapted groups within the *maculatus* radiation consist of fast-moving, diurnal, reddish and/or black species, all with very many species. The most common of these are species of the morphologically generalised *nigroaeneus* group. *Camponotus nigroaeneus* itself is restricted to mesic habitats of southeastern Australia, and the closely related *C. aeneopilosus* is distributed along the eastern seaboard from northern Victoria to North Queensland, but otherwise the group occurs exclusively in the arid zone. In most species the gaster is covered in silvery or golden pubescence, but there are many exceptions. One of these is *C. amperi*, which occurs throughout the southern semi-arid zone. A similar, undescribed species is widespread on cracking clay soils of the semi-arid tropics. A least two species of the *nigroaeneus* group are strongly iridescent throughout.

The final two arid-adapted groups that I place within the *maculatus* radiation are the closely related *ephippium* and *pellax* groups. In both cases the major workers are partly phragmotic, and their occipital corners extend backwards as rounded lobes. Species of the *ephippium* group have a characteristically concave mesosomal profile. Three distinct complexes can be recognised (Table 5). In the *ephippium* complex the vertexal corners are distinctly angled laterally. *Camponotus ephippium* occurs throughout the eastern arid zone, up to central Qld where it co-occurs with the closely-related *C. dromas*, which is distributed throughout the semi-arid tropics. Several uniformly black species with golden gasters occur in North Queensland, and another such species occurs in the southern Kimberley. Species of the *tasmani* complex have rounded rather than angled heads laterally, and occur primarily in the southern arid zone. In the *capito* complex, the mesosoma is highly polished, very markedly concave in profile, and only sparsely hairy. Most species are reddish with contrasting black gaster, and also occur in the southern arid zone. Lastly, the *pellax* group consists of numerous relatively small species from the monsoonal tropics. Species of the *pellax* complex have red foreparts and black gaster, and occur primarily in the western monsoonal zone. At least two species have a strongly iridescent gaster. Species of the *bigenus* complex are uniformly black, and occur primarily in the eastern monsoonal zone.

Several non-arid species groups of the *maculatus* radiation also occur in arid Australia, including the tropical *novaehollandiae* group (Andersen, 2000) and cosmopolitan *claripes* and *rubiginosus* groups. However, these are not considered here.

Monomorium

The exceptional diversity of the *Monomorium* fauna from arid Australia is not at all reflected in the recent revision of Australian *Monomorium* by Heterick (2001), who recognised a total of only 59 species throughout Australia. Many of Heterick's 'species' were described as being extremely widespread and highly variable, and most ant taxonomists would consider them each to represent several to many valid species. The higher-level classification of species that I propose here (Table 6) also differs significantly from that presented by Heterick (2001).

nigrum radiation

This is an extremely rich radiation of very small, mostly generalist species with 11-segmented antennae, and smooth and shiny mandibles having three or four teeth. All other Australian species groups of *Monomorium* have 12-segmented antennae, and were previously referred to the now synonymised genus *Chelaner*. Species of the *nigrum* radiation are ubiquitous in Australian ant communities outside the coolest and wettest habitats, but are particularly diverse and abundant in the arid zone and seasonal tropics. The *nigrum* group

(considered by Heterick (2001) to represent a single variable species, *M. fieldi*) consists of very many blackish species that are predominantly smooth and shiny (Plate 9, Andersen, 2000), with most occurring in the tropical north. They are extremely challenging taxonomically, but several complexes can be recognised. The *nigrum* complex comprises tiny species with short antennal scapes, glabrous hind femora, and often a short and obliquely angled propodeum. They occur throughout higher rainfall areas of northern Australia. The *fieldi* complex contains larger species with longer scapes (approximately reaching the vertexal margin), and have at least a few erect hairs on the hind femora. A third complex (with no described species) comprises a small number of species from the Top End of the NT with broad heads, short scapes, and small petiolar nodes. One species is weakly polymorphic, and two others have conspicuous sculpturing on the propodeum.

Table 6. Classification, distribution and diversity of major species-groups of *Monomorium* that occur primarily or exclusively in arid or seasonally arid Australia. Figures are numbers of species in the TERC collection. Distribution is described as predominantly northern (N; occurring primarily within the northern arid zone), southern (S; occurring primarily in the southern arid zone), monsoonal (M; occurring primarily in the monsoonal tropics) or widespread (W; well-represented throughout arid Australia).

