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 1a 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 (e.g. 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, Myrmicinae, 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. 2014a), 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. 2014a, 2014b) 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 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. dentriculatum (Mayr, 1887) + Oxypeoccus Santschi, 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 cryptobiotic (blind, soil dwelling) species that were initially identified as Monomorium, but which are also superficially similar 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. rothsetti Forel, 1902 (Sparks et al. 2014a, 2014b).

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. 2014a). 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 (donithorpeii form), M. fieldi (nigrus 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 Errormyrmex latiodis (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 (Streomyrmyx Emery, 1901, Trichomyrmex
**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'-TAAACCTTCAAGG TGACCAAAAAATCA-3' (Folmer et al. 1994) and Jerry 5'- CACATTTATTTGGTTTTTGG-3' (Simon et al. 1994)/ Ben 5'-GCTACTACATAATGTATCATG-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'-TGCACNGTGAACRACYTGCTGGATGCG-3' (Ward and Downie 2005) and Wg1032R 5'-ACYTGCNGC AGCACCTARTGAA-3' (Abouheif and Wray 2002) and for elongation factor 1α (EF1αF2) using the primers F2–557F 5'-GAACGTGAACCTGTATCAYTACSAT-3' and F2–1118R 5'-TAACTCTGAAGGGGAAGACCRAG-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 MgCl2, 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). 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 Solenopsisini (sensu Ward et al. 2015) (Figs 1–4, S1–2). Two separate *Monomorium* clades were recovered with strong

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Table 1. Summary of models used for the Bayesian analysis of the six separate datasets

<table>
<thead>
<tr>
<th>Analysis</th>
<th>No. samples</th>
<th>COI pos. 1</th>
<th>COI pos. 2</th>
<th>COI pos. 3</th>
<th>EF1αF2</th>
<th>wg</th>
</tr>
</thead>
<tbody>
<tr>
<td>COI+EF1αF2+ wg (all taxa)</td>
<td>50</td>
<td>SYM+I=G</td>
<td>GTR+I=G</td>
<td>HKY+I=G</td>
<td>K80+G</td>
<td>K80+I</td>
</tr>
<tr>
<td>COI+EF1αF2+ wg (reduced taxa)</td>
<td>21</td>
<td>GTR+I=G</td>
<td>HKY+I=G</td>
<td>HKY+I=G</td>
<td>K80+I</td>
<td>K80+G</td>
</tr>
<tr>
<td>EF1αF2+ wg</td>
<td>26</td>
<td>GTR+I=G</td>
<td>GTR+I=G</td>
<td>HKY+I=G</td>
<td>K80+I</td>
<td>K80+G</td>
</tr>
<tr>
<td>COI-only</td>
<td>85</td>
<td>GTR+I=G</td>
<td>GTR+I=G</td>
<td>GTR+I=G</td>
<td>K80+I</td>
<td>K80+G</td>
</tr>
<tr>
<td>COI+wg</td>
<td>38</td>
<td>GTR+I=G</td>
<td>GTR+I=G</td>
<td>HKY+I=G</td>
<td>K80+I</td>
<td>K80+G</td>
</tr>
<tr>
<td>COI+EF1αF2</td>
<td>26</td>
<td>SYM+G</td>
<td>SYM+G</td>
<td>HKY+I=G</td>
<td>K80+I</td>
<td>K80+G</td>
</tr>
</tbody>
</table>
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 Monomorium rothsteini Forel, 1902 complex and Monomorium sordidum Forel, 1902, both of which have 12-segmented antennae. It also included the three non-Australian species, Monomorium floricola, Monomorium pharaonis and Monomorium 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 Monomorium antarcticum and Monomorium 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.
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* (McAreeay, 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 ‘carnatum’ form of *M. sydneyense* from northern Australia was monophyletic,
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 leave* 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. leave* 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
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.


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


*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. rothsteinii*, 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 stinging 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. capitio* 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* McAveaney, 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. longinode Heterick, 2001 stat. nov.
C. longipes Emery, 1914 stat. rev. (NC)
C. macarthurii Heterick, 2001 stat. nov.
C. majori Heterick, 2001 stat. nov.
C. mellem Emery, 1914 stat. rev. (NC)
C. nightcapense Heterick, 2001 stat. nov.
C. nigricarpes 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. sculpturarum Clark, 1934 stat. rev.
C. shattuckii Heterick, 2001 stat. nov.
C. smithii Forel, 1892 stat. rev. (NZ)
C. striatifrons Heterick, 2001 stat. nov.
C. sublamellatum Heterick, 2003 stat. nov.
C. tricolor Emery, 1914 stat. rev. (NC)
C. xantheleema 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)

Diffs from Chelaner by: very small to medium ants, 1.0–7.5 mm. Clypeus medially raised and bicarinate, carinæe diverging or subparallel, raised and angular or rounded, palpal formula 1,2 or 2,2; number of mandibular teeth 3–4. Antennæe 11-segmented except for the M. rothsteini and M. sordidum radiations with 12-segmented antennæe, 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. Postero-dorsal 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. emeroides Sparks, 2014a
M. emepophilum 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. tenebrorum 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 antennæe plus the M. rothsteini/M. sordidum radiations with 12-segmented antennæe. Chelaner now encompasses those species with 12-segmented antennæe 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. 2014b) 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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