

Article

Unrecognised Ant Megadiversity in the Australian Monsoonal Tropics III: The *Meranoplus ajax* Forel Complex

Alan N. Andersen ^{1,*} , François Brassard ¹  and Benjamin D. Hoffmann ^{1,2} 

¹ Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia; francois.brassard.bio@gmail.com (F.B.); ben.hoffmann@csiro.au (B.D.H.)

² CSIRO Darwin Laboratory, PMB 44, Winnellie, NT 0822, Australia

* Correspondence: alan.andersen@cdu.edu.au; Tel.: +61-457-539-513

Abstract: Australia's monsoonal (seasonal) tropics are a global centre of ant diversity, but are largely unrecognised as such because the vast majority of its species are undescribed. Here we document another case of undescribed hyper-diversity within a taxon that is formally recognised as a single, widespread species, *Meranoplus ajax* Forel. We recognise 50 species among 125 specimens of *M. 'ajax'* that we CO1-barcode, integrating CO1 clustering and divergence, morphological differentiation and geographic distribution. A large proportion (44%) of these species are represented by single records, indicating that very many additional species are yet to be collected in this extremely remote and sparsely populated region. Sampling has been concentrated in the Northern Territory, where 27 of the 50 species occur. If diversity in Western Australia and Queensland were similar to that in the Northern Territory, as appears likely, then the *M. ajax* complex would comprise >100 species. In 2000, when Australia's monsoonal ant fauna was estimated to contain 1500 species, *Meranoplus ajax* was considered to represent a single species. Our previous analyses of a range of other taxa have shown that their diversity has been similarly under-appreciated in this estimate. Our findings suggest that the total number of ant species in monsoonal Australia is several thousand, which would make the region by far the world's richest known.

Keywords: ant diversity; CO1; species delineation; species complex



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1. Introduction

The Australian monsoonal (seasonal) tropics has an exceptionally diverse ant fauna, but it is not formally recognised as such [1] because only a small proportion of its species is described [2–4]. The fauna is so poorly known taxonomically because of a combination of misinterpreted morphological variability and historically limited sampling due to the region being so vast (nearly 2 million km²), remote, and sparsely populated. For example, *Melophorus rufoniger* Heterick, Castalanelli & Shattuck, *M. hirsutipes* Heterick, Castalanelli and Shattuck and *Monomorium fieldi* Forel were all recently described as morphologically variable species occurring throughout most of mainland Australia [5,6], but each has subsequently been shown to represent dozens or even hundreds of species just in the monsoonal tropics [7–9]. *Tetramorium spininode* Bolton is an example where limited collections led to an under-appreciation of ant diversity in monsoonal Australia. It was recognised in only two records when described in 1977, but the subsequent collection of hundreds of specimens has shown it to represent a group of dozens of species [10].

Here, we provide another example of where limited collections has led to an under-appreciation of ant diversity in monsoonal Australia. *Meranoplus ajax* Forel (Figure 1) belongs to the *M. diversus* F. Smith group of specialist seed-harvesters that is endemic to Australia, occurring throughout the mainland except for high-rainfall regions of the eastern and southern coasts [11,12]. *Meranoplus ajax* is distinguished by its clypeal structure, which features a medial keel-like carina occurring between a pair of lateral projections,

and it occurs throughout central and northern Australia [12]. However, the taxon clearly contains multiple species [11]. The medial clypeal carina characteristically projects beyond the anterior clypeal margin, but not always, and the structure of any projection is highly variable, as is clypeal sculpture and the structure of the lateral projections (Figure 2). The morphology of the head, dorsal shield of the promesonotum, propodeal spines and first gastric tergite are all, likewise, highly variable (Figures 3 and 4). Here, we provide an assessment of the number of species occurring in the complex, informed by extensive CO1 barcoding.



Figure 1. A species of the *Meranoplus ajax* complex carrying a grass seed. Photo credit: François Brassard.

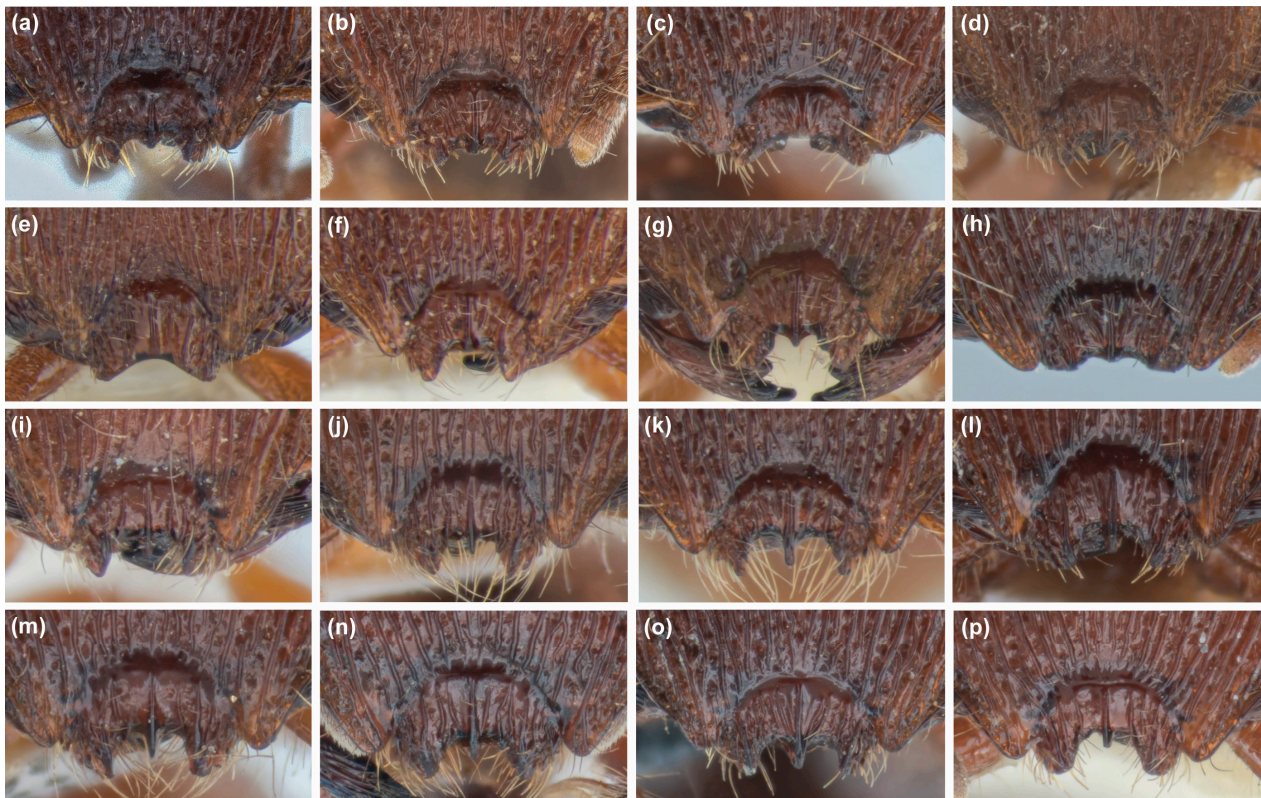


Figure 2. Examples of variation in clypeal morphology within the *Meranoplus ajax* complex. (a) sp. A1 (specimen OZBOL3871-21); (b) sp. A2 (OZBOL9207-22); (c) sp. A7 (MTROP148-23); (d) sp. A8

(MTROP146-23); (e) sp. B1 (MTROP153-23); (f) sp. B4 (MTROP147-23); (g) sp. B5 (TEMEA010-19); (h) sp. C1 (MTROP118-23); (i) sp. C3 (MTROP109-23); (j) sp. C4 (MTROP145-23); (k) sp. D2 (ASST019-18); (l) sp. E1 (MERA137-17); (m) sp. E4 (MTROP140-23); (n) sp. E5 (OZBOL3868-21); (o) sp. F1 (BEET187-23); (p) sp. X3 (MTROP108-23).