***nigrum* radiation**

carinatum group (23, N/M)
 carinatum complex (15, M)
 complex A (8, N)
eremophilum group (30, S)
laeve group (64, W)
nigrum group (24, M)
sydneyense group (7, W)
 Group A (7, E)

***rothsteini* radiation**

rothsteini group (47, W)
sordidum group (25, W)

***antarcticum* radiation**

centrale group (4, W)
flavipes group (8, S)
 flavipes complex (6, S)
 euryodon complex (2, S)
insolescens group (30, M)
lacunosum group (5, S)
longiceps group (8, S)
 legulus complex (3, S)
 longiceps complex (5, S)

***longinode* radiation**

capito group (5, N)
longinode group (2, S)

***whitei* radiation**

falcatum group (4, S)
whitei group (18, S)

The *carinatum* group also has a tropical distribution, but occurs primarily in drier habitats. The mesosoma and petiole are conspicuously sculptured, and at most sparsely hairy. The group contains two complexes (Andersen, 2000). In species of the *carinatum* complex the promesonotal dorsum is markedly flattened and broadly trapezoidal, often with distinct lateral margins. There are at least 15 species, distributed throughout the northern arid zone and semi-arid tropics. Species from the second complex (Fig. 16, Andersen, 2000; Complex A in Table 6) are smaller and the mesosoma is rounded dorsally and always glabrous. Heterick (2001) considered them all to be variants of *M. sydneyense*, which I believe belongs to a separate group. *Monomorium sydneyense* has a finely reticulate propodeum but is otherwise smooth and shiny, and is restricted to humid and sub-humid habitats of southeastern Australia (except for a recent introduction into New Zealand). It is glabrous, and in southern Victoria co-occurs with a very similar but hairy species that extends into Tasmania. Superficially similar species occur throughout Australia outside the central arid zone. I have provisionally classed them together as the *sydneyense* group, but they are very possibly polyphyletic. It is possible that *M. sydneyense* and allies are closely related to the *eremophilum* group, which comprises very many granivorous species from the southern arid zone. In all cases the median clypeal carinae project as a pair of sharp teeth. Many species, including *M. nanum*, have very large, reniform or tear-shaped eyes. Another group, with apparently no described species (Group A in Table 6), also has large, reniform eyes. However, the anterior clypeal margin of these species is not laterally denticulate, suggesting they are not granivorous. The final group in the *nigrum* radiation is the *laeve* group, whose numerous yellowish, mostly nocturnal species are ubiquitous in arid Australia.

rothsteini radiation

This is an exclusively arid-adapted radiation that seems to be allied to the *nigrum* radiation. The species have a saddle-shaped mesosoma (incorporating a deep metanotal groove), large and erect petiolar node, smooth and shiny head and promesonotum, and mandibles with three teeth. The radiation comprises two very distinct groups. Species of the *sordidum* group are highly generalised ants that strongly resemble species of the *nigrum* group. In most species the propodeum is densely sculptured, but in some from the southern arid zone it is almost entirely smooth and shiny. *Monomorium megalops* is a species from the complex with very large eyes, and occurs throughout the eastern arid zone. At least one other species has similarly large eyes.

The *rothsteini* group comprises granivorous species that are the most abundant harvester ants in arid Australia (Andersen, 2000). The group is very conservative morphologically, but there is undoubtedly very many species – apparently at least 50 and possibly many more. Several complexes can be recognised. One of these has particularly long striae on the sides of the head anteriorly (the striae extend to the lower margin of the eye), and includes three very common and widespread species. One is a particularly large and robust species that occurs throughout most of far northern Australia (it is the species studied in Andersen *et al.*, 1991, and *Monomorium* sp. 1 in Andersen *et al.*, 2000). Another has a very deeply incised anterior clypeal margin, and occurs throughout the semi-arid tropics. The third has a relatively short, narrow and dorsally tapered petiolar node, and is widespread in central Australia. In a second complex, the mesonotum is conspicuously sculptured dorsally. One such species is common throughout arid NT, and others occur in northern WA.

Most species of the *rothsteini* group have reddish foreparts with contrasting black gaster. However, in many species the foreparts are conspicuously infuscated, and some are uniformly blackish. Several such uniformly blackish species occur in northern WA. In several otherwise reddish species, peculiar black individuals can be observed foraging with normal workers. It is not clear if these represent an apterous reproductive caste from the host colony, or are parasitic species.

antarcticum radiation

This is a Gondwanan radiation of variously granivorous species that includes groups restricted to wet forests (such as the *leae* group of southern Australia and the closely related *antarcticum* group of New Zealand), as well as five major groups centred on the Australian arid zone and monsoonal tropics. In all these arid groups the mesosomal profile is a simple curve, with the propodeum at most feebly differentiated.

The *flavipes* group is closely related to the *leae* group; in both cases the mandibles have five teeth, the clypeus projects over the mandibles as a broadly rounded or blunt lobe, and the species are seed-eating omnivores. However, species of the *flavipes* group lack the differentiated propodeum of the *leae* group, and occur in drier habitats. Two complexes can be recognised, the *flavipes* complex comprising monomorphic species (as is typical for *Monomorium*) and the *euryodon* complex containing polymorphic species. Several species of the *flavipes* complex are known from subhumid habitats of southeastern Australia, another occurs throughout the southern semi-arid zone, and another is restricted to semi-arid southwestern WA. The *euryodon* complex includes at least two species, one occurring from semi-arid central Qld to western NSW, and another in semi-arid southwestern WA.

