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A multi-gene phylogeny of Australian *Monomorium* Mayr (Hymenoptera : Formicidae) results in reinterpretation of the genus and resurrection of *Chelaner* Emery

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Abstract. *Monomorium* Mayr is a speciose, cosmopolitan genus of myrmicine ants that has had a challenging systematic history, comprising numerous lineages whose relationships are problematic. This study employed an extensive sampling of mostly Australian taxa, along with exemplars of other genera of Solenopsidini, to examine relationships among the continent's *Monomorium* fauna. Sequences from elongation factor 1α F2, wingless and cytochrome oxidase subunit 1 (*COI*) were analysed using Bayesian and maximum likelihood methods. The resultant phylogeny resolved Australian *Monomorium* into two major clades separated by exemplars from other genera; one comprised predominantly species with 11-segmented antennae (corresponding to *Monomorium s. str*. in a recent study of Myrmicinae) along with three Paleotropical species. The second clade included Australian species with 12-segmented antennae, two New Zealand species and two from New Caledonia. Two Australian cryptobiotic species were resolved as sister to Clade 2. *COI* analysis indicated that some species (*M. fieldi* Forel, *M. leave* Mayr and *M. leae* Forel) possibly represent cryptic species complexes. The New Zealand *M. antipodum* Forel was recovered as a valid species, and is closely related to an eastern Australian population. We resurrect the genus *Chelaner* Emery for species in the second clade (with 12-segmented antennae) and outline morphological characters to separate *Chelaner* from *Monomorium s. str*. Fifty-three species of *Chelaner* are treated as either stat. nov. or stat. rev.

Additional keywords: species, paraphyly, Australasia, Mymicinae, New Zealand, *COI*.

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Introduction

Monomorium Mayr, 1855 is a diverse genus of myrmicine ants with a global distribution. With around 400 described species the genus exhibits a striking range in morphology from tiny, pale and unsculptured to robust, dark and heavily sculptured taxa. Workers are commonly monomorphic but polymorphic species also exists. Reproductive strategies also vary with species having winged queens or ergatoid queens, or both, and many species are polygynous. Given the number of species and the broad distribution of the genus it is impossible to generalise about its biology and ecology and there have been very few studies of this nature. What is known about the biology of the genus comes predominantly from the many studies of a single cosmopolitan species, *M. pharaonis* (Linnaeus, 1758) (e.g. Buczkowski and Bennett 2009; Solis and Bueno 2014; Tay *et al*. 2014), or from scant biological notes recorded in taxonomic treatments. Most species nest in soil, although some use rotting wood. Foraging habits vary but most species are believed to be generalist scavengers, while some species are seed harvesters and others are social parasites with corresponding morphological adaptations to these lifestyles (Ettershank 1966). Although the genus is found on all major continents, the two main centres of diversity are Africa (Bolton 1987) and Australia (Heterick 2001, 2006; Sparks *et al*. 2014*a*), while two species are among the most widely distributed tramp ant species (*M. pharaonis* and *M. floricola* Jerdon, 1851).

This large and complex genus has challenged taxonomists for more than 100 years. By the early 20th century 10 subgenera of *Monomorium* had been erected by various authors (reviewed in Bolton 1987). One of these was *Monomorium* (*Chelaner*) Emery, 1914, which was raised to generic level by Ettershank (1966) to encompass 37 of the known Australian species together with a further 10 from New Zealand, New Caledonia and New Guinea. The other 13 Australian species remained within *Monomorium sensu stricto*. After reviewing the characters

on which Ettershank had defined *Chelaner*, namely, the palpal formula and propodeal spiracle, both of which were variable in the two genera, Bolton (1987) synonymised *Chelaner* with *Monomorium*. In his review of Afrotropical *Monomorium*, Bolton (1987) proposed a species-group classification for the Afrotropical fauna and outlined three possible species-groups for the Australian fauna.

No further taxonomic work was undertaken on the Australian fauna until Heterick (2001, 2003) revised the genus, which brought the total number of recognised species to 61. Like Bolton (1987), Heterick (2001) used species-groups to associate morphologically similar taxa, but it is unclear what characters these groups were based on. Subsequent work on some of Heterick's (2001) morphologically variable species has shown some of them to represent highly diverse species complexes (Andersen *et al*. 2013; Sparks *et al*. 2014*a*, 2014*b*) and, based in part on this, Andersen (2007) estimated that the true species diversity of the Australian fauna likely runs to hundreds of species.

A recent global reassessment of myrmicine systematics based on a multi-gene phylogenetic study has resolved several critical generic-level issues associated with *Monomorium* (Ward *et al*. 2015). For example, *Trichomyrmex* Mayr, 1865 was brought out of synonymy to accommodate members of the *destructor*-group and moved to the Crematogastrini, while *Syllophopsis* Santschi, 1915 was also brought out of synonymy to include those species belonging to the *hildebrandti*-group and *fossulatum*-group. The species of *Monomorium* that were not assigned to other genera remained in four separate clades. However, the Ward *et al*. (2015) study included very few exemplar taxa from the Australasian region. *Monomorium antarcticum* (Smith F., 1858) from New Zealand, the only species of '*Chelaner*' included in the analysis, was sister to *Austromorium* Shattuck, 2009 (Australia) and these two in turn were sister to *M. denticulatum* (Mayr, 1887) + *Oxyepoecus* Santchi, 1926 (Neotropics). In contrast, *M.* nr. *fieldi* Forel, 1910a, the only Australian species included in the analysis, belonged to a clade that included Asian and African species. Some taxa previously referred to as *Chelaner* (the *rothsteini*-group and *sordidum*-group) are thought to be related to *M. fieldi* and allies (including Asian and African species) rather than to the austral (southern hemisphere) groups of typical *Chelaner* (Heterick 2001; Andersen 2007; Ward *et al*. 2015). Thus, although Ward *et al*. (2015) significantly improved knowledge of myrmicine relationships globally, there remains a pressing need for a more detailed phylogenetic assessment of Australian *Monomorium*, incorporating a more comprehensive sampling of taxa, to establish a stable natural classification for the continent's fauna.

The aims of this study were therefore to: (1) develop a multi-gene phylogeny for Australian *Monomorium*; (2) test the monophyly of the current, morphologically based species-groups, with a particular focus on resolving the status of *Chelaner*; and (3) examine the phylogenetic relationships of two Australian cryptobyotic (blind, soil dwelling) species that were initially identified as *Monomorium*, but which are also superficially similarity in some ways to *Syllophopsis* Santschi, (1915) and *Anillomyrma* Emery, 1913. A further aim of the study was to explore the genetic variation in species displaying high morphological variability to determine whether they likely represent complexes of cryptic species, as has been recently demonstrated for *M. rothsetini* Forel, 1902 (Sparks *et al*. 2014*a*, 2014*b*).

Materials and methods

Taxon selection and specimen collection

Extensive field surveys were made across the continent (2003–11) to obtain as many representatives of Australian *Monomorium* as possible. However, many taxa are rare in collections and seldom encountered in the field. Suitable specimens were available for sequencing from 30 of the 83 recognised species (Heterick 2001, 2003; Sparks *et al*. 2014*a*). *Monomorium fieldi*, *M. leae* Forel, 1913, *M. laeve* Mayr, 1876 and *M. sydneyense* Forel, 1902 are all very small, widespread, generalist species that exhibit variation in colour and sculpture. Included under these names were samples that represented as much as possible of the morphological variation attributed to these species. These taxa are here referred to by the name of the species they are morphologically allied with followed by a species code in brackets as follows: *M. fieldi* (*donisthorpei* form), *M. fieldi* (*nigrius* form), *M. fieldi* (sp. A), *M. fieldi* (sp. 18), *M. leae* (dark form), *M. leae* (light form), *M. leae* (*flavipes* form), *M. laeve* (sp. 23), *M. laeve* (sp. 24), *M. laeve* (sp. 33) and *M. sydneyense* (*carinatum* form). In addition, two undescribed taxa of blind, cryptobiotic ants were included, which were initially identified as *Monomorium* but which are also superficially similar in some characters to *Anillomyrma* and *Syllophopsis*; exemplar sequences of these latter two genera were obtained from GenBank and included in our analyses.

