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A systematic overview of Australian species of the myrmicine ant genus *Meranoplus* F. SMITH, 1853 (Hymenoptera: Formicidae)

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Abstract

This paper provides a systematic overview of the Australian *Meranoplus* F. SMITH, 1853 fauna, estimated to contain 400 species, with the great majority undescribed. Most species occur in arid and semi-arid regions, but the genus is also very rich in the monsoonal tropics. I recognise 18 informal species groups of Australian *Meranoplus*, within seven putative radiations (equivalent to subgenera). All the radiations (*M. diversus* F. SMITH, 1867, *M. excavatus* CLARK, 1938, *M. fenestratus* F. SMITH, 1867, *M. hirsutus* MAYR, 1876, *M. similis* VIEHMEYER, 1922, *M. testudineus* MCAREAVEY, 1956 and *M.* group A radiations) are proposed for the first time. The *M. diversus*, *M. dimidiatus* F. SMITH, 1867, *M. hirsutus* and *M. testudineus* groups are the same as those described in ANDERSEN (2000), as are groups A, C, D, and F. Groups B and E of ANDERSEN (2000) are now respectively referred to as complexes of the *M. testudineus* group and group C, and the *M. mjobergi* FOREL, 1915 group of ANDERSEN (2000) is now considered to be a complex within the *M. fenestratus* group. The *M. armatus* F. SMITH, 1862, *M. excavatus*, *M. froggatti* FOREL, 1913, *M. minimus* CRAWLEY, 1922, *M. puryi* FOREL, 1902, and *M. similis* groups, and groups B, E and G, are proposed for the first time. Two of the seven radiations also occur in the southern Asian and African regions, whereas the others (containing over 85 % of total species) are exclusively Australian, with occasional extensions into Papua New Guinea and eastern Indonesia. Keys are provided to informal species groups, and to species complexes within each group. More detailed, species-level information is provided for the *M. diversus* group of specialist seed harvesters, supplementing the recent revision by SCHÖDL (in press).

Key words: Formicidae, *Meranoplus*, Australia, undescribed species, informal systematic framework, diversity.

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Introduction

Meranoplus F. SMITH, 1853 is a very distinctive myrmicine genus occurring throughout the Old World tropics. It is notable for its highly developed protective morphology, featuring a promesonotal shield that extends over the propodeum, as well as very deep antennal scrobes capable of enclosing the antennae. The promesonotal shield typically has two pairs of lateral projections, a pair of posterolateral projections, and a smaller median pair of posterior projections. These projections are variously enveloped in translucent flanging. In some species this protective morphology is accompanied by specialist "playing dead" behaviour: when disturbed the ants retract their antennae into the scrobes, tuck their legs under the promesonotal shield, and lie motionless in a foetal position (HÖLLDOBLER 1988). As far as I am aware, such elaborate protective morphology does not occur in any other group of ground-foraging ants, but is reminiscent of that occurring independently in two lineages of arboreal ants from tropical rain forest: *Cataulacus* F. SMITH, 1854 in the Old World and Cephalotini in the New World.

Species of *Meranoplus* are stocky, short-limbed and rather slow-moving ants that nest in soil and forage almost exclusively on the ground. They almost always occur in low abundance, contributing a minor proportion of total ant biomass even where they are locally diverse. Most species are generalist omnivores, with many feeding opportunistically on seeds. Some, including all members of the *M. diversus* F. SMITH, 1867 group, are specialist granivores (ANDERSEN & al. 2000).

The relatively modest *Meranoplus* faunas of Africa (8 described species) and the Oriental region (14 described species) have undergone modern revisions by BOLTON (1981) and SCHÖDL (1998) respectively. However, the exceptionally rich Australian fauna is extremely poorly known taxonomically. TAYLOR (1990) reviewed the status of published names and recognised 26 valid worker-based species (plus three queen-based names designated as species inquirendae), and this was raised to 27 by SCHÖDL (2004), who recognised *M. curvispina* FOREL, 1910 as a valid species. However, it is widely appreciated that the named species represent just a fraction of the Australian *Meranoplus* fauna, which I estimate contains about 400 species (ANDERSEN in press). The vast majority of species occur in arid and semi-arid regions, most of which remain poorly collected. A very substantial number of species occur in higher rainfall regions of northern Australia (indeed, several species groups are centred there), with some even occurring in tropical rain forest. In contrast, diversity declines very markedly in cooler and wetter southern Australia, and the genus is mostly absent from wet forests of the cool temperate zone. Only three species are known from Tasmania.

Schödl embarked on a comprehensive revision of Australian species, commencing with the highly distinctive *M. diversus* group of specialist granivores. His revision of this group recognised 25 species, with 19 newly described (SCHÖDL in press). However, further work was tragically cut short by Schödl's untimely death in April 2005.

In honour of Stefan Schödl, I present here a comprehensive systematic overview of Australian *Meranoplus*, building on the species group framework I have previously presented for monsoonal northern Australia (ANDERSEN 2000). This overview does not purport to be a formal taxonomic revision, but rather is an informal systematic framework for documenting and analysing diversity within the Australian fauna. I begin by providing a higher level classification of Australian *Meranoplus*, identifying informal species groups and putative radiations of apparently related species groups. These putative radiations can be considered equivalent to subgenera, but are not based on formal phylogenetic analysis; for convenience they will simply be referred to as radiations. I then provide an overview of each radiation and constituent species groups, including the identification of species complexes within larger groups.

Materials and methods

This overview is based on the approximately 10,000 pinned specimens of *Meranoplus* held at the CSIRO Tropical Ecosystem Research Centre (TERC) in Darwin, which contains by far the most extensive holdings of Australian *Meranoplus*. Most of the TERC collection has come from pitfall samples, collected from literally thousands of sites, primarily from semi-arid southern, eastern and northern Australia. The TERC *Meranoplus* specimens are sorted into 256 species, which are all arranged in clearly-labelled species groups, based primarily on the structure of the promesonotal shield, petiole and post-petiole. Many of the species groups are highly speciose, and these have been divided into species complexes based on further details of the promesonotal shield and waist, as well as more-specific characters such as hairiness and sculpture. In addition to the TERC specimens, I have examined all *Meranoplus* holdings at CSIRO's Australian National Insect Collection in Canberra, and these are all covered by the species groups and complexes presented here.