The *centrale* group appears to be closely related to the *flavipes* group, from which it can be distinguished by its anterior clypeal margin that is conspicuously concave medially, and longer and more cuboid petiolar node. The basal tooth of the mandibles is reduced to a small denticle or is absent altogether. As in the *flavipes* group, all species are yellowish or reddish brown. One is widely distributed in the central arid zone, from SA to northwestern Qld, with most other species occurring in southern semi-arid regions. However, at least one species is known from North Queensland and another from the Kimberley region of far northern WA.

The *lacunosum* group consists of a small number of uncommon, heavily sculptured species that otherwise resemble species of the *centrale* group. Two complexes can be recognised. In one, the propodeum is armed with teeth or short, broad spines, and the metapleural lobes are likewise produced into broad spines. This complex includes *M. lacunosum* from semi-arid southwestern WA, and an undescribed species from semi-arid northwestern Victoria. In the second complex, the propodeum is unarmed and the metapleural lobes are more flange-like than spinose. The complex comprises a small number of species known only from central Qld and central NSW.

The *longiceps* group comprises up to a dozen reddish brown, conspicuously sculptured species occurring in eucalypt (particularly mallee) woodlands throughout the southern semi-arid zone. They are major predators of eucalypt seeds (e.g. the species referred to as *Chelaner* sp. 3 in Andersen, 1982). The group contains two distinctive complexes. In the *longiceps* complex the propodeum is armed with teeth, and the petiolar node is relatively short and erect. The species resemble those of the *lacunosum* group, and presumably the two groups are closely related. The *legulus* complex contains larger species with an unarmed propodeum, a long, broadly rounded petiolar node, and a clypeus armed with a large pair of acutely angled projections.

The *insolescens* group appears to parallel the *longiceps* group in northern Australia, and is the only arid-adapted group within the *antarcticum* radiation that has a northern distribution. The group occurs throughout the monsoonal tropics, but primarily in the western monsoonal region, and is particularly diverse in the Kimberley. The group as a whole is remarkable for both its diversity and the limited distributions of its species. Of the 30 species in the TERC collection, 19 are known only from relatively small areas in the Kimberley, and most of the others appear to be restricted to similarly small areas of the northern half of the NT. Three of the latter commonly co-occur in subcoastal habitats of the Top End. Only one species within the group could be considered widely distributed – a heavily sculptured species with very large eyes occurs across semi-arid NT into northwestern Qld. This species, as well as several others that are also heavily sculptured, bears a strong resemblance to species of the *longiceps* group. However, other species of the *insolescens* group are markedly divergent. The most extreme belong to a complex of large, smooth and shiny species, with long petiolar peduncles and high nodes. These species

have angular vertexal corners with a feebly to markedly concave vertexal margin, very prominent rounded or acutely angled clypeal projections, and relatively long funicular segments (see Fig. 18 in Andersen, 2000).

longinode radiation

This is a small radiation of granivorous species that is presumably allied to the *antarcticum* radiation, and possibly belongs there. The species are heavily sculptured and typically have a long and low petiolar node. Some species of the *insolescens* group also share these features, so there is possibly a close relationship, particularly with the *capito* group. The *capito* group comprises a small number of species from the northern arid zone, characterised by a very large, longitudinally striate head, massive clypeal teeth, and reduced numbers (only 2 or 3) of mandibular teeth. The most widespread of these is *M. bifidum*, which occurs in both the Top End and the Kimberley. There are at least three other sibling species, one in the central arid zone, another in the Victoria River District, and another in the East Kimberley. *Monomorium capito* has a particularly long and low petiolar node, and is known from only a single specimen collected from remote central Western Australia (Heterick, 2001). The only other known member of the *capito* group is a remarkable species in which the head has an exceptionally low attachment to the mesosoma, the propodeum is armed with a pair of teeth, and the petiole is feebly sculptured and relatively short and high. It appears to be restricted to the Katherine region of the southern Top End.