Figure 3. Examples of morphological variation in the head, pro-mesonotal shield, and propodeal spines among species within the *Meranoplus ajax* complex. (a) sp. X1 (specimen MTROP152-23); (b) sp.

X2 (MTROP120-23); (c) sp. X3 (MTROP108-23); (d) sp. X4 (OZBOL1958-21); (e) sp. X5 (TEMEA016-19); (f) sp. X6 (OZBOL6456-22); (g) sp. X7 (MTROP138-23); (h) sp. X8 (MERA151-17); (i) sp. X9 (OZBOL6464-22); (j) sp. X10 (MTROP142-23); (k) sp. X11 (OZBOL6469-22); (l) sp. X12 (MERA147-17).

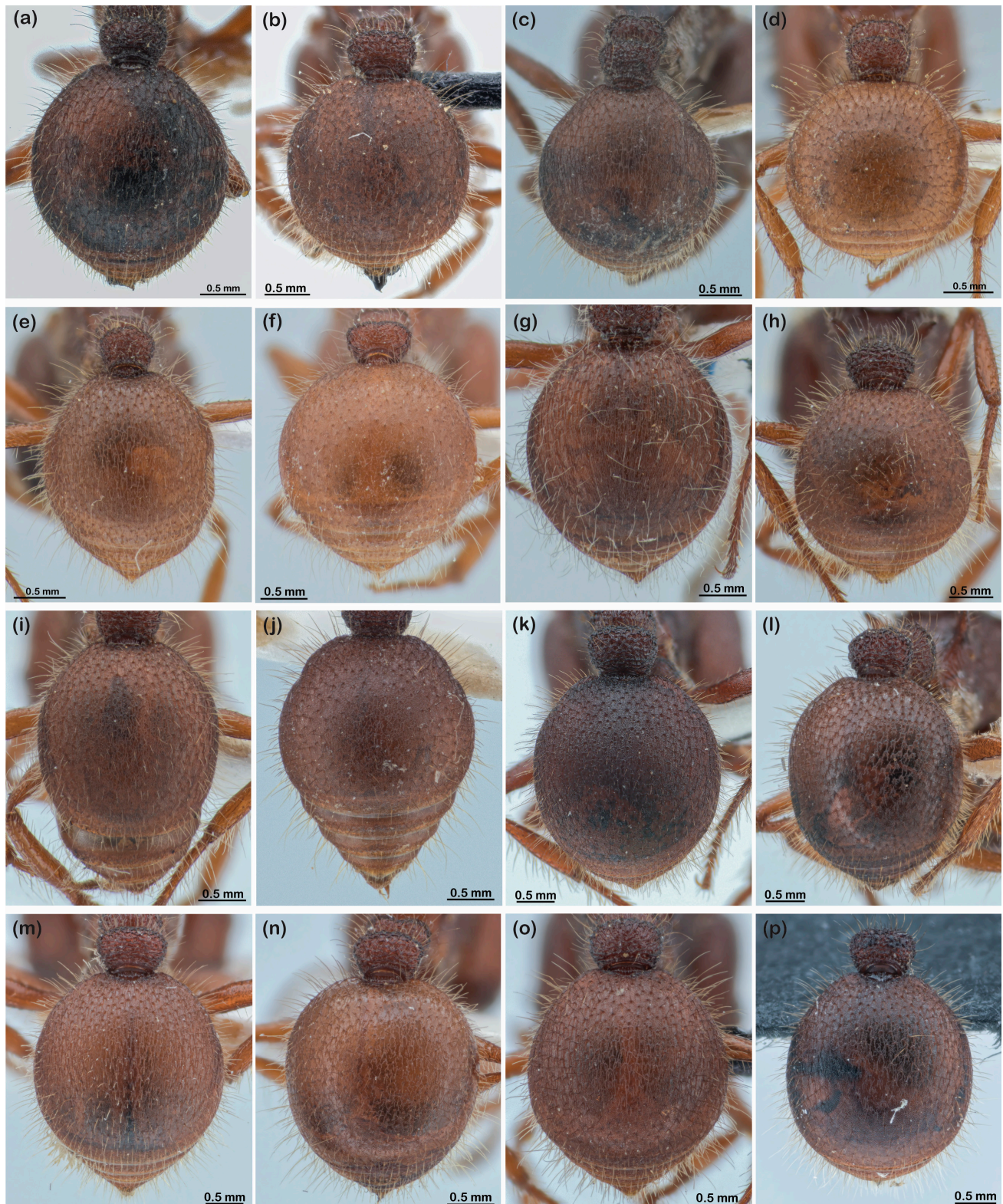


Figure 4. Examples of variation in the first gastral tergite among species of the *Meranoplus ajax* complex. (a) sp. A1 (specimen OZBOL3871-21); (b) sp. A2 (OZBOL9207-22); (c) sp. A5 (TEMEA009-19);

(d) sp. B5 (TEMEA010-19); (e) sp. B6 (MTROP154-23); (f) sp. C3 (MTROP109-23); (g) sp. C7 (OZBOL1960-21); (h) sp. D2 (ASST019-18); (i) sp. D4 (MTROP131-23); (j) sp. E2 (ASST017-18); (k) sp. E5 (OZBOL3868-21); (l) sp. F4 (TEMEA004-19); (m) sp. X2 (MTROP120-23); (n) sp. X5 (TEMEA016-19); (o) sp. X6 (OZBOL6456-22); (p) sp. X10 (MTROP142-23).

2. Materials and Methods

Our study was based on the approximately 500 pinned specimens of the *M. ajax* complex in the ant collection held at the CSIRO laboratory in Darwin, which represents the great majority of all records of the taxon. We obtained CO1 sequences from 125 specimens collected from throughout monsoonal Australia (Supplementary Table S1). Geographic coverage of samples was extremely patchy (Figure 5), as reflects available specimens. Samples were very much concentrated in the western monsoonal zone, with very few samples east of central Northern Territory outside far North Queensland, making the ca. 1 million km² southeastern monsoonal region almost unsampled (Figure 5).