Dorsal and lateral photographs were taken of selected species using a Polaroid digital camera mounted on a Zeiss Stemi 2000-C stereo microscope and automontage software.

Throughout this paper I use the following abbreviations for Australian States and Territories:

NSW New South Wales
NT Northern Territory
QLD Queensland
SA South Australia
WA Western Australia
VIC Victoria

Higher level classification of Australian *Meranoplus*

I recognise 18 species groups of Australian *Meranoplus*, within seven radiations (Tab. 1; see there also for a complete list of taxon authorities of described species). All the radiations are proposed for the first time. The *M. diversus*, *M. dimidiatus*, *M. hirsutus* and *M. testudineus* groups are the same as those described in ANDERSEN (2000), as are groups A, C, D and F. Groups B and E of ANDERSEN (2000) are now respectively referred to as complex A of the *M. testudineus* group and complex A of group C, and the *M. mjobergi* group of ANDERSEN (2000) is now considered to be a complex within the *M. fenestratus* group. All other species groups, and all species complexes within groups, are proposed for the first time.

Fig. 1: Lateral view of *M. ajax* (*M. diversus* group).

Fig. 2: Dorsal and lateral views of *M. hirsutus*.

Species from two of the seven radiations appear to be closely allied to species from southern Asia and Africa, whereas all others (over 85 % of total species) seem to belong to distinctively Australian radiations.

Key to species groups of Australian *Meranoplus*:

1 Frontal carinae short, extending just beyond mid-line of head; eyes placed at mid-line; large to very large specialist granivores with enormous heads and a highly modified clypeus (Fig. 1; *M. diversus* radiation). ..... *M. diversus* group

– Frontal carinae long, extending to or near to vertex of head; eyes placed well behind mid-line. 2

Fig. 3: Dorsal and lateral views of *Meranoplus* sp. near *dimidiatus*.

Fig. 4: Dorsal and lateral views of *M. mjobergi*.

2 Petiole triangular in profile, with anterior and posterior faces markedly broader than high and predominantly smooth and shiny, with or without feeble rugae (*M. hirsutus* radiation). 3

– Petiole variously triangular to cuboid, with its posterior face sculptured throughout and dull, not predominantly smooth and shiny, and usually not markedly broader than high. 6

3 Promesonotal dorsum with extremely long and spinose lateral and posterior projections, all about as long as width of promesonotal dorsum or longer (rainforest, North QLD). ... *M. armatus* group

– Projections on promesonotal shield not so long and spinose. 4

4 Promesonotal shield with three completely enclosed translucent "windows", bordered by opaque margins, on each side (rainforest, North QLD). ..... group G

– Translucent "windows" of promesonotal shield not all bordered by opaque margins, or entirely absent. 5

5 Promesonotal shield very strongly developed, with very extensive translucent flanging, and densely clothed with long hairs; eyes of moderate size, occupying less than one-third of sides of head (northern Australia; Fig. 2). .... *M. hirsutus* group

– Promesonotal shield not so strongly developed and with only sparse erect hairs; eyes often larger, occupying one-third or more of sides of head (widespread; Fig. 3). ..... *M. dimidiatus* group

6 Clypeus not projecting beyond apices of frontal lobes, with dorsal face rounding into a transversely concave, laterally rounded anterior face that at most feebly projects beyond anterior clypeal margin; petiole without anteroventral tooth; posterior face of post-petiole usually strongly concave (Figs. 4, 5; *M. fenestratus* radiation). .....*M. fenestratus* group

– Clypeus projecting well beyond apices of frontal lobes, wedge-shaped, with apex of wedge acutely angled and laterally denticulate, forming an apparent anterior clypeal margin that projects well forward of actual anterior clypeal margin; petiole often with anteroventral tooth; posterior face of post-petiole often convex. 7

7 Promesonotal shield very strongly developed, with each side completely enclosing two prominent, circular or elliptical, translucent "windows" that are entirely or mostly bordered by opaque margins; second funicular segment conspicuously longer than wide; petiolar node triangular in profile, with at most a very feeble dorsal face (*M. testudineus* radiation). 8

Fig. 5: Dorsal and lateral views of *M. pubescens*.

Fig. 6: Dorsal and lateral views of *M. testudineus*.

– Promesonotal shield not so strongly developed, with at most a single fully enclosed "window" on each side, and any second (posterior) "window" not bordered by an opaque margin; second funicular segment often as wide as long; petiolar node triangular or rectangular in profile, sometimes with a very distinct dorsal face. 9

8 First gastric tergite with conspicuous anterior flanging; posterior face of petiole with at most sparse rugae (northern Australia; Fig. 6). .... *M. testudineus* group

– First gastric tergite without anterior flanging; posterior face of petiole regularly costate (widespread; Fig. 7). ..... *M. froggatti* group

9 Propodeal spines entirely lacking; promesonotal dorsum rectangular, 1.5 times as wide as long, straight-sided and virtually entirely opaque; integument smooth and shiny (group A radiation, part; Top End of NT; Fig. 8). ..... group A

– Propodeum armed with distinct spines. 10

10 Post-petiole transverse and reflexed, with a flattened dorsal surface that projects backwards; erect hairs in the form of stiff, blunt, black bristles (*M. similis* radiation, part; northern arid zone; Fig. 9). ..... *M. minimus* group

– Post-petiole not transverse and reflexed. 11

11 Eyes very small, only as long as length of first funicular segment (*M. excavatus* radiation, part). ..... group B

– Eyes markedly longer than length of first funicular segment. 12

12 Eyes large to very large, occupying about one third or more of sides of head, and strongly asymmetrical, with a convex dorsal margin and straight or slightly concave ventral margin. 13

– Eyes not so large, or, if occupying about one third, then sides of head roughly elliptical, with similar dorsal and ventral margins. 14