The *longinode* group consists of two or three species from southern WA. These species have a similar mesosoma and petiole to *M. capito*, but have smaller, more coarsely and irregularly sculptured heads, and the anterior clypeal margin has short, bluntly rounded lobes rather than prominent teeth.

whitei radiation

This radiation comprises specialist granivores of the southern arid zone, and its relationship to other radiations of Australian *Monomorium* is unclear. The *whitei* group consists of large-headed species with a prominent promesonotum that is markedly higher than the propodeum in profile. *Monomorium whitei* is a very large, polymorphic species that occurs throughout the southern arid zone, from southwestern Qld to southern WA. It has a reddish brown head and mesosoma, with contrasting yellowish brown gaster. There are several other very similar taxa in the region that vary in coloration and sculpturing, indicating a complex of unresolved sibling species. *Monomorium bicornis* is a closely related mid-size, uniformly black species occurring throughout southeastern semi-arid Australia. A sibling species with a longitudinally striate head and contrasting yellow-brown gaster occurs in southern WA. Most of the diversity within the *whitei* group resides in several complexes of small, monomorphic species that have radiated primarily in southern WA. One of these complexes is characterised by very long and elongate eyes, and includes *M. anthracinum*.

The *falcatum* group consists of a handful of small, stout species with foveolate heads and the presence of propodeal denticles or spines. Two distinct complexes can be recognised. Species of the *falcatum* complex (including *M. falcatum* and *M. elegantulum*) have 12-segmented antennae and prominent propodeal spines, and are represented throughout the southern arid zone. Species of the *decuria* complex have 10-segmented antennae and the propodeum is armed with small denticles only; they are restricted to southwestern WA.

Rhytidoponera

Rhytidoponera is widespread in the Australian region, and includes several species-groups occurring primarily or exclusively in wet forests. However, it is particularly diverse in arid Australia, where it is virtually ubiquitous. Species of *Rhytidoponera* are mid-sized to very large ants with highly generalised habits, and are most abundant at relatively unproductive sites for

ants where behavioural dominance (especially by *Iridomyrmex*) is relatively low. In the arid zone they are particularly important components of local ant communities on poorly drained soils or at rocky sites (Andersen, 2003). Most species in arid Australia belong to exclusively arid-adapted species-groups (and indeed radiations; Table 7), and there is very little penetration into arid Australia from forest species-groups.

Table 7. Classification, distribution and diversity of major species-groups and complexes of *Rhytidoponera* that occur primarily or exclusively in arid or seasonally arid Australia. Figures are numbers of species in the TERC collection. Distribution is described as predominantly northern (N; occurring primarily within the northern arid zone), southern (S; occurring primarily in the southern arid zone), monsoonal (M; occurring primarily in the monsoonal tropics) or widespread (W; well-represented throughout arid Australia).

***tyloxys* radiation**

tenuis group (16, M)
tyloxys group (12, N)
 dubia complex (5, N)
 tyloxys complex (7, N)

***metallica* radiation**

anceps group (1, S)
metallica group (37, S)
 metallica complex (33, S)
 borealis complex (4, M)
flavipes group (2, S)

***mayri* radiation**

aurata group (12, M)
convexa group (62, W)
foveolata group (13, W)
 foveolata complex (9, S)
 micans complex (4, N)
mayri group (18, W)
taurus group (21, M)

***reticulata* radiation**

reticulata group (20, M)
 Group A (6, N)

tyloxys radiation

This radiation consists of two species-groups with highly reduced (often absent) hind tibial spurs. The *tyloxys* group is arguably the most distinctive of all groups within *Rhytidoponera*, and seems to be an outlier within the genus both morphologically and biologically. The long, narrow head, very large eyes and massive mandibles suggest a high degree of specialisation, but details of their biology are not known. Two clearly defined complexes can be recognised. In the *tyloxys* complex the petiolar node is armed with a dorsal spine. In *R. tyloxys* the spine is reduced to a short, angular projection; this species occurs throughout the northern arid zone and semi-arid tropics. A species with a more prominent spine is extremely widespread (but uncommon) throughout the central arid zone. A very similar species occurs in the Kimberley region, but

differs in having an elaborate rather than simple anterior clypeal margin. In two other species from the Kimberley the petiolar spine is extremely long and thin.

In the *dubia* complex the petiole is broadly rounded dorsally (Fig. 9b, Andersen, 2000). *Rhytidoponera dubia* is restricted to the Top End and northern Victoria River District of the NT, where it is usually found foraging on low vegetation. A similar but larger species occurs throughout the northern half of the NT and into the Gulf region of northwestern Qld. A larger species again occurs throughout the central arid zone, and is the only species of the *tyloxys* group known from SA.