Non-Australian species were included to inform broader biogeographic relationships among Australian species and those outside the continent, as follows: three from the Paleotropics (*M. floricola*, *M. junodi* Forel, 1910a and *M. pharaonis*), two from New Caledonia (*Monomorium* spp.), three from New Zealand (*M. antarcticum*, *M. antipodum* Forel, 1901 and *M. smithii* Forel, 1892) and *Erromyrma latinodis* (Mayr, 1872) from the Indo-Malayan region, which was recently removed from *Monomorium* (Fisher and Bolton 2016). *Monomorium antipodum* is difficult to separate from *M. fieldi* and its identification in New Zealand has been the subject of some debate (Gunawardana 2005; Don 2007). The former species has not been formally recorded from Australia (http://www.ala.org.au. accessed 17 January 2015), but specimens collected in Queensland have been tentatively assigned to this species. We included a specimen of *M. antipodum* from New Zealand and one identified as *M.* c.f. *antipodum* from Australia to test the validity of the name in relation to *M. fieldi* and to determine the status of the species in Australia. The only genus deemed critical to the study for which we were unable to obtain material was *Austromorium* Shattuck.

Outgroups were chosen to represent lineages of decreasing relatedness to *Monomorium* (*sensu* Ward *et al*. 2015) and included two genera from the tribe Solenopsidini (*Myrmicaria brunnea* Saunders, W.W., 1842, *My. exigua* Andre, 1890 and *Solenopsis invicta* Buren, 1972) and three from outside the Solenopsidini (*Stereomyrmex* Emery, 1901, *Trichomyrmex*

destructor (Jerdon, 1851), *Tr. mayri* (Forel, 1902) and *Myrmica tahoensis* Weber, 1948).

Specimens were either collected in the field by the authors or donated by other institutions and researchers as ethanol-preserved specimens. A full account of specimens, their collection locality or region of origin and GenBank accession numbers are listed in Table S1, available as Supplementary Material to this paper. All vouchers are deposited in the South Australian Museum or the Queensland Museum, as indicated in Table S1.

Molecular protocols and sequence analysis

DNA was extracted from whole ants or from three legs from the right side of larger specimens using the Puregene DNA Purification Kit (Gentra Systems Inc., Minneapolis, MN). Amplification of the mitochondrial gene cytochrome oxidase I (*COI*) was obtained by polymerase chain reaction (PCR) using the primers LCOI490: 5′-GGTCAACAAATCA TAAAGATATTGG-3′ and HCOI298: 5′-TAAACTTCAGGG TGACCAAAAAATCA-3′ (Folmer *et al*. 1994) and Jerry 5′-CAACATTTATTTTGATTTTTTGG-3′ (Simon *et al*. 1994)/ Ben 5′-GCTACTACATAATAKGTATCATG-3′ (Moreau *et al*. 2006). Amplification of a fragment of the wingless gene (*wg*) was carried out for a subset of samples using primers Wg578F 5′-TGCACNGTGAARACYTGCTGGATGCG-3′ (Ward and Downie 2005) and Wg1032R 5′-ACYTCGC AGCACCARTGGAA-3′ (Abouheif and Wray 2002) and for elongation factor 1α F2 (*EF1αF2*) using the primers F2–557F 5′-GAACGTGAACGTGGTATYACSAT-3′ and F2–1118R 5′-TTACCTGAAGGGGAAGACGRAG-3′ (Brady *et al*. 2006). PCR amplifications were carried out in 25 µL containing 13.5 µL of water, 2.5 µL of PCR buffer, 2 µL of dNTP, 3 µL of $MgCl_2$, 1 µL of each primer (5 µM), 0.1 µL of AmpliTaq Gold DNA Polymerase (Applied Biosystems) and 2 µL of extracted DNA. All reactions were initially denatured at 95°C for 9 min followed by 40 cycles of 95°C for 30 s, an annealing temperature of 47°C for 30 s and an extension temperature of 72°C for 60 s. This was followed by a further extension for 6 min at 72°C.

For a small subset of samples the Finnzymes Phire Animal Tissue Direct PCR Kit was used for DNA extraction and PCR amplification using the dilution protocol and the 3-step PCR protocol with annealing temperatures between 49°C and 59°C. PCR products were visualised on an agarose gel to check for the presence of double bands that may indicate the presence of pseudogenes and purified with a PCR Clean-up DNA purification kit (MoBio Laboratories, Solana Beach, CA). Sequencing was undertaken using the ABI prism Big Dye Terminator Cycle sequencing kit (PE Applied Biosystems, Foster City, CA) and sequencing was carried out on an ABI 3730 DNA analyser.

Forward and reverse sequences were trimmed, assembled and aligned by eye using Bioedit 7.0.9 (Hall 1990) and compared with the corresponding chromatograms. Translation of the mitochondrial DNA sequences to proteins was carried out in MEGA v. 5 (Kumar *et al*. 2008) to check for the presence of stop codons that may indicate the presence of nuclear pseudogenes. As complete sequence data were only available for a subset of samples for each gene, phylogenetic analysis was performed on six separate datasets, as follows: a combined 3-gene analysis of all taxa with missing data (3-gene (all taxa)), a 3-gene analysis with fewer taxa and complete data (3-gene (reduced taxa)), *EF1αF2+wg*, a *COI*-only analysis, *COI+EF1αF2* and *COI+wg*.

For the Bayesian (BI) analyses, MrBayes v. 3.2.2 was used (Ronquist *et al*. 2012). The six datasets were each analysed separately using PartitionFinder v. 1.1.1 (Lanfear *et al*. 2012) to determine the best evolutionary model partitioning scheme using the Bayesian information criterion and the 'greedy' algorithm (Table 1). All analyses were performed for 6 million generations, sampling every 1000 generations except for the combined 3-gene (all taxa) analysis and the *COI*-only analysis, which were performed for 10 million generations. The standard deviation of split frequencies reached below 0.01 for all analyses and TRACER 1.4 (available from http://beast.bio.ed.ac.uk/Tracer, accessed January 2014) was used to evaluate convergence parameters. The effective sample size for all parameters was above 1000 and the likelihood values converged to relative stationarity within the first 1 million generations for all analyses. A burn-in of the first 25% of trees was chosen and a 50% majority-rule tree was constructed.

Maximum likelihood (ML) analyses were carried out for all six datasets using the program RAxML v. 8 (Stamatakis 2014) (http://embnet.vital-it.ch/raxml-bb/index.php). All datasets were partitioned by codon for *COI* and by gene region under a GTR+gamma model and clade support was obtained using 100 rapid bootstrap inferences. We present the trees for the six Bayesian analyses (Figs 1–4, S1 and S2) and indicate nodes with ≥95 Bayesian posterior probability and ≥70 ML bootstrapping support.

Results

Monomorium *phylogenetics*

All analyses strongly supported the monophyly of the Solenopsidini (*sensu* Ward *et al*. 2015) (Figs 1–4, S1–2). Two separate *Monomorium* clades were recovered with strong

Table 1. Summary of models used for the Bayesian analysis of the six separate datasets
COI, cytochrome oxidase subunit 1; *EF1aF*2, elongation factor 1α F2; pos., position; *wg*, wingless gene

Analysis	No. samples	*COI* pos. 1	*COI* pos. 2	*COI* pos. 3	*EF1aF2*	*wg*
COI+EF1aF2+wg (all taxa)	50	SYM+I+G	GTR+I+G	HKY+I+G	K80+G	K80+I
COI+EF1aF2+wg (reduced taxa)	21	GTR+I+G	HKY+I+G	HKY+I+G	K80+I	K80+G
EF1aF2+wg	26				K80+I	K80+G
COI-only	85	GTR+I+G	GTR+I+G	GTR+G		
CO1+wg	38	GTR+I+G	GTR+I+G	HKY+I+G		K80+I+G
COI+EF1aF2	26	SYM+G	GTR+I+G	HKY+I+G	K80+I	