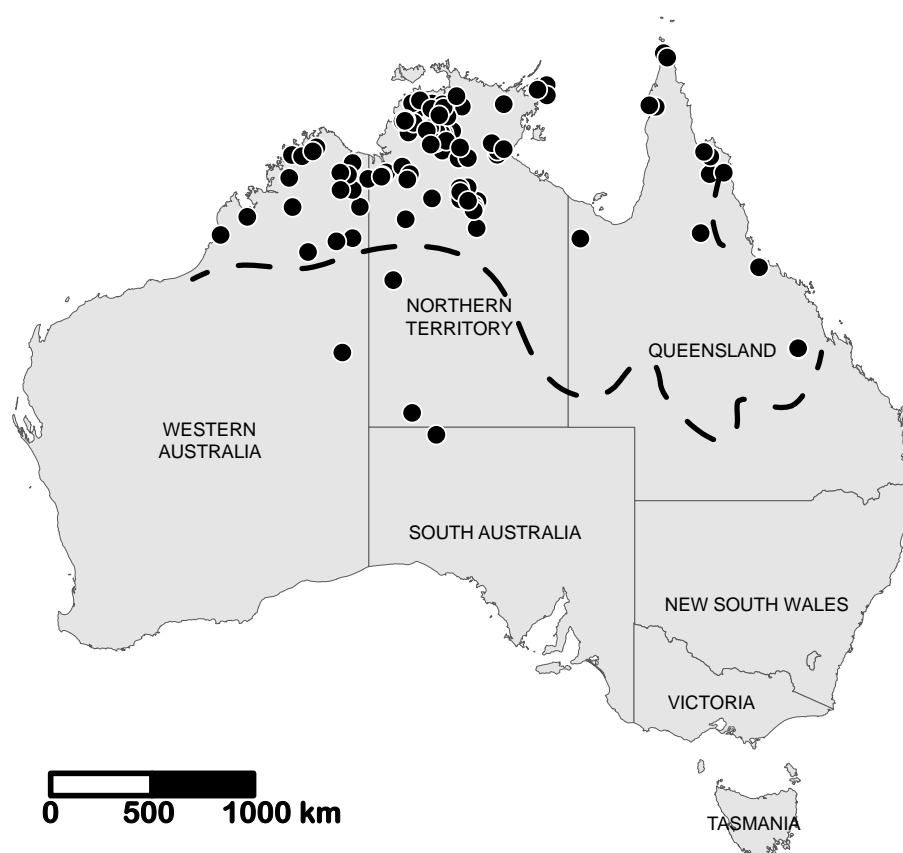


Figure 5. Collection localities (black dots) for sequenced specimens of species from the *Meranoplus ajax* complex. The dashed line represents the approximate southern boundary of the monsoonal zone, where rainfall is very heavily concentrated in a summer wet season. Total annual rainfall ranges from >1500 mm on the far northern coasts to 500 mm on the southern boundary with the central arid zone.

DNA extraction (from foreleg tissue) and CO1 sequencing were conducted through the Barcode of Life Data (BOLD) System (for extraction details, see <http://ccdb.ca/resources>; accessed on 13 February 2024). Each sequenced specimen was assigned a unique identification code that combines the batch within which it was processed, its number within the batch and the year of sequencing (e.g., OZBOL3871-21). All specimens are labelled with their respective BOLD identification numbers in the Darwin collection.

DNA sequences were checked and edited in MEGA [13], then were aligned using the UPGMB clustering method in MUSCLE [14] and translated into (invertebrate) proteins to check for stop codons and nuclear paralogues. The aligned sequences resulted in 693 base

pairs. We constructed a maximum likelihood tree in MUSCLE, using a specimen of another species from the *Meranoplus diversus* group, *M. taurus* Schoedl from Henbury Station in the NT (which we also sequenced through BOLD; MERA178-18), as the outgroup. We then produced our final figure in FigTree.

There is no specific level of CO1 divergence that can be used to define a species, but it is typically 1–3% within a species [15]. We delimited species based on the integration of morphological variation, CO1 clustering and distance, and geographic distribution [16]. We followed a species concept based on reproductive isolation and evolutionary independence as evidenced by morphological differentiation between sister (i.e., most closely related) CO1 clades (considering all available samples from the same collections as those of sequenced specimens) and sympatric distribution.

We imaged a bar-coded specimen of each recognized species using a Leica DMC5400 camera mounted on a Leica M205C dissecting microscope. We took image montages using the Leica Application suite v. 4.13 and stacked them in Zerene stacker.

3. Results

We recognize 50 species among our 125 sequenced specimens (Figure 6). Most (37) of the species occur in one of six clades (A–F). Clade A contains eight species, where the clypeal carinae at most extends only weakly beyond the anterior margin, never as a spinose projection (Figure 7). There are two subclades each with four species, one known only from central Northern Territory (spp. A–D) and the other from far North Queensland (Figure 8a). Clade B contains six species (Figure ??), all from North Queensland (Figure 8b). In sp. B5 the clypeal carina extends as a short, triangular projection (Figure ??e) and in the other species it projects feebly beyond the anterior margin at most. Clade C comprises seven species (Figure 10) from the western monsoonal zone, with one (sp. C7) extending into South Australia (Figure 8c). Clypeal structure is highly variable—in most cases the clypeal carina does not extend beyond the anterior margin—but in spp. C2 and C6 it extends as a short, spinose projection (Figure 10b,f). Clade D, likewise, comprises seven species with highly variable clypeal morphology (Figure 11), but all known only from the Northern Territory (Figure 8d). Clade E comprises five species having similarly variable clypeal morphology (Figure 12), with four occurring in the Northern Territory and the other (sp. E4) in the adjacent eastern Kimberley region of Western Australia (Figure 8e). Finally, Clade F comprises four species from the far north of the Northern Territory (Figure 8f), three with a spinose clypeal projection and the other (sp. F3) without (Figure 13). The thirteen miscellaneous species falling outside the six major clades (spp. X1–13) are dispersed throughout the CO1 tree (Figure 6). There is high morphological variation among them (Figure 3), as to be expected given the variation within each of the major clades. A disproportionate number (spp. X5–11, X13) of the miscellaneous species occur in the Kimberley (far northern) region of Western Australia (Figure 14), most of which fall at the base of the CO1 tree (Figure 6).