The *tenuis* group seems much closer to mainstream *Rhytidoponera* both morphologically and biologically. It consists of a large number of relatively small and gracile species from the monsoonal zone (Fig. 9c, Andersen, 2000), apparently only one of which is described. Most have rather limited distributions. A species with a densely punctate first gastric tergite is common throughout the Top End of the NT, and a similar species occurs in central Qld. In *Rhytidoponera tenuis* the first gastric tergite has feeble striations over dense background punctation; it is restricted to the broader Townsville/Cairns region of North Queensland. In several species the first gastric tergite is coarsely striate but otherwise shiny anteriorly, and densely punctate posteriorly. In several other species the first gastric tergite is striate throughout.

metallica radiation

This is a radiation of smaller species occurring primarily in southern Australia. Most of the species belong to the extremely rich but morphologically conservative *metallica* group. *Rhytidoponera metallica* as I understand the species is a metallic green, highly opportunistic species occurring in a wide range of open habitats throughout southeastern Australia. It is an extremely common urban ant throughout the region, and is familiar to many people because of its relatively painful sting. Very many similar species occur in the southern arid zone. In some the mesosoma has bulging pronotal shoulders and an extended 'neck'. A relatively smooth and shiny species with sparse hairs occurs throughout the western semi-arid zone. Most species have prominent, backward projecting occipital lobes, but in others these lobes are reduced or absent. A species with coppery pink iridescence is widespread in the central arid zone, and other species are brilliantly blue. A smaller number of species, including *R. tasmaniensis* from mesic habitats of the southeast, and *R. inornata* from the southwest, lack iridescence altogether.

All the above species appear to be seed-eating omnivores. A separate complex of non-granivorous, usually non-iridescent species occurs in the northern monsoonal tropics. The most common of these are *R. borealis* (Fig. 9a, Andersen, 2000), *R. brunnea* and *R. trachypyx*, which co-occur along with an uncommon undescribed species in the the Top End of the NT. *Rhytidoponera brunnea* was synonymised with *R. borealis* by Brown (1958), but can be distinguished by its short and high petiolar node, and finer sculpturing on the occipital lobes. Both species also occur in the northern Kimberley, along with another undescribed species with small eyes and reduced occipital lobes. At least two undescribed species with bluish iridescence and an unusually projecting clypeus occur in Cape York Peninsula.

The *flavipes* group consists of a small number of species from the southwestern arid zone. They are more gracile, less coarsely sculptured ants with relatively narrow heads and very large eyes, giving them the general appearance of species of the *tyloxys* group.

The final group within the *metallica* complex considered here is the *anceps* group. *Rhytidoponera anceps* is a relatively small species with a cuboid petiolar node and large eyes. It has a remarkably disjunct distribution, with distant populations in southern WA and central Qld. Another complex (*victoriae* complex) in the *anceps* group is extremely common in mesic habitats throughout the eastern seaboard, and is not considered here. There is a small number of other groups within the *metallica* radiation that occur exclusively in eastern forests (e.g. *impressa* group, Ward, 1980), and these are likewise not considered here.

mayri radiation

This is the major arid-adapted radiation within the genus, and includes all the larger species of arid Australia. The most common representatives are species of the extremely rich but morphologically uniform *convexa* group, which occurs throughout most of inland Australia. The species are mid-sized for *Rhytidoponera*, and have a characteristically short, high and dorsally flattened node, and a relatively simple occipital vertex. Within the group, there are one or more complexes of somewhat larger, less coarsely sculptured species that have rectangular heads with a distinctly concave vertexal margin. The head is variously punctate and foveolate, but never coarsely rugose. One of these is *R. maniae*, a very common ant throughout semi-arid southeastern Australia. In more typical species, the head is coarsely reticulate-rugose, and not so broad behind the eyes (Fig. 9g, Andersen, 2000). One complex of species (*R. violacea* and allies) from central and southern WA is conspicuously iridescent. *Rhytidoponera rufithorax* is a distinctive reddish brown species with contrasting dark brown gaster that occurs throughout the semi-arid tropics. It co-occurs throughout its range with an extremely similar but uniformly blackish (gaster sometimes paler brown) species. *Rhytidoponera convexa* is a relatively hairy species from central and North Queensland. *Rhytidoponera pilosula* is a particularly hairy, uniformly blackish species from southwestern Qld and northwestern NSW. A very similar species is highly abundant in Mitchell grasslands of northwestern Qld and semi-arid NT.

The *foveolata* group appears to be closely allied to the *convexa* group, especially to the first complexes described above. They are larger, more robust species, with broadly rectangular heads, usually with a concave vertexal margin. Species of the *micans* complex are finely but densely punctate throughout, with scattered, shallow foveolae, and occur in the central and northern arid zones. Species of the *foveolata* complex are more coarsely sculptured, and occur in the southern arid zone.