13 Antennal scapes long, with entire first funicular segment surpassing posterior margin of eye when antennae retracted; promesonotal shield rather poorly developed posteriorly, with posterolateral spines less than half the length of propodeal spines (group A radiation, part; central and northern Australia). ..... group E

– Antennal scapes shorter, surpassing posterior margin of eye by less than length of first funicular segment; promesonotal shield consistently developed throughout, with posterolateral

Fig. 7: Dorsal and lateral views of *Meranoplus* sp. (*M. froggatti* group, complex C).

spines at least half the length of propodeal spines (*M. excavatus* radiation, part; widespread). ..... group D

14 Promesonotal dorsum (not including projections and translucent flanging) markedly wider than long, with relatively short (length of eye or shorter) white, curved or semi-appressed hairs; petiole truncate, with distinct dorsal face; clypeus often either shagreened or with coarse rugae; head and mesosoma dark chocolate brown, often with contrasting tan gaster (*M. excavatus* radiation, part; northern Australia; Fig. 10). .... group F

– Promesonotal dorsum square or longer than wide; if markedly wider than long then colour not dark chocolate brown, or hairs long and erect; petiole with or without distinct dorsal face; clypeus usually smooth and shiny, at most with a few rather feeble, longitudinal rugae. 15

15 Propodeal spines considerably longer than posterolateral spines of promesonotal shield; mesosoma reddish brown, and usually with hairs that are as long or longer than eye length (*M. excavatus* radiation, part; widespread). ... *M. puryi* group

– Propodeal spines about the same length as posterolateral spines of promesonotal shield; if considerably shorter, then total body length <2 mm and mesosoma yellowish, usually with hairs shorter than eye length. 16

Fig. 8: Dorsal and lateral views of *Meranoplus* sp. (group A).

16 Petiole cuboid, with dorsal face at least half as long as anterior face, and with distinct carina on its anterior margin; first gastric tergite with conspicuous anterior flanging; larger (total length about 3 mm), orange-coloured species with very extensive translucent flanging on promesonotal shield (*M. similis* radiation, part). .... *M. similis* group

– Petiole triangular in profile, at most with short, oblique dorsal face, usually with an angular or broadly rounded apex; first gastric tergite without conspicuous anterior flanging; smaller (about 2.5 mm or less), mostly brown, reddish brown or yellowish species (*M. excavatus* radiation, part). 17

17 Lateral and posterior surfaces of petiole (and usually also post-petiole) coarsely and uniformly costate; in posterior view, petiole broader than post-petiole, and broadest dorsally, with dorsum flat or even slightly concave, never conspicuously convex medianly; promesonotal shield with very extensive translucent flanging laterally (northern Australia; Fig. 11). ..... group C

– Petiole not coarsely and uniformly costate, or, if so, then same width as post-petiole and convex medianly; promesonotal shield usually without such extensive translucent flanging laterally (widespread). ..... *M. excavatus* group

Fig. 9: Dorsal and lateral views of *M. minimus*.

Overview of species radiations, groups and complexes of Australian *Meranoplus*

The *Meranoplus hirsutus* radiation

This is a morphologically diverse radiation whose species have a distinctively triangular and smooth petiole. It seems surprising that such petiolar morphology has been conserved within an otherwise diverse radiation, but it very much appears to be the case. This character is shared with many African and Asian species of the genus, indicating that they might belong to this radiation, too. I recognise four Australian groups, three of which typically occur in tropical rain forest and have relatively few species. Two of these have very extensive promesonotal shields. In one (group G), the shield uniquely encompasses three fully enclosed translucent windows on each side. This group is extremely rare, comprising two undescribed species known from a handful of specimens collected from North Queensland rain forest. In the second, the *M. hirsutus* group, the shield has two pairs of large "windows" (but at least posterior pair without opaque margins) on each side. *Meranoplus hirsutus* is a very common and widespread rain forest species, occurring from North Queensland to northern New South Wales (TAYLOR 1990, 2006). Three other undescribed species from North Queensland rain forest are described elsewhere in this volume (TAYLOR 2006). The group also includes two known savanna species, one of which occurs throughout semi-arid northern Australia, with the other restricted to Western Australia's Kimberley region.

The exceptionally spinose *M. armatus* group is the third Australian rain forest group within the radiation, and occurs in both North Queensland and New Guinea (TAYLOR 1990, 2006). Two Australian species are known, *M. armatus*

Fig. 10: Dorsal and lateral views of *Meranoplus* sp. (group F).

(illustrated in BEATON & TAYLOR 1996, and TAYLOR 2006) and an undescribed species, both of which are very rare.

In contrast to the above, the richer (16 species in the TERC collection, Tab. 1) *M. dimidiatus* group occurs only in arid and semi-arid regions. The species have at most moderately developed, and often very reduced, promesonotal shields. Such shield reduction reaches an extreme in the *M. dimidiatus* complex, whose species have a box-shaped mesosoma without lateral projections (Fig. 3). These species are strongly reminiscent of *M. magretti* ANDRÉ, 1884, *M. bicolor* (F. SMITH, 1875) and allies from Africa and southern Asia (BOLTON 1981, SCHÖDL 1998).

I recognise five Australian complexes within the *M. dimidiatus* group:

Key to species complexes of the *M. dimidiatus* group:

1 Dorsum of promesonotum densely clothed in silky, white semi-appressed hairs. ..... complex A

– Dorsum of promesonotum with sparse and erect hairs. 2

2 Dorsum of promesonotum with at most very feeble and rounded lateral projections, not forming a distinct shield (northwestern Australia). ..... *M. dimidiatus* complex

– Dorsum of promesonotum with well-developed angular projections, forming a distinct shield (southern semi-arid zone). 3

Fig. 11: Dorsal and lateral views of *Meranoplus* sp. (group C).