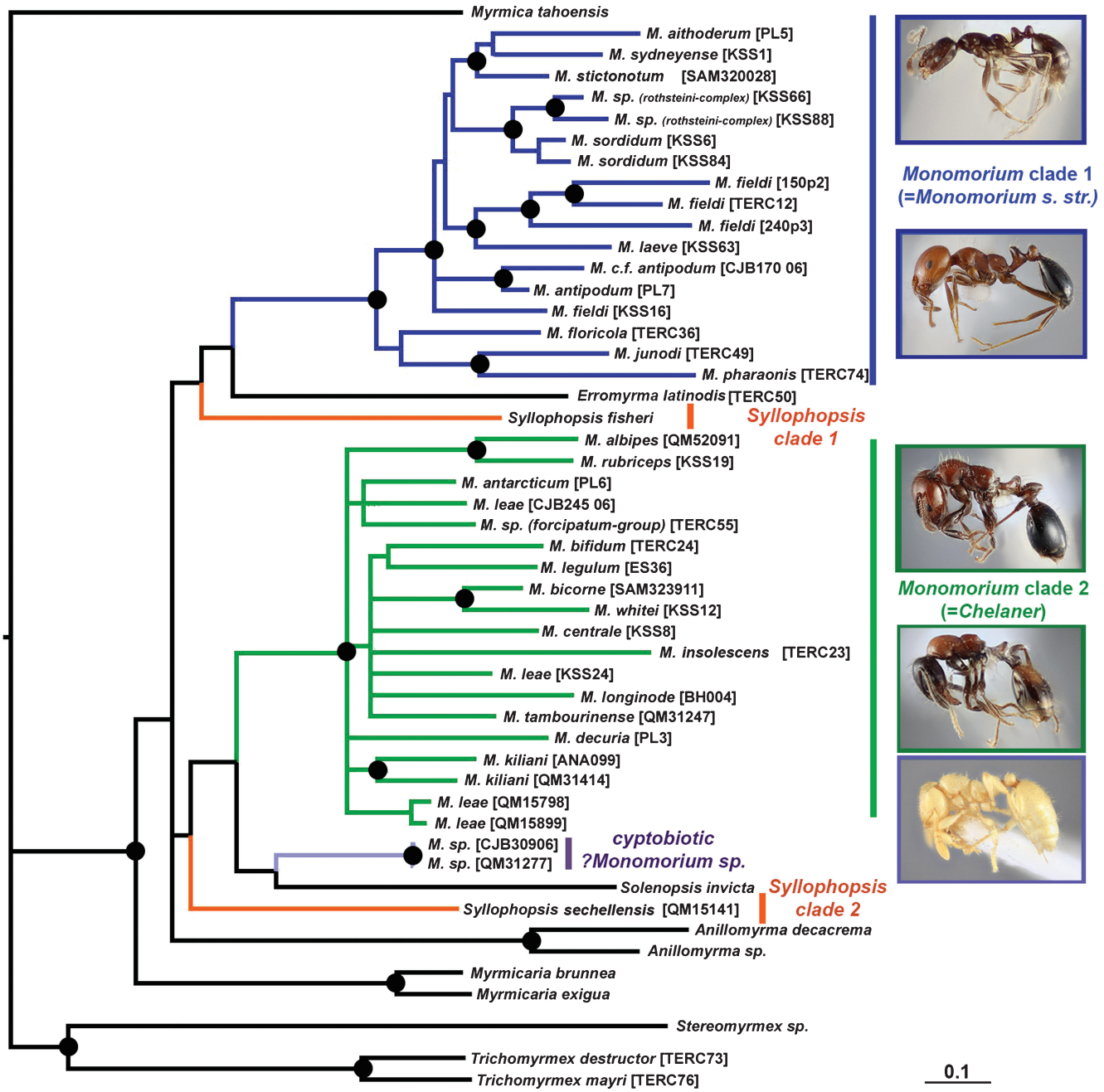

Fig. 1. Bayesian tree of the 3-gene analysis (*COI*, *EF1αF2* and *wg*) for all samples (including missing data). Solid circles denote nodes with ≥95 Bayesian posterior probability and ≥70 maximum likelihood bootstrapping support. Specimen codes follow the taxon names.

support in all analyses (Figs 1–3) except for *COI* (Fig. 4), which had variable support between the Bayesian and ML analyses for Clade 2 (posterior probability (PP) 0.77, bootstrapping support (BS) 0.22) (Fig. 4). Clade 1 contained the small, Australian and New Zealand species that have 11-segmented antennae, as well as the *M. rothsteini* Forel, 1902 complex and *M. sordidum* Forel, 1902, both of which have 12-segmented antennae. It also included the three non-Australian species, *M. floricola*, *M. pharaonis* and *M. junodi*. This clade corresponds to the 'core' *Monomorium sensu* Ward *et al.* (2015).

Clade 2 comprised the remaining Australian *Monomorium* species, all with 12-segmented antennae, as well as *M. antarcticum* and *M. smithii* from New Zealand and the two New Caledonian species. The taxonomically uncertain, undescribed, de-pigmented, blind taxa (?*Monomorium* spp. (CJB30906 and QM31277)) were sister to Clade 2 with strong support in multi-gene analyses (3-gene, complete data) (Fig. 2), *EF1αF2+wg* (Fig. 3) and *COI*+ *EF1αF2* (Fig. S1)), but not in the 3-gene, all taxa tree (with missing data) (Fig. 1) or in the *COI*-only tree (Fig. 4) where support for alternative relationships was weak.

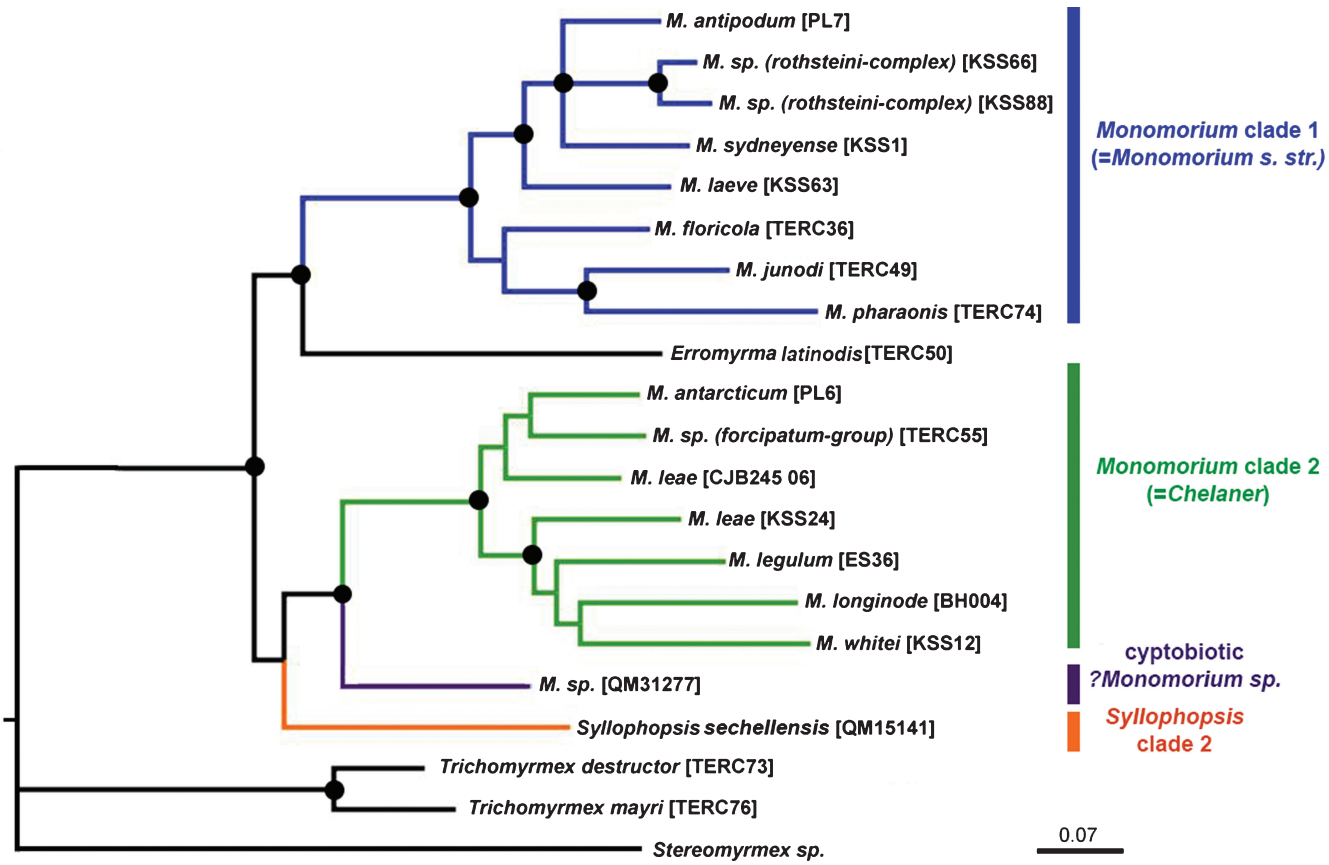

Fig. 2. Bayesian tree of the 3-gene analysis (cytochrome oxidase subunit 1, elongation factor 1α F2 and wingless) with complete data for all taxa. Solid circles denote nodes with ≥95 Bayesian posterior probability and ≥70 maximum likelihood bootstrapping support. Specimen codes follow the taxon names.

Although these cryptobiotic taxa are superficially similar in some characters to *Syllophopsis* and *Anillomyrma*, we found no evidence for a close relationship to these genera.