The *mayri* group consists of numerous, very large species with prominently crested heads. They typically construct 'volcano' nests, often at the bases of shrubs. *Rhytidoponera mayri* is widespread in the southeastern arid zone, but most other species have more limited distributions. In the monsoonal tropics the group is largely replaced by species of the closely related *aurata* and *taurus* groups (Andersen, 2000). In the latter the vertexal lobes are produced as prominent horn-like projections (Fig. 9h, Andersen, 2000). *Rhytidoponera taurus* is widely distributed in the central and northern arid zones, but virtually all other species are restricted to the monsoonal tropics. The group is particularly rich in northern WA, where apparently at least a dozen species occur. In the *aurata* group (Plate 5, Andersen, 2000) the horns are reduced to acute vertexal angles. With two exceptions, all species appear to be restricted to either the Top End or Kimberley. One of the exceptions is a uniformly reddish brown species that occurs throughout the monsoonal zone, and the other is a uniformly blackish brown species occurring in the Top End, Victoria River District and Kimberley.

reticulata radiation

This is a tropical radiation containing two arid-adapted species-groups, each with a cuboid petiolar node and long, spinose sub-petiolar process. In the *reticulata* group the head is at most slightly crested and the vertexal corners are not prominently lobed. *Rhytidoponera reticulata* (Fig. 9e in Andersen, 2000) is a slightly crested species that is very common throughout the Top End. A very similar but more feebly crested, more densely hairy and less coarsely sculptured species occurs in semi-arid NT and northwestern Qld. Most other species occur in northern WA.

The other species-group within this radiation (Group A in Table 7) comprises species with the general appearance of those of the *reticulata* group, but with conspicuous vertexal crests or lobes. There are six known species, none of which are described. All occur in the semi-arid tropics, mostly in the NT.

CONCLUSION

This chapter has presented a systematic overview of the five major genera contributing to the remarkable ant diversity in arid Australia. For some genera (*Melophorus* and *Iridomyrmex*) this represents their first comprehensive treatment at the species-group level. For others (*Monomorium*, *Camponotus*) the analyses significantly challenge recent taxonomic work, particularly at the species level. All the genera contain very difficult species complexes whose final resolution remains a long way off. Many species-groups and indeed entire genera are highly conservative morphologically, often making it difficult to determine relationships between groups, and sometimes to assign species to species-groups. The application of molecular techniques would be highly informative here, but unfortunately has had very limited use in Australian ant taxonomy. The use of molecular techniques would also be important for investigating relationships between Australian and other species-groups in genera such as *Monomorium* and *Rhytidoponera*.

The five major genera considered here exhibit highly divergent biogeographical profiles (Fig. 4). The most extreme is shown by *Iridomyrmex*, where the overwhelming majority (85%) of species belong to groups that are widely distributed throughout arid Australia (Fig. 4a). This is perhaps explained by the genus being an ancient autochthonous element of the Australian ant fauna that has radiated within Australia over a very long period of geological time. In contrast, *Monomorium* has a far more even biogeographical profile, with substantial proportions of species from both southern and northern species-groups (Fig. 4d). *Monomorium* has a complex biogeographical history within Australia, apparently including relatively recent incursions of tropical elements from South-East Asia (*nigrum* radiation), as well as Gondwanan stock (e.g. *antarcticum* radiation).

Melophorus and *Rhytidoponera* both belong to entirely Gondwanan taxa (Melophorini and Ectatomminae respectively), but both contain a substantial proportion of species from northern groups within Australia (Figs 4b, e). For *Rhytidoponera*, this can be explained by the predominantly tropical distribution of ectatommines generally. However, all other melophorines occur primarily in cool-temperate climates, so in *Melophorus* the prominence of northern over southern Australian elements is surprising.

The biogeographical history of *Camponotus* in Australia, where the arid zone supports a high proportion of species from southern species-groups (Fig. 4c), is unclear. The *aurocinctus*, *whitei* and *discors* radiations appear to be endemic to Australia. The *subnitidus* radiation occurs in South-East Asia and possibly also southern Africa. The *maculatus* radiation (which possibly includes groups assigned to the *discors* radiation in Table 5) occurs throughout the Old World. Within this radiation, the *novaehollandiae* group would seem to be a geologically recent incursion into Australia from South-East Asia, given its prevalence throughout that region and its exclusively tropical distribution within Australia. As previously noted, its major workers lack the notched anterior clypeal margin that is characteristic of other Australian groups within the *maculatus* radiation, which all appear to be endemic to Australia. It is therefore possible that the latter evolved within Australia from Gondwanan stock.

It is one thing to describe the remarkable ant diversity in arid Australia; it is another to explain it. An answer to the fundamental question of why ant diversity is so remarkably high in arid Australia remains elusive. However, it is possibly related to unusually high ant productivity and behavioural dominance over evolutionary time, perhaps driven by an unusually high supply of plant exudates, ultimately in response to low soil fertility and erratically pulsed rainfall (Andersen, 2003). Highly productive communities are also typically highly diverse, due to interaction selection producing numerous highly specialised taxa (Greenslade, 1983). It is clear that interaction selection has played a major role in shaping the arid Australian ant fauna at higher taxonomic levels, with the extent of morphological, physiological and behavioural specialisation exhibited by genera such as *Meranoplus*, *Melophorus* and *Cerapachys* being

unparalleled in other arid ant faunas (Andersen, 2003). However, the extent to which this might explain exceptional diversity at the species level remains unclear.