3 Post-petiole entirely smooth and shiny; in profile parallel-sided and about twice as high as long (southwestern WA). .....complex B

– Post-petiole conspicuously sculptured, not twice as high as long, often bulbous. 4

4 Propodeal spines conspicuously longer than posterolateral spines of promesonotal shield (throughout southern semi-arid zone). ... complex C

– Posterolateral spines of promesonotal shield as long as or longer than propodeal spines (central and southern WA). ..... complex D

The *Meranoplus fenestratus* radiation

This radiation includes a single Australian group (the *M. fenestratus* group), which has unusual clypeal structure for *Meranoplus*, lacking an acutely angled and often laterally toothed "apparent" anterior clypeal margin that projects well forward of the actual anterior clypeal margin. Similar clypeal structure also occurs in *M. belli* FOREL, 1902 and *M. castaneus* F. SMITH, 1857 from South-East Asia, *M. mayri* FOREL, 1910 from Madagascar, and *M. leveillei* EMERY, 1883 and allies from New Caledonia, suggesting they also belong to this radiation. The *M. fenestratus* group occurs throughout the Torres Strait Islands and in New Guinea, which is consistent with this link.

I recognise five Australian complexes within the *M. fenestratus* group:

Key to species complexes of the *M. fenestratus* group:

1 Shield rather feebly sculptured, giving it a generally smooth appearance. 2

– Shield conspicuously sculptured, either densely punctate or rugose, not at all with a generally smooth appearance. 3

2 Head and mesosoma dark chocolate brown; shield wider than long or square (monsoonal tropics). ..... *M. mjobergi* complex

– Head and mesosoma more reddish brown; shield longer than wide (southern semi-arid zone). ... . complex A

3 Posterior margin of promesonotal shield with uniformly extensive translucent flanging, sometimes concave medially but never with prominent pair of medial projections; post-petiole very strongly reflexed, with a flat dorsal face that is twice as wide as long; petiole usually with short dorsal face, only about one third as long as anterior face, or shorter (northern Australia). ..... *M. pubescens* complex

– Posterior margin of promesonotal shield not so extensively flanged, with conspicuous pair of median projections; post-petiole not so strongly reflexed, with dorsal face at least feebly convex; dorsal face of petiole usually at least half as long as anterior face. 4

4 Petiole cuboid, with dorsal face straight in profile; promesonotal shield usually with sparse and relatively fine rugae (widespread). .... *M. fenestratus* complex

– Petiole with oblique dorsal face in profile; promesonotal shield more coarsely rugose (southern Australia). ..... *M. ferrugineus* complex

The *Meranoplus diversus* radiation

This comprises the *M. diversus* group, which appears to have no close relative similar in external worker morphology. When Schödl was undertaking his revision he unfortunately had to cancel his visit to Darwin because of ill health, and was forced to complete his work without TERC material. The TERC collection has about 1500 pinned specimens of the *M. diversus* group, representing 23 of the 25 species recognised by SCHÖDL (in press) from material in other collections, and in many cases significantly extending the described ranges of these species (Tab. 2). Many species described by SCHÖDL (in press) have been published in the ecological literature under various code numbers, and the identities of these are provided in Table 3. The TERC collection has an additional 18 undescribed species.

I recognise 10 complexes within the *M. diversus* group (SCHÖDL in press did not identify species complexes), including one (complex A) without a described species:

Key to species complexes of the *M. diversus* group:

1 Promesonotal shield with relatively feebly projections laterally and posteriorly, with posterolateral spines reduced to short triangular or blunt lobes. 2

– Promesonotal shield strongly projecting laterally and posteriorly, with very prominent posterolateral projections. 5

2 Apparent clypeal margin with prominent pair of blunt lateral teeth, without any median projection or median keel-like carina; mandibles with four teeth. 3

– Apparent clypeal margin with prominent pair of blunt lateral teeth, either uniformly concave between lateral angles, or with prominent angular or rectangular projection; mandibles with three teeth. 4

3 Eyes very large, occupying about one-third the sides of head; head rectangular, distinctly wider than long; colour uniformly yellowish brown; relatively small species (total length ≤ 3.5 mm). . ..... complex A

– Eyes of normal size, occupying about one-quarter or less the sides of head; head approximately square, not distinctly wider than long; colour reddish brown, with gaster slightly paler; larger species (total length ≥ 3.5 mm). ....*M. orientalis* complex

4 Clypeus with prominent, median keel-like carina that may or may not extend beyond apparent clypeal margin to form an acutely angled or rounded median projection. .... *M. ajax* complex

– Clypeus with two to several less prominent carinae, two of which often form the lateral margins of a rectangular, feebly projecting dorsal lobe. ..... *M. unicolor* complex

5 Posterior face of petiole irregularly rugose, or with widely spaced, rather irregular longitudinal rugae; head, and waist blackish brown, contrasting with yellow-brown gaster. 6

– Posterior face of petiole regularly and densely costate; body uniformly reddish brown or bicoloured. 7

6 Apparent clypeal margin very broadly concave, with lateral pair of acutely angled projections that only just extend beyond apices of frontal lobes; mandibles with 5 teeth. .... *M. mcarthuri* complex

– Apparent clypeal margin more narrowly concave, with a more median pair of broad and blunt projections that extend well beyond apices of frontal lobes; mandibles with 4 teeth. ... . *M. taurus* complex

7 Apparent clypeal margin with rounded median projection, with or without additional pair of lateral projections. ..... *M. tricuspidatus* complex

– Apparent clypeal margin uniformly concave between pair of lateral projections. 8

8 Projecting lobes of apparent anterior clypeal margin widely spaced, with distance between apices greater than half the distance between apices of frontal lobes. 9

– Projecting lobes of apparent anterior clypeal margin not so widely spaced, with distance between apices at most half the distance between apices of frontal lobes. ..... *M. diversus* complex

9 Apparent clypeal margin uniformly concave between lateral projections. .... *M. convexius* complex

– Apparent clypeal margin straight medially. ... .*M. deserticola* complex

Most of the undescribed species of the *M. diversus* group within the TERC collection belong to the *M. ajax* and *M. unicolor* complexes, with four and seven undescribed species respectively. Keys to all known (described and undescribed) species of these complexes are given below.