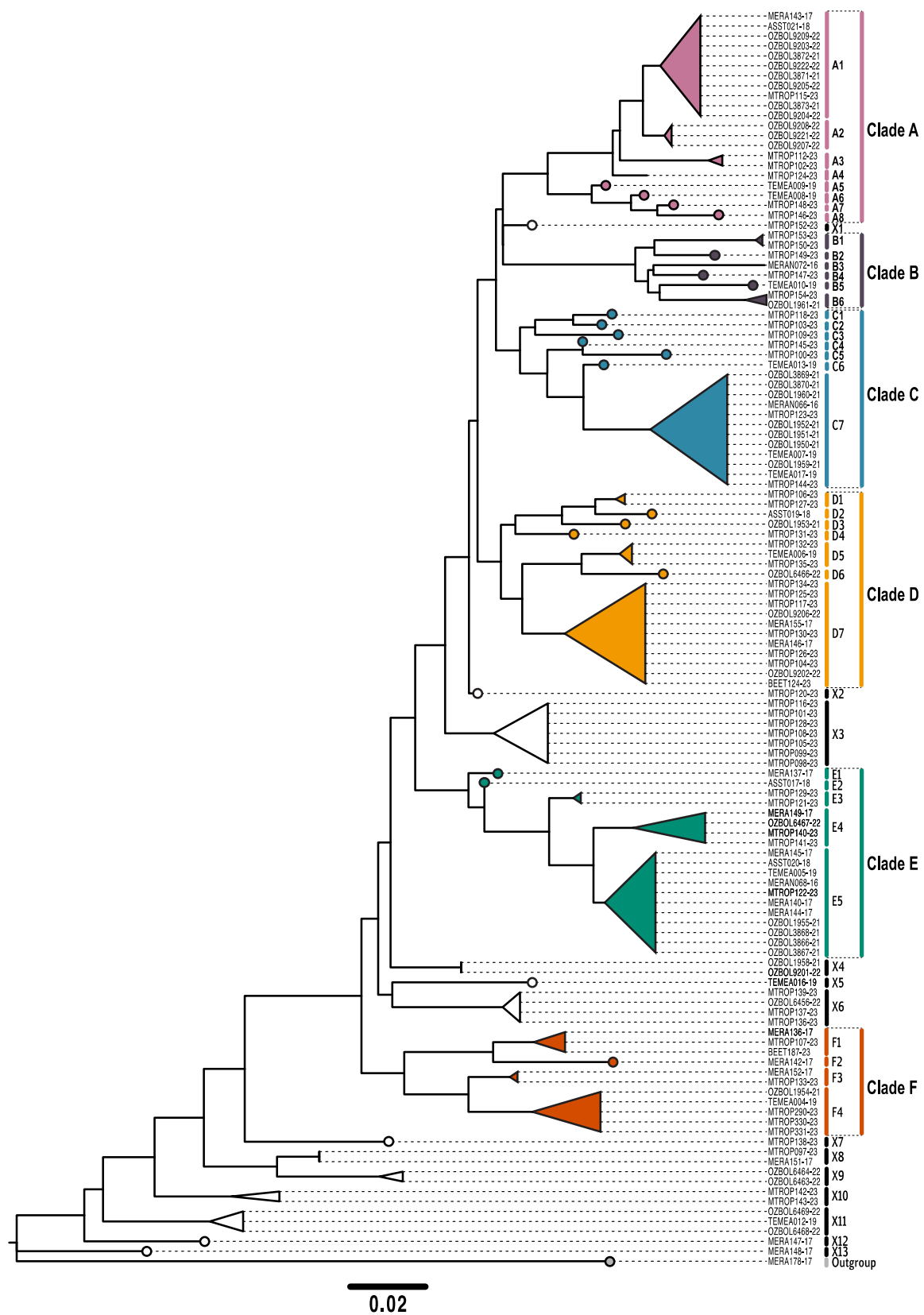


Figure 6. CO1 tree constructed by maximum likelihood. Showing the 126 sequenced specimens of the *Meranoplus ajax* complex, identifying six major clades (A–F) and recognising 50 species (coded A1, etc.).



Figure 7. Images of the heads, promesonotal shields and propodeal spines of species of the *Meranoplus ajax* complex from Clade A. (a) sp. A1 (OZBOL3871-21); (b) sp. A2 (OZBOL9207-22); (c) sp. A3 (MTROP112-23); (d) sp. A4 (MTROP124-23); (e) sp. A5 (TEMEA009-19); (f) sp. A6 (TEMEA008-19); (g) sp. A7 (MTROP148-23); (h) sp. A8 (MTROP146-23).

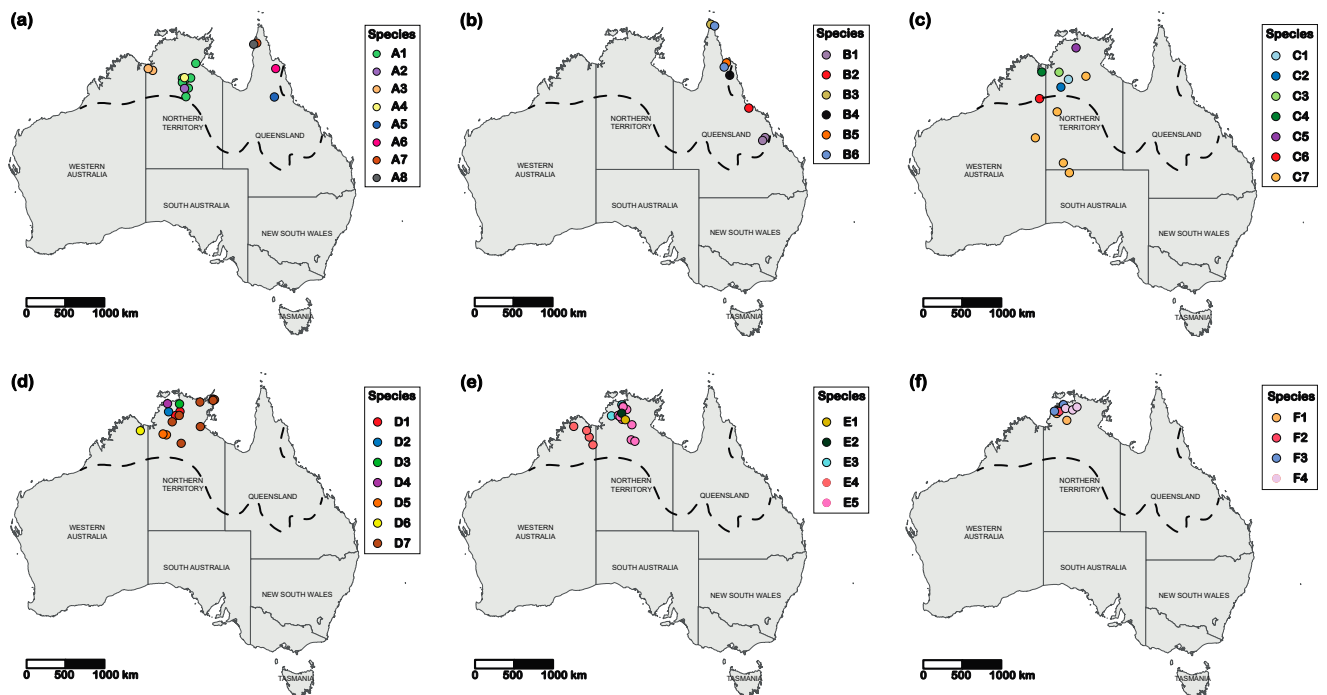


Figure 8. Collection localities for sequenced specimens of the *Meranplus ajax* complex occurring in the six major CO1 clades. (a) Clade A; (b) Clade B; (c) Clade C; (d) Clade D; (e) Clade E; (f) Clade F. The dashed line represents the approximate southern boundary of the monsoonal zone.