The position of *E. latinodis* was also unclear with all analyses except *COI+wg* (Fig. S2), placing it as sister to Clade 1 with variable support. The position of *M. decuria* Heterick, 2001 was also unclear, with the 3-gene, all taxa analysis (Fig. 1) and *COI+wg* (Fig. S2) placing it as a well-supported member of Clade 2 but the *COI*-only analysis placing it as sister (along with *E. latinodis*) to Clade 1+*My. brunnea* but with low support. *Monomorium decuria* is unique among Australian *Monomorium* as it is the only species to have 10-segmented antennae but is otherwise morphologically similar to *M. falcatum* (McAreavey, 1949) (Heterick 2001; Andersen 2007), which has 12-segmented antennae and is allied morphologically with those species in Clade 2.

The two *Syllophopsis* species were not recovered as monophyletic in the two analyses that included both species. However, support was generally low for the critical nodes, and that *COI* was missing for *Sy. fisheri* (Heterick, 2006) likely contributed to this unexpected result.

Australian Monomorium *species-groups*

To further examine relationships among the Australian species, analysis of the *COI*-only sequences was undertaken for the much larger sampling of species and, where available, multiple morphotypes of each species.

The monophyly of the *M. monomorium*-group *sensu* Heterick (2001) was well supported within Clade 1 (Fig. 4). However, within Clade 2 the *rubriceps*-group, *longinode*-group and *kiliani*-group of Heterick (2001) were not recovered as monophyletic, but support values were generally low and relationships must be considered provisional in light of this. Groups that were recovered as monophyletic with good support included of the *bicorne*-group, the New Zealand species, *M. antarcticum* and *M. smithii*, and a sister-group relationship between two species, *M. rubriceps* and *M. albipes*, in the *rubriceps*-group. Nothing could be inferred for the status of the *insolescens*-group, which contains a single species, or the *falcatum*-group, which was represented here by only one species (*M. decuria*). Relationships of the two species from New Caledonia and the remaining species in Clade 2 were poorly resolved.

Monomorium *species complexes*

Within Clade 1, the *COI* analysis indicated that the *M. rothsteini* and *M. sordidum* species complexes, which bear close morphological affinities to one another, formed a monophyletic group (Fig. 4). The '*carinatum*' form of *M. sydneyense* from northern Australia was monophyletic,

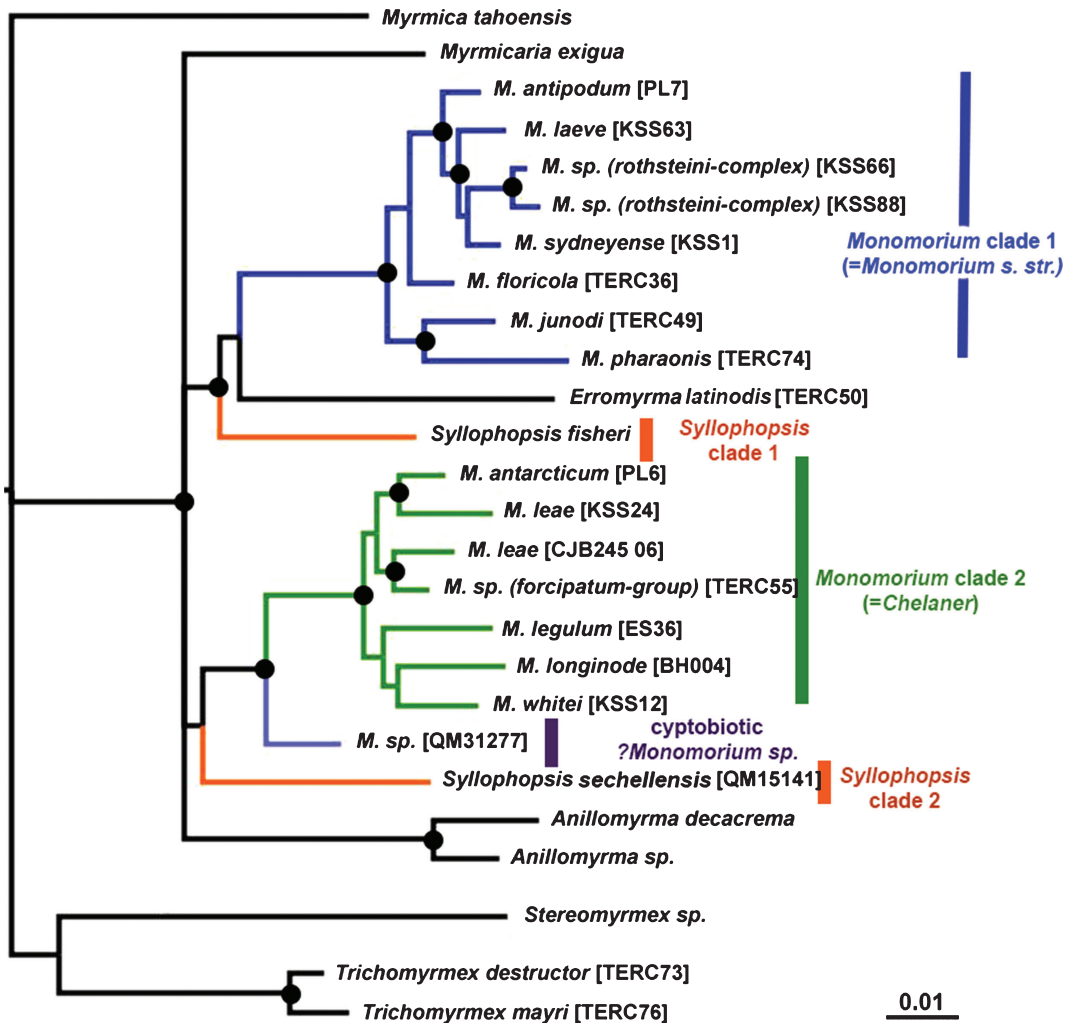

Fig. 3. Bayesian tree of the concatenated elongation factor 1α F2 and wingless data. Solid circles denote nodes with ≥95 Bayesian posterior probability and ≥70 maximum likelihood bootstrapping support. Specimen codes follow the taxon names.

with the more typical form from southern Australia (KSS1) having a more distant sister relationship. However, the lineages belonging to *M. fieldi* and *M. leave* were problematic. The majority of *M. fieldi* samples formed a well-supported group that was further divided into five well-supported lineages with relatively deep divergences. However, one *M. fieldi* sample (KSS16) was resolved as a member of a clade that included samples of *M. leave* and *M. sydneyense*, although these relationships were not well supported. *Monomorium laeve* comprised three separate lineages, but again this was not well supported. The two *M. stictonotum* (Heterick, 2001) samples were recovered as monophyletic although with poor support (PP 0.62), while *M. antipodum* from New Zealand and *M.* cf. *antipodum* from Australia formed a well-supported clade separate to the *M. fieldi* clades described above.

With a greater number of species represented but fewer duplicates, species paraphyly was less apparent in Clade 2. *Monomorium leae* was represented by three distinctive morphological types, but support was lacking for the critical nodes with the exception of the '*flavipes*' form that was recovered as part of a weakly supported clade (PP 0.81) containing species from four of Heterick's (2001) species-groups but no other *M. leae* morphotypes.

Taxonomic changes

The phylogenetic results here support the monophyly of an Australasian clade (Clade 2), hereafter referred to as the '*Chelaner*' clade. The majority of these species are morphologically united by having 12-segmented antennae, a palpal formula of 2,3 and a mandibular tooth count of 3–7 (Heterick 2001, 2003). Members of the *monomorium*-group clade (Clade 1) overlap morphologically with the *Chelaner* clade in having a mandibular tooth count of 3 or 4, but having a palpal formula of 1,2 or 2,2, and 11-segmented antennae distinguishes most species from the Australasian *Chelaner* clade. However, *M. crinitum* Heterick, 2001, *M. petiolatum* Heterick, 2001, *M. sculpturatum* Clark, 1934, *M. shattucki* Heterick, 2001 and *M. tambourinense* Forel, 1915 from the