Key to species of the *M. ajax* complex:

1 Median carina projecting beyond apparent clypeal margin. 2

– Median carina not projecting beyond apparent clypeal margin. 5

2 Median projection of apparent clypeal margin with acute apex, formed entirely by projecting median carina (widespread in northern Australia). ..... *M. ajax*

– Median projection of apparent clypeal margin with rounded apex, formed by projecting lateral as well as median carinae (northwestern Australia). 3

3 Posterolateral projections of promesonotal shield long and digitate (Kimberley WA). ..... sp. A

– Posterolateral projections of promesonotal shield short and broadly and bluntly triangular. 4

4 Distance between posterolateral and median posterior spines of promesonotal shield equal to distance between median posterior spines (Kimberley WA). ..... sp. B

– Distance between posterolateral and median posterior spines of promesonotal shield shorter than distance between median posterior spines (Tanami Desert NT). ..... sp. K

5 Frontal area irregularly striate-rugose; first gastric tergite conspicuously striate, with background sculpture feebly punctate and shiny. ... . *M. snellingi*

– Frontal area reticulate-rugose; first gastric tergite densely punctate and dull, with or without feeble striations (northeastern Arnhem Land, NT). ..... sp. C

Key to species of the *M. unicolor* complex:

1 Posterolateral corners of promesonotal shield produced into conspicuous, bluntly triangular projections. 2

– Promesonotal shield lacking distinct posterolateral angles, let alone conspicuous projections. 8

2 Median portion of clypeus with a closely approximated pair of longitudinal carinae, often

forming a weakly raised dorsal lobe that occupies no more than one-fifth of the space between apices of frontal lobes. 3

– Median portion of clypeus with several longitudinal carina, and dorsal lobe broad, occupying about one-third of space between apices of frontal lobes (sometimes no distinct dorsal lobe). 6

3 Median clypeal lobe projecting beyond apparent anterior clypeal margin (northern Kimberley, WA). ..... sp. D

– Median clypeal margin not projecting beyond apparent anterior clypeal margin, which is uniformly concave. 4

4 First gastric tergite with scattered shallow foveolae, otherwise only feebly shagreened and predominantly smooth and shiny; eyes squarish, about as wide as long (Top End NT). ..... sp. E

– First gastric tergite coarsely shagreened or conspicuously striate, not predominantly smooth and shiny; eyes markedly longer than wide (northern Kimberley WA). 5

5 Head wider than long; median pair of clypeal carina not forming a distinct dorsal lobe; frontal area partly reticulate rugose; first gastric tergite conspicuously striate. ..... sp. F

– Head longer than wide; median pair of clypeal carina forming a distinct dorsal lobe; frontal area striate rugose throughout; first gastric tergite at most feebly striate. ..... sp. G

6 First gastric tergite conspicuously striate; posterior half of head foveolate and with irregularly striate rugae. 7

– First gastric tergite punctate, without conspicuous striations; posterior half of head coarsely reticulate rugose (Top End NT, Kimberley WA). . ..... *M. berrimah*

7 Apex of petiolar node acutely angled in profile, with anterior face distinctly concave; median projections on posterior margin of promesonotal shield strongly developed; sculpture on head and shield very coarse (Desert Uplands QLD). ..... sp. H

– Apex of petiolar node blunt in profile, with anterior face straight or convex; median projections on posterior margin of promesonotal shield feebly developed; sculpture on head and shield much finer (throughout drier regions of northern Australia, WA, NT, QLD). ..... *M. unicolor*

8 Sculpture relatively fine throughout: head and promesonotal shield with relatively fine, longitudinal rugae, petiole mostly punctate, and first gastric tergite finely striate (Gulf region QLD). ....sp. I

– Sculpture very coarse throughout: head reticulate rugose posteriorly, promesonotal shield and petiole coarsely rugose, and first gastric tergite coarsely striate (central QLD). ..... sp. J

The *Meranoplus* group A radiation

This radiation consists of two very rare species groups (A and E) that have no described species. Group A is known from only a handful of specimens of two closely related species occurring in the sandstone escarpment of western Arnhem Land. The species are quite unlike any other known *Meranoplus*, possessing a short but wide promesonotal shield without lateral processes, lacking propodeal spines, and having all dorsal surfaces predominantly smooth and shiny (Fig. 8). Group E consists of two very large-eyed species, each known from single collections. They may prove to be unrelated to each other, and also unrelated to group A.

The *Meranoplus testudineus* radiation

The *M. testudineus* radiation consists of the closely related *M. froggatti* and *M. testudineus* groups, which have very extensively flanged promesonotal shields incorporating two lateral pairs of large, fully enclosed translucent "windows".

The relatively common and species-rich *M. froggatti* group occurs primarily in the southern semi-arid zone, but extends into northern Western Australia. I recognise five complexes within the group:

Key to species complexes of the *M. froggatti* group:

1 Head with sparse and irregular striae, with dull shagreening or densely punctate background sculpture (central and western Australia). 2

– Head coarsely rugose, with integument often shiny between rugae (southern and eastern Australia). 3

2 Posterior face of petiole very densely and uniformly costate. ..... complex A

– Posterior face of petiole with rather sparse and irregular rugae. ..... complex B

3 Promesonotal shield with conspicuous elliptical or crescentic infuscated patch located forward of centre, unless entirely dark brown. .... *M. froggatti* complex

– Promesonotal shield with very feeble or no infuscated patch. 4

4 Promesonotal shield with very long erect hairs, as long as height of petiole or longer (eastern Australia). ..... complex C

– Promesonotal shield with relatively short erect hairs, shorter than height of petiole (southwestern Australia). ..... *M. rugosus* complex

The promesonotal shield is especially strongly developed in the spectacular turtle ants (ANDERSEN 2002) of the predominantly northwestern *M. testudineus* group. With one exception (species C below), the species are very uncommon. I recognise six species, arranged into four complexes:

Key to species of the *M. testudineus* group:

1 Propodeum armed with long, dorsally lamellate spines. 2

Tab. 1: List of radiations, groups and complexes of Australian species of *Meranoplus*, based on specimens held at CSIRO's Tropical Ecosystems Research Centre in Darwin. Figures in parentheses represent numbers of species held in the TERC collection (as of April 2006). The positions of all valid, worker-based species names are indicated. *Meranoplus linae* SANTSCHI, 1928 is only provisionally assigned to the *M. aureolus* complex of the *excavatus* group, as I have not seen a type specimen.