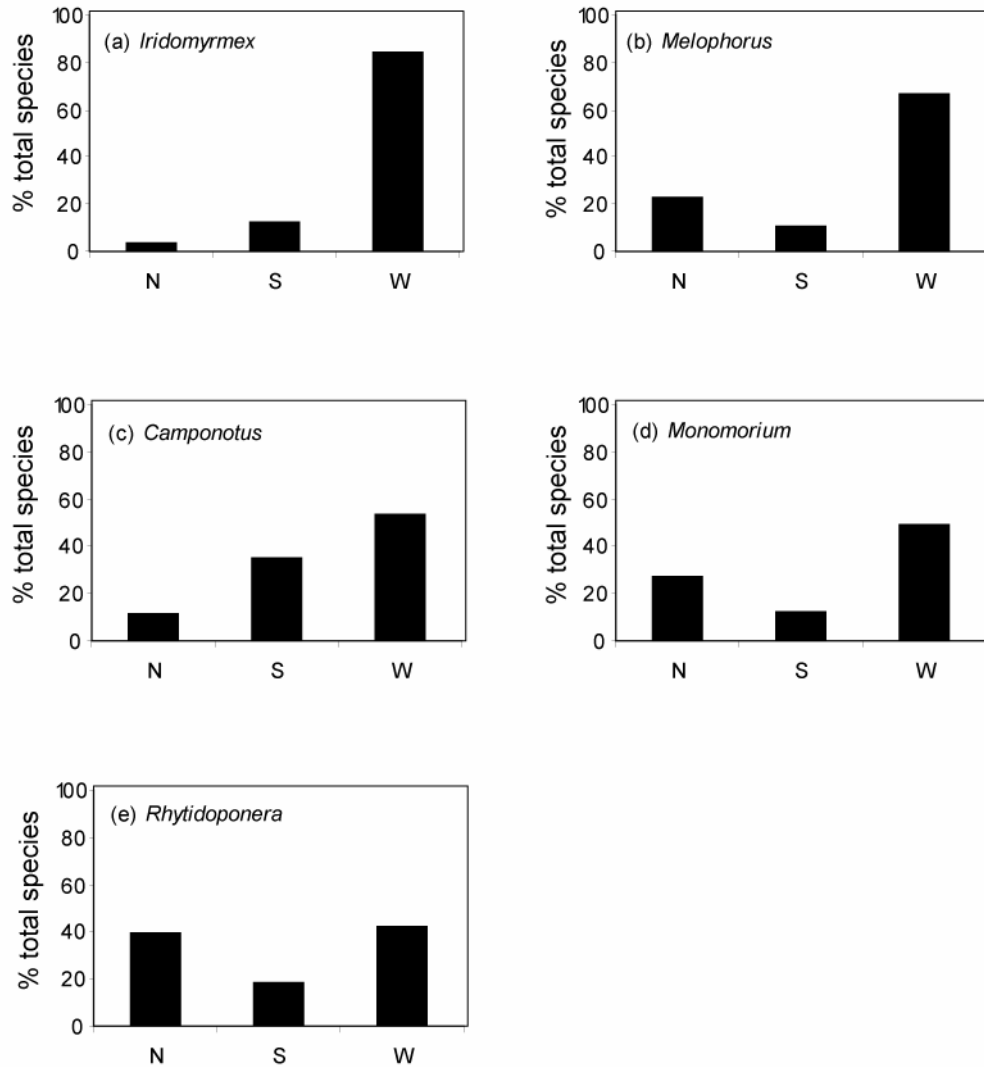


Fig. 4. Proportions (%) of species belonging to northern (N), southern (S) and widespread (W) species-groups in terms of their distributions in arid Australia. Data are from Tables 3-7 (data for northern species-groups also include those occurring primarily in monsoonal Australia).

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Appendix 1. Key to species-groups of *Melophorus*, based on minor workers unless otherwise stated.