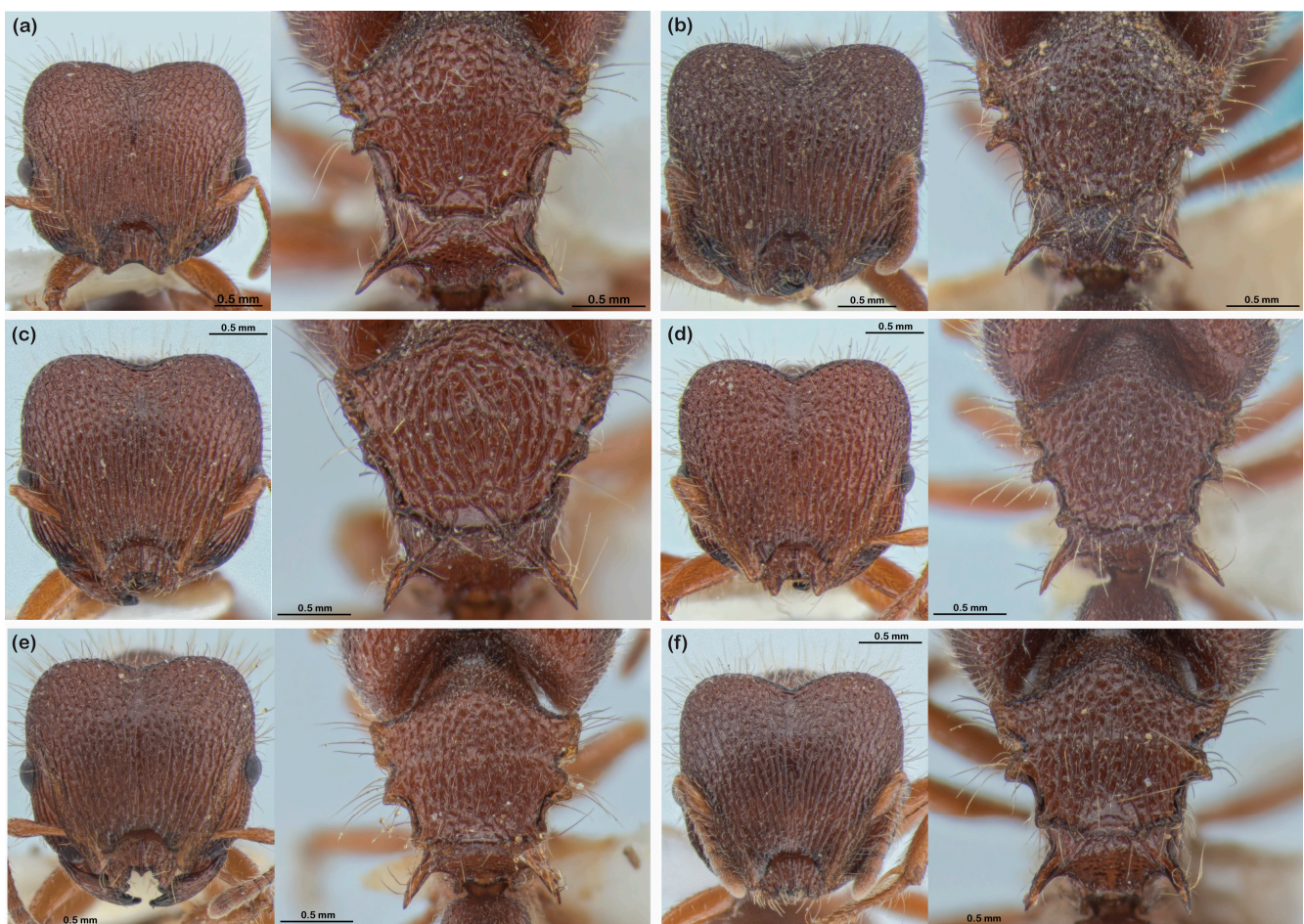


Figure 9. Images of the heads, promesonotal shields, and propodeal spines of species of the *Meranoplus ajax* complex from Clade B. (a) sp. B1 (MTROP153-23); (b) sp. B2 (MTROP149-23); (c) sp. B3 (MERAN072-16); (d) sp. B4 (MTROP147-23); (e) sp. B5 (TEMEA010-19); (f) sp. B6 (MTROP154-23).

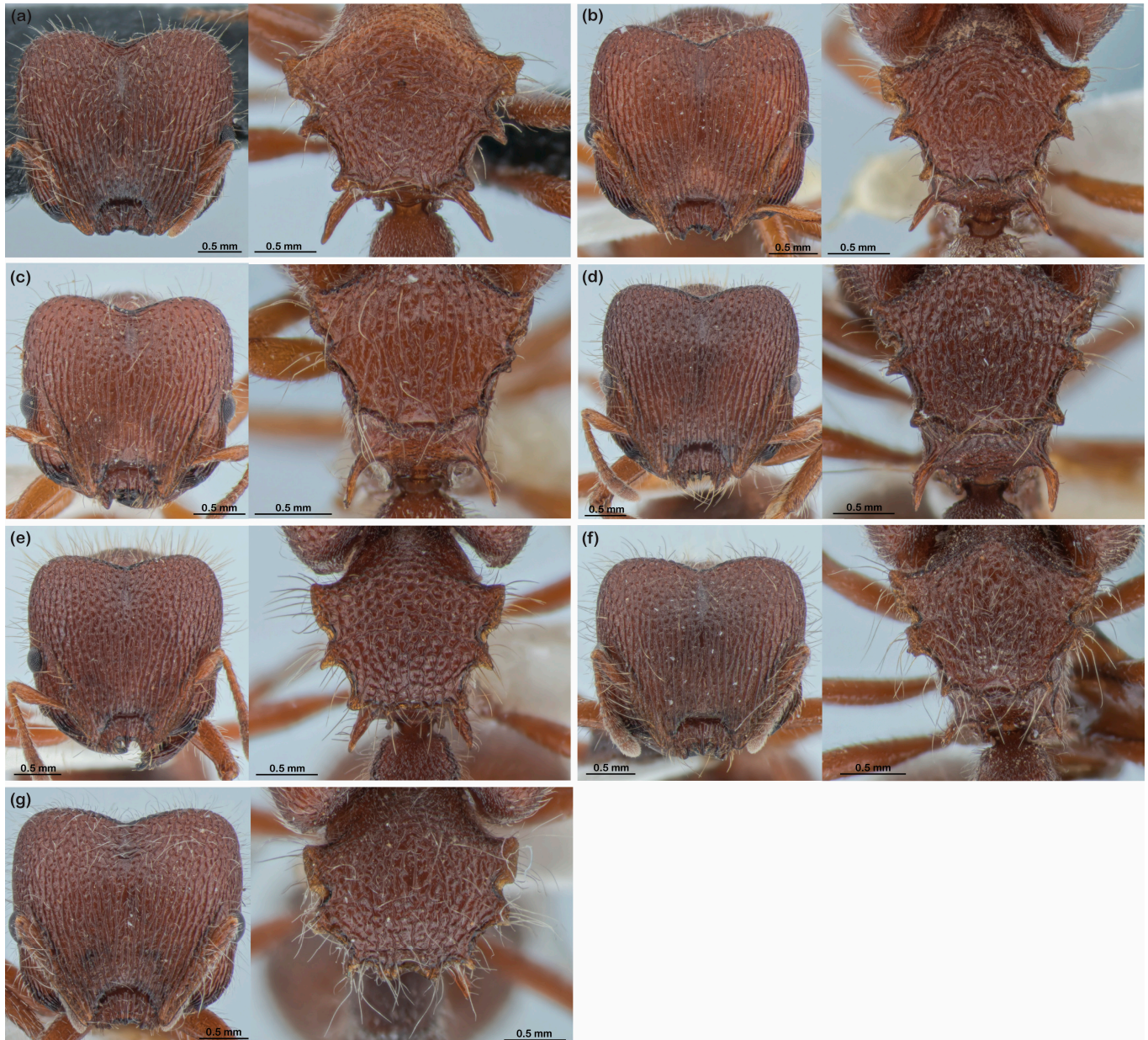


Figure 10. Images of the heads, promesonotal shields, and propodeal spines of species of the *Meranoplus ajax* complex from Clade C. (a) sp. C1 (MTROP118-23); (b) sp. C2 (MTROP103-23); (c) sp. C3 (MTROP109-23); (d) sp. C4 (MTROP145-23); (e) sp. C5 (MTROP100-23); (f) sp. C6 (TEMEA013-14); (g) sp. C7 (OZBOL1960-21).