***Meranoplus hirsutus* radiation (21)**
Meranoplus armatus group (1): *M. armatus* FR. SMITH, 1862
Meranoplus dimidiatus group (16): *M. dimidiatus* complex (4) – *M. dimidiatus* FR. SMITH, 1867; complex A (3); complex B (1); complex C (6); complex D (2)
Meranoplus hirsutus group (3): *M. hirsutus* MAYR, 1876
Group G (1)
***Meranoplus fenestratus* radiation (28)**
Meranoplus fenestratus group (28): *M. pubescens* complex (5) – *M. pubescens* (FR. SMITH, 1853); *M. mjobergi* complex (8) – *M. mjobergi* FOREL, 1915; *M. fenestratus* complex (7) – *M. fenestratus* FR. SMITH, 1867, *M. oceanicus* FR. SMITH, 1862; *M. ferrugineus* complex (6) – *M. ferrugineus* CRAWLEY, 1922, *M. hilli* CRAWLEY, 1922; complex A (2)
***Meranoplus diversus* radiation (41)**
Meranoplus diversus group (41): *M. ajax* complex (6) – *M. ajax* FOREL, 1915, *M. snellingi* SCHÖDL, in press; *M. convexius* complex (4) – *M. convexius* SCHÖDL, in press, *M. digitatus* SCHÖDL, in press, *M. naitsabes* SCHÖDL, in press; *M. deserticola* complex (3) – *M. crassispina* SCHÖDL, in press, *M. deserticola* SCHÖDL, in press; *M. diversus* complex (8) – *M. christinae* SCHÖDL, in press, *M. diversoides* SCHÖDL, in press, *M. diversus* FR. SMITH, 1867, *M. oxleyi* FOREL, 1915, *M. wilsoni* SCHÖDL, in press; *M. mcarthuri* complex (1) – *M. mcarthuri* SCHÖDL, in press; *M. orientalis* complex (2) – *M. duyfkeni* FOREL, 1915, *M. orientalis* SCHÖDL, in press; *M. taurus* complex (5) – *M. angustinodis* SCHÖDL, in press, *M. arcuatus* SCHÖDL, in press, *M. occidentalis* SCHÖDL, in press, *M. taurus* SCHÖDL, in press, *M. variabilis* SCHÖDL, in press; *M. tricuspidatus* complex (2) – *M. discalis* SCHÖDL, in press, *M. mars* FOREL, 1902, *M. tricuspidatus* SCHÖDL, in press; *M. unicolor* complex (9); *M. berrimah* SCHÖDL, in press, *M. unicolor* FOREL, 1902; complex A (1)
Group A radiation (4)
Group A (2)
Group E (2)
***Meranoplus testudineus* radiation (24)**
Meranoplus froggatti group (18): *M. froggatti* complex (5) – *M. barretti* SANTSCHI, 1928, *M. froggatti* FOREL, 1913; *M. rugosus* complex (4) – *M. rugosus* CRAWLEY, 1922; complex A (3); complex B (3); complex C (3)
Meranoplus testudineus group (6): *M. testudineus* complex (1) – *M. testudineus* MCAREAVEY, 1956; complex A (1); complex B (3); complex C (1)
***Meranoplus similis* radiation (6)**
Meranoplus minimus group (3): *M. minimus* CRAWLEY, 1922
Meranoplus similis group (3): *M. similis* VIEHMEYER, 1922
***Meranoplus excavatus* radiation (132)**
Meranoplus excavatus group (52); *M. excavatus* complex (17) – *M. excavatus* CLARK, 1938; *M. aureolus* complex A (22), *M. aureolus* CRAWLEY, 1921, *M. linae* SANTSCHI, 1928; complex A (3); complex B (2); complex C (2); complex D (7)
Meranoplus puryi group (17): *M. curvispina* complex (6) – *M. curvispina* FOREL, 1910; *M. puryi* complex (3) – *M. minor* FOREL, 1902, *M. puryi* FOREL, 1902; complex A (7); complex B (1)
Group B (1)
Group C (14): complex A (5); complex B (3); complex C (4); complex D (2)
Group D (42): complex A (3); complex B (7); complex C (5); complex D (9); complex E (5); complex F (13)
Group F (6): complex A (3); complex B (3)

– Propodeal spines reduced to small teeth; all dorsal surfaces coarsely foveolate (complex A; Top End of NT). ..... sp. A

2 First gastric tergite flanged along entire length; translucent windows of promesonotal shield as wide as minimum mesonotal width (*M. testudineus* complex; northern Kimberley).. *M. testudineus*

– Flanging of first gastric tergite restricted to anterior half; translucent windows of promesonotal shield not nearly as wide as minimum mesonotal width. 3

3 Head coarsely rugose; almost entire first gastric tergite striate (complex C; southern WA). ..... sp. F

– Head sparsely striate; striations on first gastric tergite restricted to anterior third, or absent (complex B; northern Australia). 4

4 First gastric tergite parallel-sided. 5

Tab. 2: Significant extensions to ranges described by SCHÖDL (in press) of species of the *M. diversus* group, from specimens held in the CSIRO Tropical Ecosystems Research Centre collection. NSW = New South Wales; NT = Northern Territory; Qld = Queensland; SA = South Australia; WA = Western Australia.