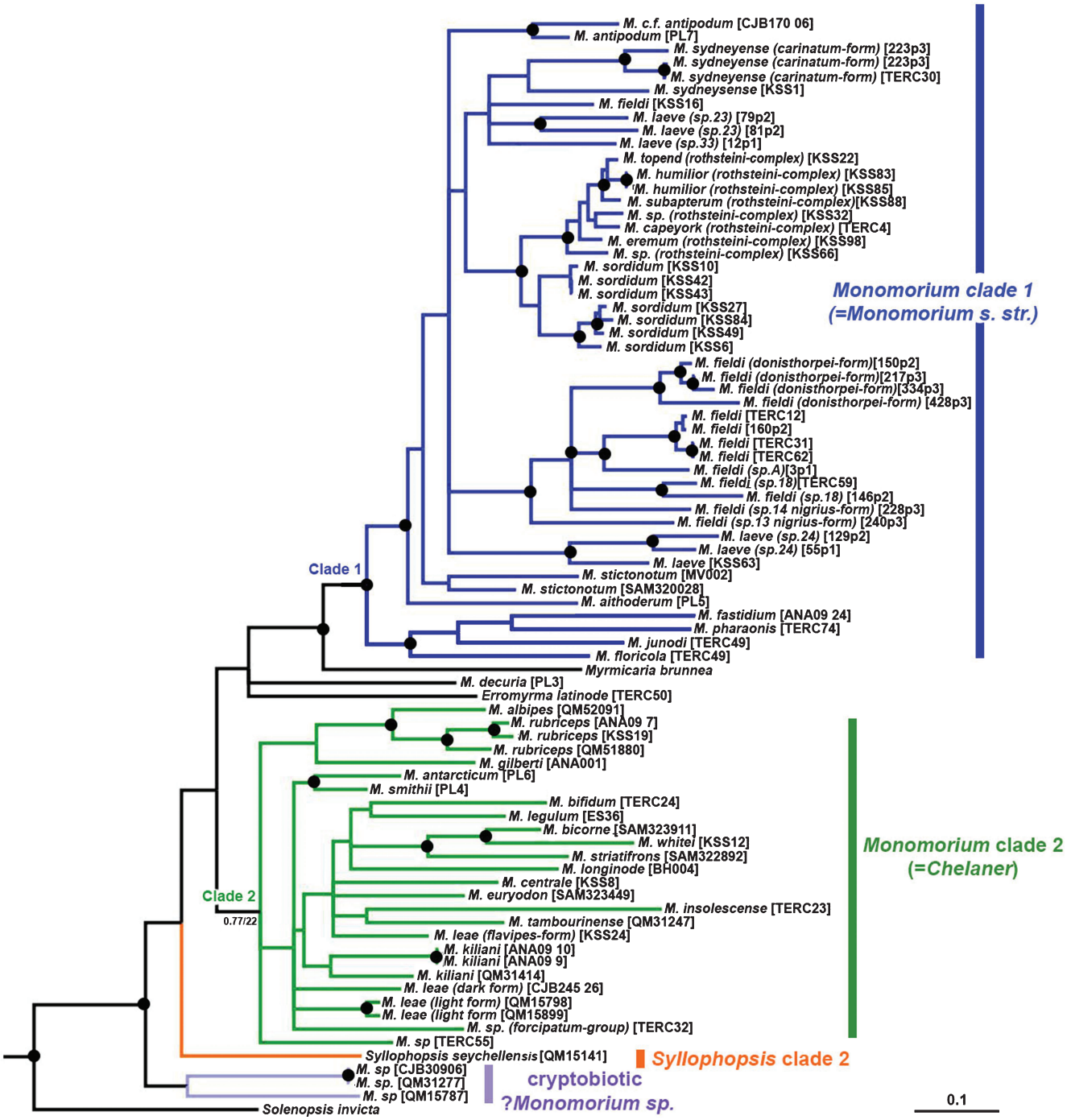

Fig. 4. Bayesian tree of the cytochrome oxidase subunit 1 (*COI*-only) data for all samples. Solid circles denote nodes with ≥95 Bayesian posterior probability and ≥70 maximum likelihood bootstrapping support. Outgroup taxa represented by *Trichomyrmex desctructor* and *T. mayri* not shown. Specimen codes follow the taxon names.

Chelaner clade have a palpal formula of 2,2 and together with having 12-segmented antennae overlap in both these characters with members of the *M. rothsteini* complex and *M. sordidum* from Clade 1. Our analyses provide strong molecular support for the placement of the *M. rothsteini* complex and *M. sordidum* in the *monomorium*-group as proposed by Heterick (2001) on other morphological grounds, and the presence of 12-segmented antennae most likely represents a character reversal on this branch. Four of the five species listed above were not available for our molecular analysis but bear strong morphological affinities to *M. kiliani* Forel, 1902 (in the case of *M. crinitum*, *M. petiolatum* and *M. shattucki*) or *M. leae*

(in the case of *M. sculpturatum*). The one species available for sequencing, *M. tambourinense*, was strongly supported as a member of the *Chelaner* clade.

Monomorium decuria has 10-segmented antennae and is the only Australian species with this character. As previously mentioned, it is otherwise very similar morphologically to *M. falcatum*, which has 12-segmented antennae. Our *COI+wg* analysis provided the strongest support for the placement of this species in the *Chelaner* clade and until further evidence is available we conclude that this species is best placed in this group, as proposed by both Heterick (2001) and Andersen (2007).

Based on the results above, we propose that a more workable classification for the group is to remove *Chelaner* Emery as a junior synonym of *Monomorium s. l.* and resurrect it as a valid genus-level taxon.

Chelaner Emery, stat. rev.

Monomorium subgenus *Chelaner* Emery, 1914: 410. Type: *Monomorium* (*Chelaner*) *forcipatum* Emery, by subsequent designation of Emery (1921).

Chelaner Emery; Ettershank, 1966; raised to generic rank.

Monomorium subgenus *Notomyrmex* Emery, 1915: 190; synonymy by Ettershank (1966).

Schizopelta McAvreavey, 1949: 14, synonymy by Ettershank (1966).

Monomorium subgenus *Chelaner* Emery; synonymy by Bolton (1987) but without recognising *Chelaner* as a subgenus.

Diagnosis (worker)

Small to medium ants 2–7 mm in length, commonly monomorphic but with size variation in some species. Clypeus bicarinate with a median clypeal seta, carinae subparallel, converging or diverging, frontal margin overhanging mandibles, with or without a pair of clypeal teeth, clypeal margin may be rounded or deeply concave. Antennae 12-segmented or 10-segmented (*C. decuria*) with a 3-segmented club. Palpal formula 2,3 or 2,2, mandibular tooth count 3–7. Eyes well developed, small to large, circular or oval.

Promesonotal suture not extending on to dorsal surface, rarely complete dorsally. Metanotal groove moderately to deeply impressed or very shallow. Propodeum rounded to slightly concave on the dorsal and posterior surfaces, which may be distinctly carinate or with barely raised, rounded ridges, propodeum less commonly dentate (variably so in *C. insolescens* Wheeler, 1934) or spinose (*C. sculpturatum* and *C. sublamellatum* Heterick, 2003). Metapleural gland and lobes well developed.

Petiole pedunculate, node large, quadrate and parallel-sided or more triangular with a rounded apex. Post-petiole node present, high and rounded with distinct anterior and posterior surfaces or, less commonly, low with a gently sloping anterior surface (*C. crinitum*, *C. kiliani*, *C. petiolatum*, *C. tambourinense*).

Colour ranges from pale yellow to dark amber, red and black. Sculpture highly variable from smooth and glossy to punctures restricted to mesopleuron, to head, mesosoma and waist entirely punctate, reticulate or striate.

Remarks

Ettershank (1966) refers to the propodeal spiracle opening into a vestibule as a character that separates species of *Chelaner* from *Monomorium*. The first author has examined a large number of *Chelaner* species and, although the propodeal spiracle is obviously vestibulate for several species, it is not evident for many of them. This is largely due to them having a very dark or heavily sclerotised cuticle that obscures anything below the surface. Similarly, for those species that remain in *Monomorium*, none were observed to have a vestibulate spiracle, but it is often difficult to see through the cuticle to determine whether it is vestibulate or not. Bolton (1987) reviewed the characters Ettershank (1966) had used to raise *Chelaner* to genus level, referring to the palpal formula and vestibulate nature of the spiracle as the only diagnostic characters separating *Chelaner* from *Monomorium*, while all the others occurred in both genera (these included the number of antennal segments, the structure of the clypeus and the pedunculate petiole). Further evidence that this character is not particularly useful is Ettershank's (1966) observation that *M. rothsteini*, a species that clearly belongs to the *Monomorium* clade, has a vestibulate propodeal spiracle.

Although the molecular data presented above support two distinct clades, the morphological diagnoses for these two genera remain problematic in that some specimens are difficult to identify, and a more thorough examination of their morphology that scrutinises additional characters will be required in future. In this respect, male genitalia and structure of the sting apparatus (see Kugler 1978) are likely character systems worth exploring.

Included species

All species are Australian unless indicated otherwise as New Caledonia (NC), New Guinea (NG) or New Zealand (NZ).