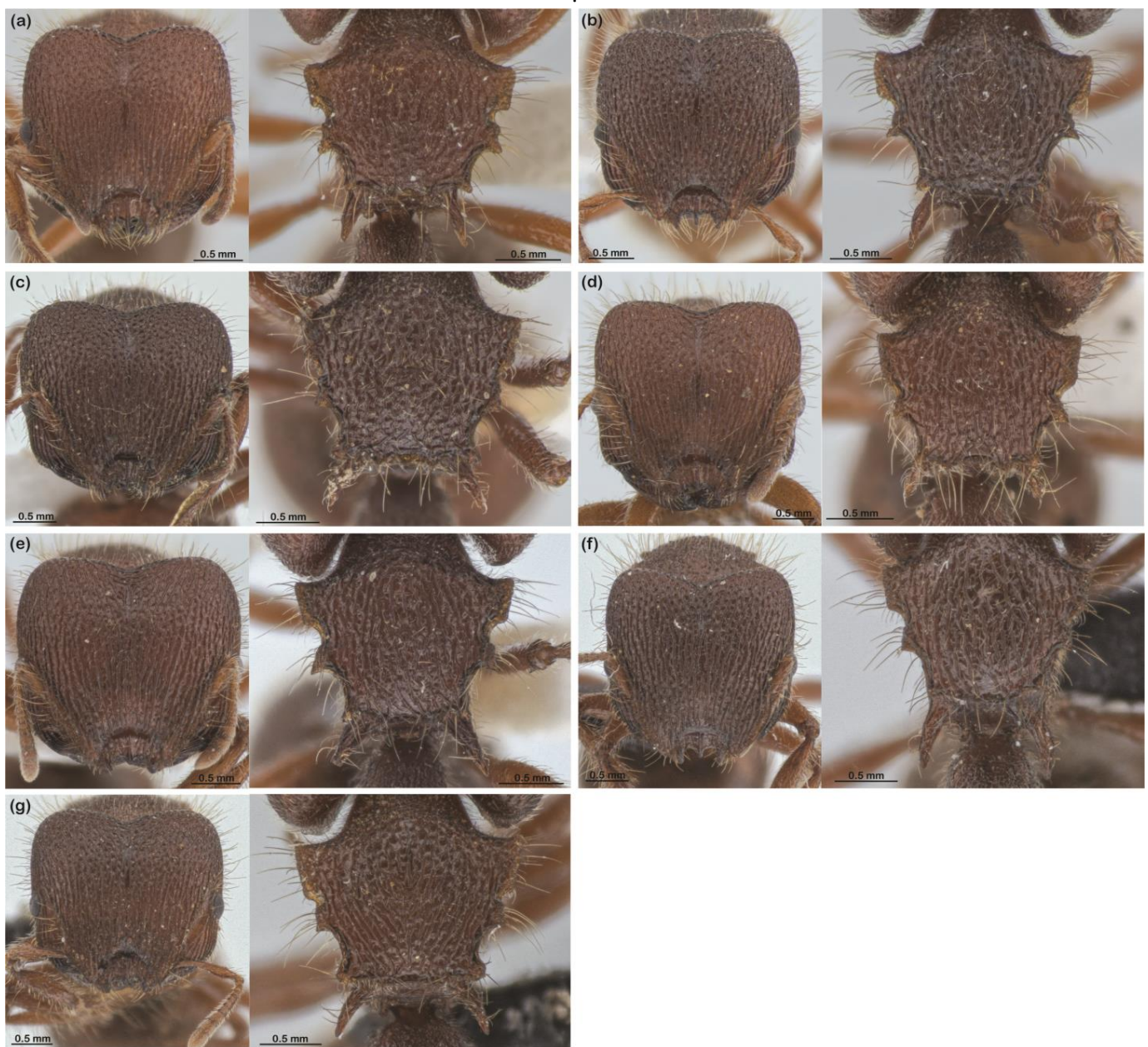


Figure 11. Images of the heads, promesonotal shields, and propodeal spines of species of the *Meranoplus ajax* complex from Clade D. (a) sp. D1 (MTROP106-23); (b) sp. D2 (ASST019-18); (c) sp. D3 (OZBOL1953-21); (d) sp. D4 (MTROP131-23); (e) sp. D5 (MTROP135-23); (f) sp. D6 (OZBOL6466-22); (g) sp. D.7 (OZBOL9206-22).