1. Hind tibia without a conspicuous apical spur 2
Hind tibia with a conspicuous apical spur 6
2. Antennal scapes relatively short, exceeding vertexal margin by at most half their total length 3
Antennal scapes very long, exceeding vertexal margin by well over half their total length . 5
3. Mesosoma glabrous **Group G**
Mesosoma covered with short erect hairs 4
4. Head and mesosoma densely punctate and dull throughout; gaster covered with short, silvery pubescence **fulvihirtus group**
Head and mesosoma smooth and shiny throughout; gaster likewise shiny, without silvery pubescence **Group I**
5. Dorsum of mesosoma markedly flattened, with distinct lateral carinae, and glabrous; distal half of antennal scapes conspicuously swollen; frontal carinae closely approximated, separated by a distance no greater than the maximum scape diameter (southwestern WA)....
..... **majeri group**
Dorsum of mesosoma not markedly flattened, without distinct lateral carinae, and covered with short erect hairs; distal half of antennal scapes not conspicuously swollen; frontal carinae separated by a distance greater than twice the maximum scape diameter (northern Australia) **anderseni group**
6. Antennal scapes very short, at most exceeding vertexal margin by a distance equal to their maximum diameter; propodeal spiracle very large, as long as at least half the maximum height of the propodeum **potteri group**
Antennal scapes exceeding vertexal margin by a distance equal to at least twice their maximum diameter; propodeal spiracle not so large, usually much shorter than half the maximum height of the propodeum 7
7. Anterior clypeus projecting over mandibles and acutely angled in profile, such that there is a V-shaped notch between the anterior clypeus and mandibles; in most cases, antennal scapes exceeding vertexal margin by well over half their total length..... 8
Anterior clypeus at most feebly projecting over mandibles, and never acutely angled in profile; in most cases, scapes exceeding vertexal margin by half or less their total length . 12
8. Mesosoma entirely glabrous 9
Mesosoma with erect hairs (sometimes confined to the pronotum)..... 11
9. Mesosoma longitudinally compressed, with a truncate propodeum that has a very short dorsal face **froggatti group**
Mesosoma elongate and saddle-shaped, with propodeum of normal length..... 10
10. Total length >4 mm; head and mesosoma uniformly red, contrasting with black gaster.....
..... **aeneovirens group**
Total length <4 mm; mesosoma at least partly brownish, not uniformly reddish **Group A**

11. Antennal scapes glabrous, and usually exceeding vertexal margin by about two-thirds their total length; second funicular segment about twice as long as wide..... **Group L**
 Antennal scapes with erect hairs, exceeding vertexal margin by about half or less their total length; second funicular segment less than twice as long as wide..... **Group B**
12. Maxillary palps relatively short, length of fourth (of six) segment about half or less that of third; mandible sometimes with more than five teeth; clypeus often bulging such that it has a distinct anterior face above the mandibles..... 13
 Maxillary palps relatively long, length of fourth (of six) segment about two-thirds or more that of third; mandibles not with more than five teeth, and clypeus not bulging such that it has a distinct anterior face above the mandibles..... 16
13. Dorsal surface of head covered with numerous short hairs; head and mesosoma heavily sculptured, at most feebly shiny..... 14
 Dorsal surface of head with scattered setae only; integument usually smooth and shiny.... 15
14. Mandibles with five teeth; foreparts brick-red, contrasting with black gaster..... **Group H**
 Mandibles with >10 teeth; color uniformly blackish..... **Group K**
15. Antennal scapes exceeding vertexal margin by about one-third their total length....**Group F**
 Antennal scapes exceeding vertexal margin by at most one-quarter their total length.....
 *wheeleri* group
16. Antennal scapes exceeding vertexal margin by well over half their total length.....
 *iridescens* group
 Antennal scapes exceeding vertexal margin by at most half their total length..... 17
17. Propodeum shorter than high (rarely, propodeal suture absent); head often dorso-ventrally compressed..... 18
 Propodeum as long or longer than high; head not dorso-ventrally compressed..... 22
18. Petiolar node short and scale-like, in profile very thin and acutely angled dorsally..... 19
 Petiolar node longer, broadly rounded dorsally in profile..... **Group J**
19. Mesosoma and gaster covered with whitish or silvery adpressed pubescence in addition to erect hairs..... **Group C**
 Mesosoma with or without erect hairs, but not covered with adpressed pubescence..... 20
20. Very small species, total length about 1.5 mm; mesosoma almost always glabrous.....
 *mjobergi* group
 Larger species, total length about 2 mm or longer; mesosoma usually hairy..... 21
21. Mesosoma barrel-shaped, without even a propodeal suture..... *hirsutus* group
 Mesosoma with conspicuous metanotal groove or depression..... **Group D**
22. Head conspicuously sculptured, dull or feebly shiny..... 23
 Head very finely and feebly scalloped, effectively smooth and shiny..... 24
23. Legs and antennal scapes clothed in long white hairs; foreparts brick-red, contrasting with black gaster..... **Group E**

Legs and scapes with at most scattered hairs; mesosoma brownish or black ..***bruneus* group**

24. Tibiae clothed with long (longer than maximum tibial diameter) fine, erect hairs, giving them a bottle-brush appearance***pillipes* group**
 Tibiae with very sparse or no long, erect hairs 25
25. Propodeum very short (about one-quarter total mesosoma length), prominently rounded, and often markedly lower than promesonotum in profile, giving the mesosoma a strongly biconvex profile ***perthensis* group**
 Propodeum not so short (about one-third total mesosoma length) and prominently rounded, only slightly lower than promesonotum in profile.....***fieldi* group**