Species	Range described by SCHÖDL (in press)	Additional range
M. arcuatus	SA and southern WA	Alice Springs / West McDonnell Ranges region of NT
M. berrimah	Top End NT	Kimberley WA
M. convexius	central NSW and southeastern QLD	central QLD
M. crassispina	northern SA, Kimberley WA	southern NT
M. deserticola	south-central WA, southwestern NT, northwestern SA	Pilbara WA
M. diversus	northwestern SA, central WA	southwestern WA
M. mars	southern NT, northeastern SA, central and southeastern QLD, northeastern NSW	Gulf regions of NT and QLD
M. naitsabes	central NT	QLD Gulf region, central WA
M. orientalis	southeastern QLD	Charters Towers region of northeastern QLD
M. oxleyi	Top End NT, Kimberley WA	Victoria River District NT, Gulf region QLD
M. snellingi	Top End NT	Kimberley NT
M. wilsoni	eastern QLD, northeastern NSW	central QLD

– Sides of first gastric tergite markedly convex (Kimberley WA). ..... sp. E

5 Colour reddish brown (arid and semi-arid northern Australia - WA, NT and QLD). ..... sp. C

– Colour pale yellow (Top End of NT). ..... sp. D

The *Meranoplus similus* radiation

This is a small radiation of medium-sized, usually orange-brown species with extensive translucent flanging on the promesonotal shield. The *M. minimus* group consists of three known species: *M. minimus* from the Top End of the NT, a less common species also from the Top End, and a species from Queensland's Cape York Peninsula. They bear a strong resemblance to species from the *M. fenestratus* group (including having a reflexed and dorsally flattened post-petiole), but lack that group's unusual clypeal structure.

The *M. similis* group is also known from three species: *M. similis* from the southeastern arid zone, and two species each known from single records, in the Tanami Desert of the NT, and Kimberley region of WA respectively.

The *Meranoplus excavatus* radiation

This is by far the largest radiation of Australian *Meranoplus*, contributing over half of all known species, and including all the small, "mainstream" Australian taxa. I recognise six species groups within the radiation (Tab. 1).

***Meranoplus excavatus* group:** This is a very rich group of small to very small species that occurs throughout inland Australia. I recognise six complexes (see below), two of which (complexes A and B; collectively with 25 species in the TERC collection) are restricted to northern Australia, with three (complexes C and D, and the *M. excavatus* complex; collectively with 19 species in the TERC collection) occurring primarily in southern Australia, and the remaining (complex E; 7 species in the TERC collection) being widespread. *Meranoplus excavatus* is a small yellowish species that occurs throughout the southern semi-arid zone.

Key to species complexes of the *M. excavatus* group:

1 Lateral and posterior faces of petiole regularly and densely costate (northern Australia). .... *M. aureolus* complex

– Lateral and posterior faces of petiole not regularly and densely costate. 2

2 Promesonotal shield markedly wider than long, and with lateral pair of fully enclosed circular or elliptical translucent windows that have opaque outer margins; body covered with silky, white, semi-appressed hairs (Top End of NT). ..... complex A

– Promesonotal shield not markedly wider than long, or, if so, then without a lateral pair of fully enclosed circular or elliptical translucent windows that have opaque outer margins. 3

3 Mesosoma dark chocolate or reddish brown, contrasting with paler yellowish or reddish brown gaster. ..... complex B

– Mesosoma yellowish, concolourous with gaster..... 4

4. Promesonotal shield without posterolateral projections. ..... complex C

– Promesonotal shield with distinct posterolateral teeth or other projections. 5

5 Posterior margin of promesonotal shield with extensive translucent flanging that joins apices of posterolateral projections, uninterrupted by a median pair of projections. … *M. excavatus* complex

– Posterior margin of promesonotal shield with extensive flanging only between median projections, or with virtually no flanging. .... complex D

Tab. 3: Identities of species of the *M. diversus* group that have been published using various code numbers in the ecological literature.

Species	Published species code	References
M. ajax	*Meranoplus* (*diversus* gp.) sp. 3	ANDERSEN (1993a), ANDERSEN & al. (2000)
M. berrimah	*Meranoplus* (*diversus* gp.) sp. 2	ANDERSEN & al. (2000), ANDERSEN & al. (2004)
M. convexius	*Meranoplus* sp. B (*diversus* gp.)	ANDERSEN & al. (2003)
M. diversoides	*Meranoplus* sp. A (*diversus* gp.)	HOFFMANN (2000, 2003)
M. naitsabes	*Meranoplus* sp. C (*diversus* gp.)	ANDERSEN & al. (2002)
M. oxleyi	*Meranoplus* sp. B (*diversus* gp.) *Meranoplus* (*diversus* gp.) sp. F	HOFFMANN (2000, 2003) ANDERSEN (1993b)
M. snellingi	*Meranoplus* sp. *Meranoplus* (*diversus* gp.) sp. 1 *Meranoplus* ?*unicolor*	ANDREW (1986) ANDERSEN (1991), ANDERSEN & PATEL (1994), ANDERSEN & al. (2000) ANDERSEN & al. (2004)
M. taurus	*Meranoplus* sp. OB (*diversus* gp.)	READ & ANDERSEN (2000)

***Meranoplus puryi* group:** Species of the *M. puryi* group, with characteristically long propodeal spines, occur primarily in higher rainfall regions, and include all three known Tasmanian species of *Meranoplus* (*M. curvispina*, *M. puryi*, and *M.* sp. near *minor*). *Meranoplus curvispina* is extremely widespread, distributed from southern Western Australia through South Australia to Tasmania and Victoria, and northwards through New South Wales to southern Queensland (see SCHÖDL 2004). I recognise three complexes within the *M. puryi* group, as outlined below. One of these (the *M. puryi* complex) is noteworthy in that it occurs primarily in higher rainfall, forested habitats, with at least one species known from Papua New Guinea.

Key to species complexes of the *M. puryi* group:

1 Propodeal spines twice as long as posterolateral spines of promesonotal shield, or longer. 2

– Propodeal spines only about 1.5 times as long as posterolateral spines of promesonotal shield. . ..... *M. puryi* complex

2 Posterolateral spines of promesonotal shield digitate, longer than width at base (eastern and southern Australia). ..... *M. curvispina* complex

– Posterolateral spines of promesonotal shield short and broadly triangular, no longer than width at base (northwestern Australia). ... complex A

Group B: This is represented by a single known species, with unusually small eyes. It is known only from a single specimen collected in the Barkly Tableland of the NT.