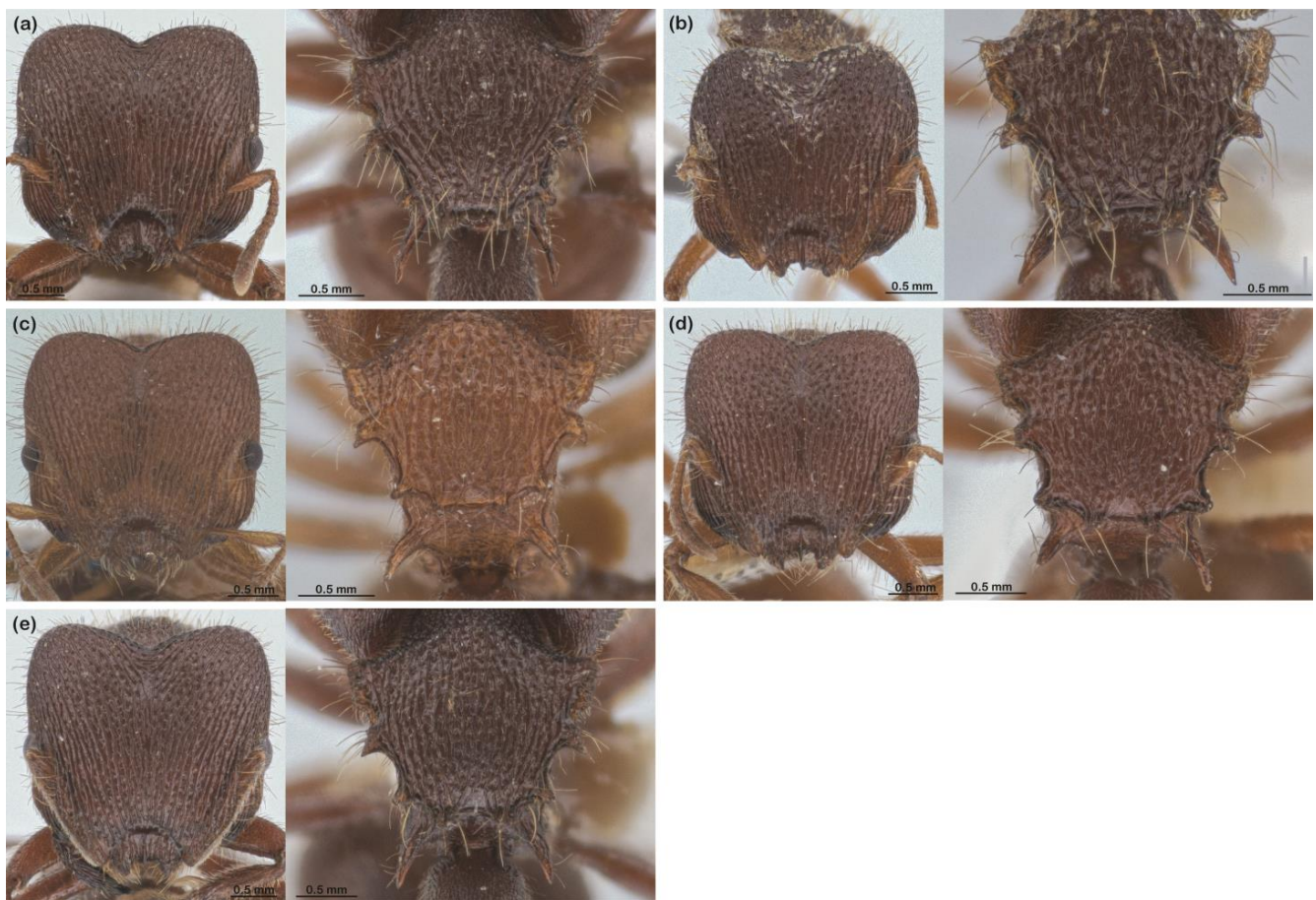


Figure 12. Images of the heads, promesonotal shields, and propodeal spines of species of the *Meranoplus ajax* complex from Clade E. (a) sp. E1 (MERA137-17); (b) sp. E2 (ASST017-18); (c) sp. E3 (MTROP129-23); (d) sp. E4 (MTROP140-23); (e) sp. E5 (OZBOL3868-21).

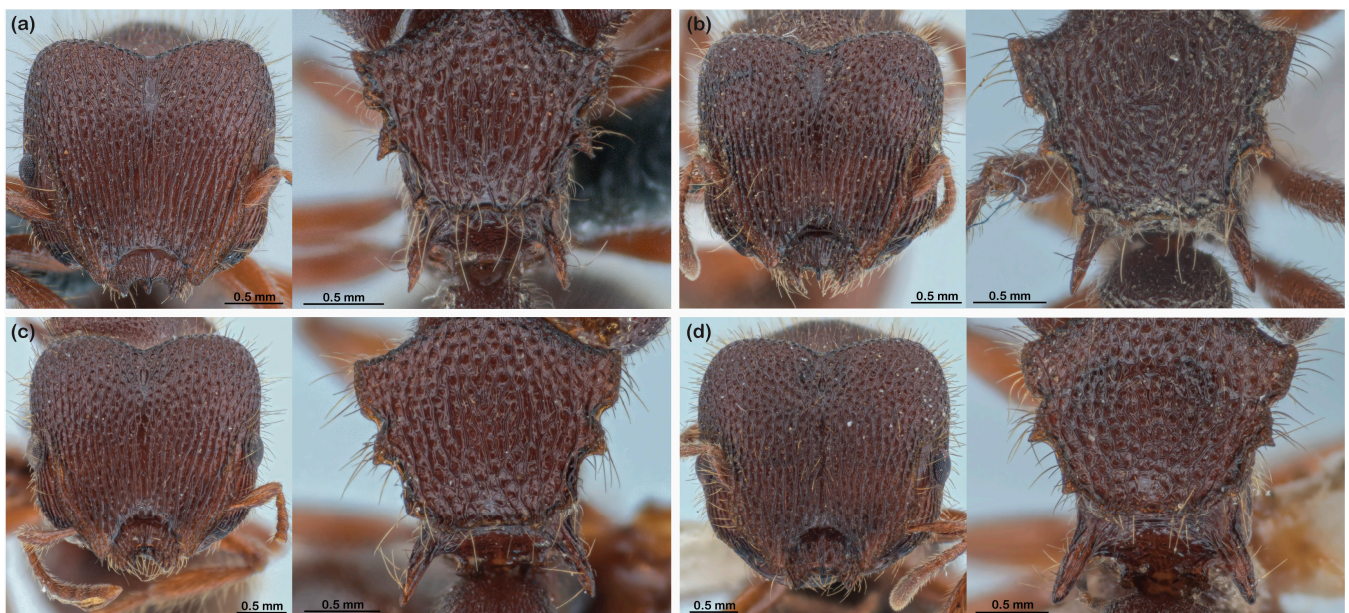


Figure 13. Images of the heads, promesonotal shields, and propodeal spines of species of the *Meranoplus ajax* complex from Clade F. (a) sp. F1 (BEET187-23); (b) sp. F2 (MERA142-17); (c) sp. F3 (MERA152-17); (d) sp. F4 (TEMEA004-19).

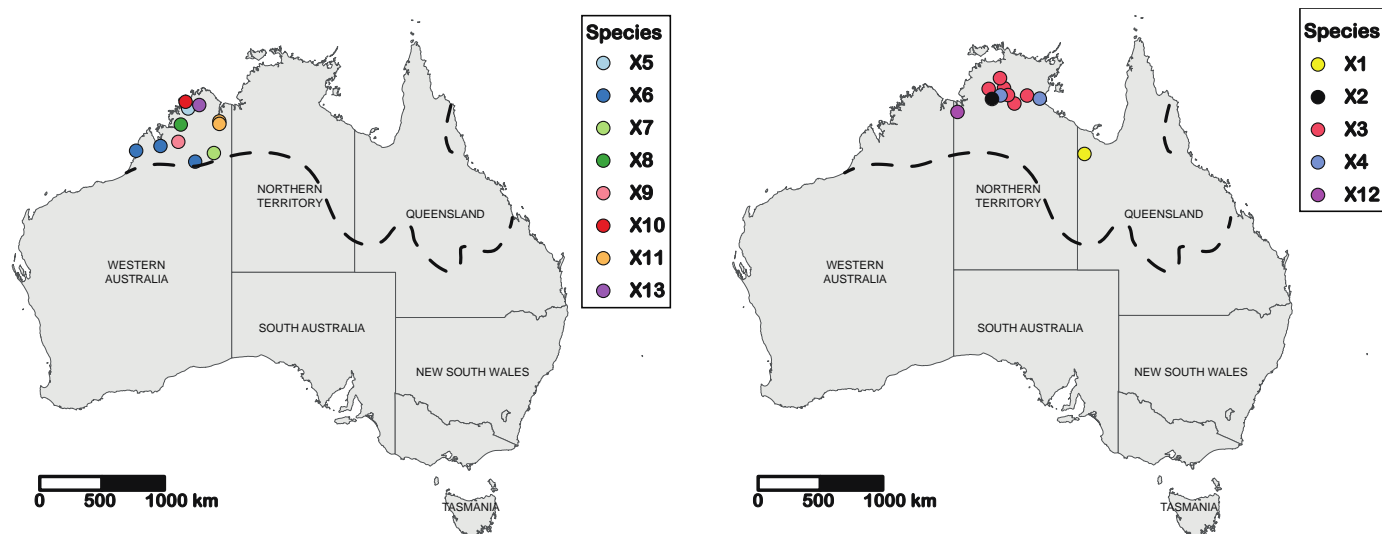


Figure 14. Collection localities for sequenced specimens of the 13 miscellaneous species of the *Meranoplus ajax* complex (spp. X1–13). The dashed line represents the approximate southern boundary of the monsoonal zone.