C. albipes Heterick, 2001 **stat. nov.**
C. antarcticum Smith F., 1858 **stat. rev.** (NZ)
C. anthracinum Heterick, 2001 **stat. nov.**
C. aper Emery, 1914 **stat. rev.** (NC)
C. aper dubium Emery, 1914 **stat. rev.** (NC)
C. bicorne Forel, 1907 **stat. rev.**
C. bifidum Heterick, 2001 **stat. nov.**
C. bihamatum Heterick, 2001 **stat. nov.**
C. brachythrix Heterick, 2001 **stat. nov.**
C. burchera Heterick, 2001 **stat. nov.**
C. capito Heterick, 2001 **stat. nov.**
C. centrale Forel, 1910b **stat. rev.**
C. crinitum Heterick, 2001 **stat. nov.**
C. croceiventre Emery, 1914 **stat. rev.** (NC)
C. decuria Heterick, 2001 **stat. nov.**
C. draculai Heterick, 2001 **stat. nov.**
C. durokoppinense Heterick, 2001 **stat. nov.**
C. edentatum Emery, 1914 **stat. rev.** (NG)
C. elegantulum Heterick, 2001 **stat. nov.**
C. euryodon Heterick, 2001 **stat. nov.**
C. falcatum McAreavey, 1949 **stat. rev.**
C. flavonigrum Heterick, 2001 **stat. nov.**
C. forcipatum Emery, 1914 **stat. rev.** (NC)
C. gilberti Forel, 1902 **stat. rev.**
C. insolescens Wheeler, 1934 **stat. rev.**
C. kiliani Forel, 1902 **stat. rev.**
C. lacunosum Heterick, 2001 **stat. nov.**

C. leae Forel, 1913 **stat. rev.**
C. legulum Heterick, 2001 **stat. nov.**
C. longiceps Wheeler, 1934 **stat. rev.**
C. longinode Heterick, 2001 **stat. nov.**
C. longipes Emery, 1914 **stat. rev.** (NC)
C. macarthuri Heterick, 2001 **stat. nov.**
C. majori Heterick, 2001 **stat. nov.**
C. melleum Emery, 1914 **stat. rev.** (NC)
C. nightcapense Heterick, 2001 **stat. nov.**
C. nigriceps Heterick, 2001 **stat. nov.**
C. parantarcticum Heterick, 2001 **stat. nov.**
C. petiolatum Heterick, 2001 **stat. nov.**
C. pubescens Heterick, 2001 **stat. nov.**
C. punctulatum Heterick, 2003 **stat. nov.**
C. ravenshoense Heterick, 2001 **stat. nov.**
C. rubriceps Mayr, 1876 **stat. rev.**
C. rufonigrum Heterick, 2001 **stat. nov.**
C. sculpturatum Clark, 1934 **stat. rev.**
C. shattucki Heterick, 2001 **stat. nov.**
C. smithii Forel, 1892 **stat. rev.** (NZ)
C. striatifrons Heterick, 2001 **stat. nov.**
C. sublamellatum Heterick, 2003 **stat. nov.**
C. tambourinense Forel, 1915 **stat. rev.**
C. tricolor Emery, 1914 **stat. rev.** (NC)
C. whitei Wheeler, 1915 **stat. rev.**
C. xantheklemma Heterick, 2001 **stat. nov.**

Monomorium Mayr, 1855

For a complete list of synonymies see AntWiki. Available at: http://www.antwiki.org/wiki/Monomorium.

Diagnosis (*worker, Australasian species*)

Differs from *Chelaner* by: very small to medium ants, 1.0–7.5 mm. Clypeus medially raised and bicarinate, carinae diverging or subparallel, raised and angular or rounded, palpal formula 1,2 or 2,2; number of mandibular teeth 3–4. Antennae 11-segmented except for the *M. rothsteini* and *M. sordidum* radiations with 12-segmented antennae, all with a 3-segmented club (and for the introduced African species *M. floricola* and *M. pharaonis*). Eyes very small and consisting of one or a few ommatidia to very large, circular oval or reniform. Posterodorsal corners of the propodeum may be smoothly rounded or angulate but never dentate or spinose. Petiole pedunculate, petiole and postpetiole with a high, rounded node. Colour and sculpture highly variable.

Remarks

See above under 'Remarks' for *Chelaner* for additional information on the morphological distinction of the two genera.

Included Australasian species

M. aithoderum Heterick, 2001
M. anderseni Heterick, 2001
M. antipodum Forel, 1901 (NZ)
M. arenarium Heterick, 2001
M. bogischi Wheeler, 1917
M. broschorum Sparks, 2014a
M. capeyork Sparks, 2014a
M. carinatum Heterick, 2001
M. casteneum Heterick, 2001
M. disetigerum Heterick, 2001
M. eremoides Sparks, 2014a
M. eremophilum Heterick, 2001
M. eremum Sparks, 2014a
M. fieldi Forel, 1910
M. geminum Sparks, 2014a
M. hertogi Sparks, 2014a
M. hoffmanni Sparks, 2014a
M. humilior Forel, 1910b
M. kidman Sparks, 2014a
M. laeve Mayr, 1876
M. leda Forel, 1915
M. maryannae Sparks, 2014a
M. megalops Heterick, 2001
M. merepah Sparks, 2014a
M. micula Heterick, 2001
M. mitchell Sparks, 2014a
M. nanum Heterick, 2001
M. oodnadatta Sparks, 2014a
M. pilbara Sparks, 2014a
M. rothsteini Forel, 1902
M. silaceum Heterick, 2001
M. sordidum Forel, 1902
M. speculum Sparks, 2014a
M. stagnum Sparks, 2014a
M. stictonotum Heterick, 2001
M. subapterum Wheeler, 1917
M. sydneyense Forel, 1902
M. tenebrosum Sparks, 2014a
M. topend Sparks, 2014a
M. torrens Sparks, 2014a

Discussion

This study supports the resurrection of *Chelaner* as a genus separate from *Monomorium s. str*. and provides a preliminary taxonomic framework for the species occurring in Australia, New Zealand, New Caledonia and New Guinea. As now defined, *Monomorium s. str.* contains the speciose radiations of small, generalist species with 11-segmented antennae plus the *M. rothsteini*/*M. sordidum* radiations with 12-segmented antennae. *Chelaner* now encompasses those species with 12-segmented antennae and a palpal formula of 2,3 or rarely 2,2. As so defined, this genus is endemic to Australasia with a significant radiation on the Australian continent, one species recorded from New Guinea and two from New Zealand, although it has been suggested that *C. antarcticum* may represent a species complex (Jones *et al*. 1988; Don and Jones 1993). There are six species and one subspecies described from New Caledonia; however, many more are known from collections.

Our results support most of the taxonomic changes made to the genus by Ward *et al*. (2015) with the exception of the placement of the *hildebrandti*-group and *fossulatum*-group within *Syllophopsis* (represented here by *S. fisheri* and *S. sechellensis*). The *EF1αF2+wg* analysis resolved *S. fisheri* as sister to *Monomorium* Clade 1 and *S. sechellensis* as sister to *Monomorium* Clade 2. The Ward *et al*. (2015) analysis, which employed a greater number of nuclear markers, also

did not provide strong support for the monophyly of *Syllophopsis* and morphological affinity was provided as a secondary line of evidence for their association. *Syllophopsis* species have characteristics typical of cryptobiotic ants (e.g. very small body size, pale colour, reduced or absent eyes) and their morphological affinity may be a result of convergence associated with living in such habitats. Additional sampling for sequencing that spans the geographic range of these two species-groups, in addition to careful morphological assessment, is required to fully resolve the relationships among these taxa. Our analyses also indicate that the two blind, cryptobiotic, soil-dwelling taxa from Australia, initially assigned to *Monomorium*, are sister to Clade 2 (*Chelaner*) and are unrelated to *Syllophopsis* or *Anillomyrma*. Even though these two cryptobiotic taxa bear some resemblance to species of *Syllophopsis*, and they share numerous characters with *Anillomyrma*, namely, depigmented integument, a complete lack of eyes, enlarged fore coxae, short broad fore femora and tibiae, and the absence of the anteroventral process on the petiole (Bolton 1987; Eguchi *et al*. 2010), these similarities are now best interpreted as convergences associated with living in similar habitats. As to whether these two species represent an early branching lineage of *Chelaner* that went underground, or possibly a new genus, will require future studies incorporating much greater taxon sampling and the use of additional nuclear markers.