Group C: This is a very species-rich but entirely undescribed group of the northern monsoonal tropics, occurring primarily in the Victoria River District and Top End of the Northern Territory (14 known species) and the Kimberley region of Western Australia (7 known species). I recognise five complexes:

Key to species complexes of group C:

1 Body densely covered with fine, white, silky curved to adpressed hairs. 2

– Body more sparsely covered with thicker, darker erect hairs. 3

2 Hairs exceptionally dense and semi-adpressed, with fur-like appearance that is strongly reminiscent of *Triglypothrix*. ..... complex A

– Hairs sparser, longer, and more erect, not fur-like. ..... complex B

3 Post-petiole irregularly rugose; hairs mostly semi-adpressed and shorter than eye-length. ... . complex C

– Post-petiole regularly costate; hairs mostly erect and about eye-length. 4

4 Post-petiole with transverse costae; head and mesosoma dark chocolate brown, contrasting with yellow-brown gaster. ..... complex D

– Post-petiole with longitudinal costae; colour uniformly orange. ..... complex E

Group D: Species of the extremely rich group D have very large (often exceptionally so) eyes, and occur throughout semi-arid Australia. The group is especially diverse in the eastern semi-arid zone, where more than 35 species occur. I recognise six complexes within the group:

Key to species complexes of group D:

1 Promesonotal shield densely clothed with fine, white hairs. 2

– Promesonotal shield with sparse, short and relatively stout hairs. 5

2 Hairs on promesonotal shield mostly erect and about as long as eye length or longer. 3

– Hairs on promesonotal shield mostly appressed or semi-appressed, with erect hairs shorter than eye length. 4

3 Posterior margin of promesonotal shield extensively and uniformly bordered with translucent flanging, without conspicuous pair of median projections. ..... complex A

– Posterior margin of promesonotal shield with a conspicuous pair of median projections. .... complex B

4 Median posterior projections of promesonotal shield either not discernible, or their bases confluent with those of posterolateral projections. . ..... complex C

– Promesonotal shield with distinct pair of median posterior projections, whose bases are distinct from those of posterolateral projections. .... complex D

5 First gastric tergite with erect, black setae (southern semi-arid zone). ..... complex E

– First gastric tergite without erect, black setae. . ..... complex F

Group F: This is a relatively small group of entirely undescribed species centred on the monsoonal tropics. It occurs primarily in denser habitats, often in patches of rainforest or riparian vegetation. At least one species is known from Papua New Guinea.

Conclusion

Australia has an exceptionally diverse *Meranoplus* fauna, which, like Australia's other "megadiverse" ant genera (ANDERSEN 2003), is centred on arid and (especially) semi-arid regions. Some relatively small groups (e.g. the *M. hirsutus* and *M. puryi* groups) occur primarily in mesic eastern and southern Australia; these regions have been relatively well-collected for ants, and are unlikely to yield a large number of *Meranoplus* species additional to those already in collections. However, most groups occur in remote and poorly collected "outback" Australia, and are therefore likely to include very many uncollected species. This is particularly the case for the groups of small and inconspicuous species within the *M. excavatus* radiation.

Given that this is the first systematic overview of such a diverse genus, some of the proposed species groups and relationships between groups are inevitably provisional. Further taxonomic work, including the use of molecular methods, are required to confirm them, and to clarify relationships with the non-Australian *Meranoplus* fauna. I hope this overview will provide a stimulus for undertaking such work, and for describing the very many undescribed species, following in Stefan Schödl's footsteps.

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Zusammenfassung

Es wird ein systematischer Überblick über die australische Fauna der Gattung *Meranoplus* F. SMITH, 1853 gegeben, welche geschätzte 400 Arten enthält; die Mehrzahl davon ist unbeschrieben. Die meisten Spezies bewohnen aride oder semi-aride Regionen, aber die Gattung ist auch in den vom Monsun beeinflussten Tropen reich vertreten. Ich erkenne innerhalb von sieben mutmaßlichen Radiationen, welche Untergattungen entsprechen könnten, 18 informelle australische Artengruppen. Alle Radiationen (Radiationen von *M. diversus* F. SMITH, 1867, *M. excavatus* CLARK, 1938, *M. fenestratus* F. SMITH, 1867, *M. hirsutus* MAYR, 1876, *M. similis* VIEHMEYER, 1922, *M. testudineus* MCAREAVEY, 1956 und der Gruppe A) werden zum ersten Mal vorgeschlagen. Die Artengruppen des *M. diversus*, *M. dimidiatus* F. SMITH, 1867, *M. hirsutus* und *M. testudineus* sowie die Gruppen A, C, D und F sind identisch mit jenen, die von ANDERSEN (2000) beschrieben worden sind. Die Artengruppen B und E bei ANDERSEN (2000) werden hier als Artenkomplexe der *M. testudineus*-Gruppe bzw. der Gruppe C behandelt, und die Gruppe des *M. mjobergi* FOREL, 1915 bei ANDERSEN (2000) wird nun als Artenkomplex in die *M. fenestratus*-Gruppe gestellt. Die Gruppen des *M. armatus* F. SMITH, 1862, *M. excavatus*, *M. froggatti* FOREL, 1913, *M. minimus* CRAWLEY, 1922, *M. puryi* FOREL, 1902 und *M. similis* sowie die Gruppen B, E und G werden erstmals vorgeschlagen. Zwei der sieben Radiationen kommen auch im südlichen Asien und in Afrika vor. Hingegen sind die anderen fünf, welche über 85 % aller Arten enthalten, ausschließlich australisch oder kommen vereinzelt noch in Papua Neuguinea und im östlichen Indonesien vor. Bestimmungsschlüssel werden für die informellen Artengruppen und für die Artenkomplexe innerhalb jeder Gruppe vorgeschlagen. Ausführliche Information bis auf Artniveau wird für die *M. diversus*-Gruppe gegeben, eine Gruppe spezialisierter Samenernter; dies ergänzt die neue Revision durch SCHÖDL (in Druck).

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