4. Discussion

We have recognised a remarkable 50 species among the limited sample of specimens analysed. Such high diversity cannot be considered an artefact of inadequate sampling of variation occurring across species ranges. More than half (27) of our recognised species occur in the Northern Territory, where sampling intensity is high. Within the Northern Territory, sampling has been concentrated in the Top End (northern quarter) where 16 species occur, only two of which are known further south. All eleven species collected from Queensland belong to CO1 clades or subclades that do not contain species from the Northern Territory or Western Australia, and so are clearly not conspecific with any of them. Eight of the nine species known only from Western Australia do not belong to any of the five CO1 clades containing Northern Territory species and so cannot be conspecific with any of them. *Meranoplus 'ajax'* is therefore clearly a hyper-diverse complex of dozens of species. None of the 50 species that we recognise among our sequenced specimens are cryptic in the sense of having no clear morphological differentiation [17].

Given that our sequenced specimens represent such a limited sample across the distributional range of the complex, very many additional species undoubtedly occur. This is particularly the case given the almost complete lack of overlap in occurrence of sequenced species from Western Australia, Northern Territory, and Queensland, and is reflected by a very large proportion (22 of the 50 species) of them being represented in the Darwin collection by single records. More than half of our sequenced species occur in the Northern Territory, but this matches the geographical variation in sampling intensity and therefore does not necessarily reflect patterns of regional diversity. Although far fewer species were collected from Western Australia (13) and Queensland (11), these figures would undoubtedly increase markedly with increased sampling intensity. This is especially the case for Queensland, most of which is not represented by samples. If diversity in Queensland and Western Australia were similar to that in the Northern Territory, as appears likely, then the *M. ajax* complex would comprise >100 species.

The six major CO1 clades show clear geographic structure: Clade A has two subclades, one from the Northern Territory and the other from North Queensland; species from Clade B are known only from far eastern Queensland; species from Clade C occur primarily from the central monsoonal region, with one (C7) extending into the central arid zone; and species from Clades D–F all occur primarily or exclusively in the Top End of the Northern Territory. This is indicative of extensive speciation within different regions of the monsoonal zone. Only one species (C7) is known from outside the monsoonal zone,

occurring widely in the central arid zone, including in South Australia. Many of the species have broadly overlapping distributions. The most intensively sampled area is the Darwin-Kakadu-Nitmiluk region of the western top end of the Northern Territory, and 15 of our recognised species (C5, D1-4, D7, E1-3, 5, F1-4, X3) occur there.

Clypeal structure was highly variable, both within and among the six major CO1 clades. In clades A and B, the medial carina tended to project at most feebly beyond the anterior margin, whereas each of the other clades included species with spinose projections as well. Such variability within a clade indicates that clypeal structure is evolutionarily labile. Variation in clypeal structure is presumably related to variation in the preferred seeds of these granivorous species. The limited available information suggests that different species within the *M. diversus* group are highly selective in their seed preferences. *Meranoplus snellingi* Schödl specialises on seeds of the annual grass *Sorghum intrans* [18], and three species occurring at the same site in Kakadu National Park all had very different seed preferences [19]. It is possible that such seed specialisation has driven clypeal specialisation and species radiation.

Our finding of such hyper-diversity in the *M. ajax* complex continues to build the case for unparalleled ant diversity in monsoonal Australia. Our unpublished CO1 data and morphological analysis of other species of the *M. diversus* group from monsoonal Australia, including *M. unicolor* Forel, *M. snellingi* Schödl and *M. berrimah* Schödl, show that each represents diverse species complexes. Our data suggest that the *M. diversus* group has >150 species in Australia's monsoonal zone. The *M. aureolus* Crawley group, with only one described species [11], appears to be even more diverse. For example, a recent synopsis of the entire ant fauna of the Top End [20] lists eight species of the *M. diversus* group (as we have shown here, this is only a fraction of those actually occurring) but 34 species of the *M. aureolus* group (includes species incorrectly assigned to the *M. puryi* and *M. excavata* groups).

Two decades ago the total size of Australia's monsoonal ant fauna was an estimated 1500 species [2]. In this estimate, *Meranoplus ajax* was considered to represent a single species. Our subsequent analyses of other taxa from a range of genera (including *Monomorium*, *Melophorus*, *Camponotus* and *Tetramorium*) have shown that their diversity has also been greatly under-estimated [3,5–7]. It is not possible to give a precise estimate of the total number of ant species in monsoonal Australia, but our findings suggest that it is several thousand. This would make the region by far the world's richest known.

Such a finding upturns the conventional understanding that regional ant faunas are richest in tropical forest biomes [1]. Ant diversity is considered to be especially high in the Amazon Basin and in Brazilian Atlantic Forest [21]. Approximately 1000 described ant species are known from the Brazilian Amazon, which at >4000 km² is more than twice the area of monsoonal Australia [22]. Ant diversity in Brazilian Atlantic forest is similarly high [21]. There are many undescribed species in these biomes, especially within *Azteca*, *Hypoponera*, *Pheidole*, and *Solenopsis* [21]. However, there is no evidence that levels of undescribed diversity are anywhere near as high or as extensive as in monsoonal Australia. For example, an extensive CO1 analysis of the ant fauna of southern Atlantic forest revealed that its size was likely only 6–10% larger than currently recognised [23]. For the many taxa in monsoonal Australia analysed, this figure is one or more orders of magnitude, not just a fraction.

A key factor contributing to high ant diversity in tropical rainforests is the vertical stratification of ant species, with specialist cryptobiotic, epigaeic and arboreal communities, each highly diverse [22,24,25]. Tropical rainforests, therefore, functionally have multiple faunas, stacked on top of each other and with little or no interaction between them. In contrast, all the hyper-diverse taxa in monsoonal Australia are epigaeic, with no vertical stratification and, therefore, all interacting where they co-occur. This makes the extreme hyper-diversity in monsoonal Australia even more remarkable.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16020126/s1>, Supplementary Table S1: List of specimens of the *Meranoplus ajax* complex sequenced in this study and their collection locations. Specimens are identified by their BOLD ID codes and arranged according to species.

Author Contributions: A.N.A. conceived the study, led the development of the Darwin ant collection, and wrote the first draft of the manuscript. F.B. prepared Figures and contributed to the writing of the paper. B.D.H. helped develop the Darwin ant collection and contributed to the writing of the paper. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The CO1 data presented in this study are available on request from the corresponding author.

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Conflicts of Interest: The authors declare no conflicts of interest.

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