There is now a growing understanding of the broader systematic relationships among genera in the Solenopsidini. However, resolving the species-level taxonomy for both *Chelaner* and Australian *Monomorium* remains a mammoth task. Evidence presented here and elsewhere (Andersen *et al*. 2013; Sparks *et al*. 2014*b*) shows that taxa previously considered to be single variable species are in fact diverse species complexes. In this respect, the species *M. fieldi*, *M. laeve* and *M. sydneyense* are perhaps the most in need of taxonomic reassessment. They have continent-wide distributions, and their small size and simplified morphology makes species delimitation challenging without input from concurrent molecular studies. Although many studies have demonstrated the utility of *COI* in clarifying species boundaries (e.g. Dinsdale *et al*. 2010; Ng'endo *et al*. 2013; Song *et al*. 2016), the limitations of mtDNA (e.g. nuclear paralogues, male-biased gene flow or introgression) or using a single marker to infer species trees means there is a pressing need to develop novel nuclear markers that are informative at the species level.

Our results support the validity of the New Zealand *M. antipodum* as a separate species from *M. fieldi. Monomorium antipodum* formed a clade with a morphologically similar Australian specimen, and its affinity with the latter taxon is supported by analysis of venom chemistry (Don *et al*. 2001). This relationship means that it is likely to have been introduced from Australia, as suggested by Brown (1958). However, further molecular and morphological analysis is required to confirm that it is indeed conspecific with an Australian population.

We set out to provide a more stable and broadly acceptable systematics framework for the Australian species of *Monomorium.* However, this study highlights some of the difficulties in undertaking phylogenetic research on such a large and complex group of ants, for which many of the species are rare. The conclusions that can be made about the broader relationships among genera, and species groups within *Chelaner* in particular, are limited by the taxa that were available for study. Although we did not set out to undertake a phylogenetic study of southern hemisphere *Monomorium* and its relatives, the inclusion of other closely related genera (e.g. *Oxyepoecus* and *Austromorium*) would help place *Chelaner* in a broader phylogenetic context. Additionally, species level sampling across both *Monomorium* and *Chelaner* would need to be far more comprehensive if the relationships among species are to be adequately resolved. Here we were able to sample just 30 species that were suitable for DNA analysis out of the 83 known species, despite extensive field collection over many years.

This study also highlights that a greater number and variety of genetic markers will be required to adequately resolve both the deeper relationships among genera and among some of the more recently evolved lineages as support was weak at some deep and shallow nodes in different parts of the trees derived from our analyses. Next generation sequencing technologies are now coming on stream that make this feasible and cost-effective, although it was not possible at the time the current study was undertaken. Recent next generation sequencing studies have greatly expanded the available markers for phylogenetic and phylogenomic analyses of spiders (e.g. Rix *et al*. 2017), various insect orders (e.g. Kawahara and Breinholt 2014; Peters *et al*. 2017) and families including Formicidae (Blaimer *et al*. 2015).

Despite these limitations, our analyses have contributed to a more stable taxonomic basis for a speciose Australian component of the Solenopsidini. It is hoped that this study will initiate more detailed systematics research on *Monomorium* and its relatives in the future. Given the demonstrated limitations of comparative morphology for these small ants, an integrative approach is necessary; one that incorporates fine-scale comprehensive field sampling, a much greater array of solenopsidine taxa from the south-west Pacific and other southern hemisphere continents, the incorporation of ecophysiological results such as comparative venom chemistry, in addition to the development of a wider array of species-level molecular markers. In this way, there may be hope for resolving the taxonomy of this dominant and ecologically significant component of the Australian ant fauna.

Conflicts of interest

The authors declare no conflicts of interest.

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References

Abouheif, E., and Wray, G. A. (2002). Evolution of the gene network underlying wing polyphenism in ants. *Science* **297**, 249–252. doi:10.1126/science.1071468

Andersen, A. N. (2007). Ant diversity in arid Australia: a systematic overview. In 'Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson – 50 Years of Contributions'. (Eds R. R. Snelling, B. L. Fisher and P. S. Ward.) *Memoirs of the American Entomological Institute* **80,** 19–51.

Andersen, A. N., Arnan, X., and Sparks, K. (2013). Limited niche differentiation within remarkable co-occurrences of congeneric species: *Monomorium* ants in the Australian seasonal tropics. *Austral Ecology* **38**, 557–567. doi:10.1111/aec.12000

Blaimer, B. B., Brady, S. G., Ted, R., Schultz, T. R., Lloyd, M. W., Fisher, B. L., and Ward, P. S. (2015). Phylogenomic methods outperform traditional multi-locus approaches in resolving deep evolutionary history: a case study of formicine ants. *BMC Evolutionary Biology* **15**, 271. doi:10.1186/s12862-015-0552-5

Bolton, B. (1987). A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology* **54**, 263–452.

Brady, S. G., Schultz, T. R., Fisher, B. L., and Ward, P. S. (2006). Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 18172–18177. doi:10.1073/pnas.0605858103

Brown, W. L. (1958). A review of the ants of New Zealand. *Acta Hymenopterologica* **1**, 1–50.

Buczkowski, G., and Bennett, G. (2009). Colony budding and its effects on food allocation in the highly polygynous ant, *Monomorium pharaonis*. *Ethology* **115**, 1091–1099. doi:10.1111/j.1439-0310.2009.01698.x

Clark, J. (1934). Ants from the Otway Ranges. *Memoirs of the National Museum of Victoria* **8**, 48–73. doi:10.24199/j.mmv.1934.8.03

Dinsdale, L., Cook, C., Buckley, Y. M., and De Barro, P. (2010). Refined global analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) mitochondrial cytochrome oxidase 1 to identify species level genetic boundaries. *Annals of the Entomological Society of America* **103**, 196–208. doi:10.1603/AN09061

Don, W. (2007). 'Ants of New Zealand.' (Otago University Press: Dunedin, New Zealand.)

Don, A. W., and Jones, T. H. (1993). The stereochemistry of 3-butyl-5-(5-hexenyl)-pyrrolizidine from populations of *Monomorium antarcticum* (Smith) (Hymenoptera: Formicidae) and its possible role as a unique taxonomic character. *New Zealand Entomologist* **16**, 45–48. doi:10.1080/00779962.1993.9722649

Don, A. W., Jones, T. H., Flournoy, R. C., and Zottig, V. E. (2001). Venom chemistry of *Monomorium antipodum* Forel (Hymenoptera: Formicidae) from New Zealand and its relevance to the taxonomy of the species. *New Zealand Entomologist* **24**, 49–52. doi:10.1080/00779962.2001.9722080

Emery, C. (1914). Les Fourmis de la Nouvelle-Caledonie er des Iles Loyalty. In 'Forschungen in Neu-Caledonien und auf den Loyalty-Inseln'. *Zoologie* **1**, 393–437.

Eguchi, K., Tuan, V. B., General, D. M., and Alpert, G. D. (2010). Revision of the ant genus *Anillomyrma* Emery, 1913 (Hymenoptera: Formicidae: Myrmicinae: Solenopsidini). *Myrmecological News* **13**, 31–36.

Emery, C. (1901). Ameisen gesammelt in Ceylon von Dr. W. Horn 1899. *Deutsche Entomologische Zeitschrift* **1901**, 113–122.

Emery, C. (1915). Noms de sous-genres et de genres proposés pour la sous-famille des Myrmicinae. Modifications à la classification de ce groupe (Hymenoptera Formicidae). *Bulletin de la Société Entomologique de France* **1915**, 189–192.

Emery, C. (1921). Hymenoptera. Fam. Formicidae. Subfam. Myrmicinae. *Genera Insectorum* **174A**, 1–94.

Ettershank, G. (1966). A generic revision of the world Myrmicinae related to *Solenopsis* and *Pheidologeton* (Hymenoptera: Formicidae). *Australian Journal of Zoology* **14**, 73–171. doi:10.1071/ZO9660073

Fisher, B. L., and Bolton, B. (2016). 'Ants of Africa and Madagascar. A Guide to the Genera.' (University of California Press: Berkley, IA.)

Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Forel, A. (1892). Die Ameisen Neu-Seelands. *Mitteilungen der Schweizerische Entomologische Gesellschaft* **8**, 331–343.

Forel, A. (1901). Variétés myrmécologiques. *Annales de la Société Entomologique de Belgique* **45**, 334–382.

Forel, A. (1902). Fourmis nouvelles d'Australie. *Revue Suisse de Zoologie* **10**, 405–548. doi:10.5962/bhl.part.13793

Forel, A. (1907). Formicidae. In 'Die Fauna Südwest-Australien. Volume 7'. (Eds W. Michaelsen and R. Hartmeyer.) pp. 263–310. (Gustav Fischer: Jena, Germany.)

Forel, A. (1910*a*). Note sur quelque fourmis d'Afrique. *Annales de la Société Entomologique de Belgique* **54**, 421–458.

Forel, A. (1910*b*). Formicides Australiens reçus de M. M. Froggatt et Rowland Turner. *Revue Suisse de Zoologie* **18**, 1–94.

Forel, A. (1913). Fourmis de Tasmanie et d'Australie récoltées par MM. Lae, Froggatt etc. *Bulletin de la Société Vaudoise des Sciences Naturelles* **49**, 173–195.

Forel, A. (1915). Results of Dr E. Mjöbergs Swedish Scientific Expeditions to Australia 1910–13. 2. *Ameisen. Arkiv för Zoologi* **9**, 1–119.

Gunawardana, D. (2005). *Monomorium fieldi* Forel (Hymenoptera: Formicidae) is the current name to use for ants previously known as *Monomorium antipodum* Forel and *Monomorium orientale* Mayr in New Zealand. *The Weta* **30**, 14–15.

Hall, T. A. (1990). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**, 95–98.

Heterick, B. E. (2001). Revision of the Australian ants of the genus *Monomorium* (Hymenoptera: Formicidae). *Invertebrate Taxonomy* **15**, 353–459. doi:10.1071/IT00003

Heterick, B. E. (2003). Two new Australian *Monomorium* Mayr (Hymenoptera: Formicidae), including a highly distinctive species. *Australian Journal of Entomology* **42**, 249–253. doi:10.1046/j.1440-6055.2003.00352.x

Heterick, B. (2006). A revision of the Malagasy ants belonging to genus *Monomorium* Mayr, 1855 (Hymenoptera: Formicidae). *Proceedings of the California Academy of Sciences* **57**, 69–202.

Jerdon, T. C. (1851). A catalogue of the species of ants found in southern India. *The Madras Journal of Literature and Science* **17**, 103–127.

Jones, T. H., Blum, M. S., Andersen, A. N., Fales, H. M., and Escoubas, P. (1988). Novel 2-ethyl-5-alkylpyrrolidines in the venom of an Australian ant of the genus *Monomorium*. *Journal of Chemical Ecology* **14**, 35–45. doi:10.1007/BF01022529

Kawahara, A. Y., and Breinholt, J. W. (2014). Phylogenomics provides strong evidence for relationships of butterflies and moths. *Proceedings. Biological Sciences* **281**, 20140970. doi:10.1098/rspb.2014.0970

Kugler, C. (1978). A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). *Studia Entomologica* **20**, 413–548.

Kumar, S., Nei, M., Dudley, J., and Tamura, K. (2008). MEGA: a biologist-centric software for evolutionary analysis of DNA and protein sequences. *Briefings in Bioinformatics* **9**, 299–306. doi:10.1093/bib/bbn017

Lanfear, R., Calcott, B., Ho, S. Y. W., and Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**, 1695–1701. doi:10.1093/molbev/mss020

Mayr, G. (1855). Formicina Austriaca. Beschreibung der bisher im österreichischen Kaiserstaate aufgefundenen Ameisen, nebst Hinzufügung jener in Deutschland, in der Schweiz und in Italien vorkommenden Arten. *Verhandlungen des Zoologisch-Botanischen Gesellschaft Wien* **5**, 273–478.

Mayr, G. (1865). 'Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1850.' (Zoologischer Theil: Vienna, Austria.)

Mayr, E. (1872). Formicidae Borneenses collectae a G. Doria er O. Deccari in Territorio Sarawak annis 1865–1867. *Annali del Museo Civico di Storia Naturale di Genova* **2**, 133–155.

Mayr, G. (1876). Die Australischen Formiciden. *Journal des Museum Godeffroy* **12**, 56–115.

Mayr, G. (1887). Südamerikanische Formiciden. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* **37**, 511–632.

McAreavey, J. (1949). Australian Formicidae. New genera and species. *Proceedings of the Linnean Society of New South Wales* **74**, 1–25.

Moreau, C. S., Bell, C. D., Vila, R., Archibald, S. B., and Pierce, N. E. (2006). Phylogeny of the ants: diversification in the age of angiosperms. *Science* **312**, 101–104. doi:10.1126/science.1124891

Ng'endo, R., Osiemo, Z. B., and Brandl, R. (2013). DNA barcodes for species identification in the hyperdiverse ant genus *Pheidole* (Formicidae: Myrmicinae). *Journal of Insect Science* **13**, 27.

Peters, R. S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., Diez, P. A., Heraty, J., Kjer, K. M., Klopfstein, S., Meier, R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Wappler, T., Rust, J., Misof, B., and Niehuis, O. (2017). Evolutionary history of the Hymenoptera. *Current Biology* **27**, 1013–1018. doi:10.1016/j.cub.2017.01.027

Rix, M. G., Cooper, S. J. B., Meusemann, K., Klopfsteim, S., Harrison, S. E., Harvey, M. S., and Austin, A. D. (2017). Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae). *Molecular Phylogenetics and Evolution* **109**, 302–320. doi:10.1016/j.ympev.2017.01.008

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**, 539–542. doi:10.1093/sysbio/sys029

Santschi, F. (1915). Nouvelles formis d'Afrique. *Annales de la Société Entomologique de France* **84**, 224–282.

Saunders, W. W. (1842). Descriptions of two hymenopterous insects. *The Transactions of the Entomological Society of London* **3**, 223–231.

Santschi, F. (1926). Deux nouvelles fourmis parasites de l'Argentine. *Folia Myrmecologica et Termitologica* **1**, 6–8.

Shattuck, S. O. (2009). *Austromorium*, a new myrmicine ant genus from Australia (Hymenoptera: Formicidae). *Zootaxa* **2193**, 62–68.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H., and Flook, P. (1994). Evolution, weighting, and phylogenetic utility of mitochondrial gene-sequences and a compilation of conserved polymerase chain-reaction primers. *Annals of the Entomological Society of America* **87**, 651–701. doi:10.1093/aesa/87.6.651

Smith, F. (1858). 'Catalogue of Hymenopterous Insects in the Collection of the British Museum. Part VI. Formicidae.' (British Museum: London, United Kingdom.)

Solis, D. R., and Bueno, O. C. (2014). Thermal tolerances of three tramp ant species (Hymenoptera: Formicidae). *Sociobiology* **59**, 213–223. doi:10.13102/sociobiology.v59i1.678

Song, C., Wang, Q., Zhang, R. L., Sun, B. J., and Wang, X. H. (2016). Exploring the utility of DNA barcoding in species delimitation of *Ploypedilum* (Tripodura) non-biting midges (Diptera: Chironomidae). *Zootaxa* **4079**, 534–550. doi:10.11646/zootaxa.4079.5.2

Sparks, K. S., Andersen, A. N., and Austin, A. D. (2014*a*). Systematics of the *Monomorium rothsteini* Forel species complex (Hymenoptera: Formicidae), a problematic ant group in Australia. *Zootaxa* **3893**, 489–529. doi:10.11646/zootaxa.3893.4.2

Sparks, K. S., Andersen, A. N., Donnellan, S. C., and Austin, A. D. (2014*b*). Navigating the mtDNA road map out of the morphological maze: interpreting morphological variation in the diverse *Monomorium rothsteini* (Forel) complex (Hymenoptera: Formicidae). *Systematic Entomology* **39**, 264–278. doi:10.1111/syen.12051

Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**, 1312–1313. doi:10.1093/bioinformatics/btu033

Tay, J. W., Neoh, K. B., and Lee, C. Y. (2014). The roles of the queen, brood and worker castes in the colony growth dynamics of the pharaoh ant *Monomorium pharaonis* (Hymenoptera: Formicidae). *Myrmecological News* **20**, 87–94.

Ward, P. S., and Downie, D. A. (2005). The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): phylogeny and evolution of big-eyed arboreal ants. *Systematic Entomology* **30**, 310–335. doi:10.1111/j.1365-3113.2004.00281.x

Ward, P. S., Brady, S. G., Fisher, B. L., and Schultz, T. R. (2015). The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology* **40**, 61–81. doi:10.1111/syen.12090

Wheeler, W. M. (1917). The phylogenetic development of subapterous and apterous castes in the Formicidae. *Proceedings of the National Academy of Sciences of the United States of America* **3**, 109–117. doi:10.1073/pnas.3.2.109

Wheeler, W. M. (1934). Contributions to the fauna of Rottnest Island, Western Australia. No. IX. The ants. *Journal of the Royal Society of Western Australia* **20**, 137–163.

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