

# The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae)

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**Abstract.** This study investigates the evolutionary history of a hyperdiverse clade, the ant subfamily Myrmicinae (Hymenoptera: Formicidae), based on analyses of a data matrix comprising 251 species and 11 nuclear gene fragments. Under both maximum likelihood and Bayesian methods of inference, we recover a robust phylogeny that reveals six major clades of Myrmicinae, here treated as newly defined tribes and occurring as a pectinate series: Myrmicini, Pogonomyrmecini **trib.n.**, Stenammini, Solenopsidini, Attini and Crematogastrini. Because we condense the former 25 myrmicine tribes into a new six-tribe scheme, membership in some tribes is now notably different, especially regarding Attini. We demonstrate that the monotypic genus *Ankylomyrma* is neither in the Myrmicinae nor even a member of the more inclusive formicoid clade – rather it is a poneroid ant, sister to the genus *Tatuidris* (Agroecomyrmecinae). Several species-rich myrmicine genera are shown to be nonmonophyletic, including *Pogonomyrma*, *Aphaenogaster*, *Messor*, *Monomorium*, *Pheidole*, *Temnothorax* and *Tetramorium*. We propose a number of generic synonymies to partially alleviate these problems (senior synonym listed first): *Pheidole* = *Anisopheidole* **syn.n.** = *Machomyrma* **syn.n.**; *Temnothorax* = *Chalepoxenus* **syn.n.** = *Myrmoxenus* **syn.n.** = *Protomognathus* **syn.n.**; *Tetramorium* = *Rhoptryomyrma* **syn.n.** = *Anergates* **syn.n.** = *Teleutomyrma* **syn.n.** The genus *Veromessor* **stat.r.** is resurrected for the New World species previously placed in *Messor*; *Sylophopsis* **stat.r.** is resurrected from synonymy under *Monomorium* to contain the species in the *hildebrandti* group; *Trichomyrma* **stat.r.** is resurrected from synonymy under *Monomorium* to contain the species in the *scabriceps*- and *destructor*-groups; and the monotypic genus *Epelysidris* **stat.r.** is reinstated for *Monomorium brocha*. Bayesian divergence dating indicates that the crown group Myrmicinae originated about 98.6 Ma (95% highest probability density 87.9–109.6 Ma) but the six major clades are considerably younger, with age estimates ranging from 52.3 to 71.1 Ma. Although these and other suprageneric taxa arose mostly in the middle Eocene or earlier, a number of prominent, species-rich genera, such as *Pheidole*, *Cephalotes*, *Strumigenys*, *Crematogaster* and *Tetramorium*, have estimated crown group origins in the late Eocene or Oligocene. Most myrmicine species diversity resides in the two sister clades, Attini and Crematogastrini, which are estimated to have originated and diversified extensively in the Neotropics and Paleotropics, respectively. The newly circumscribed Myrmicini is Holarctic in distribution, and ancestral range estimation suggests a Nearctic origin. The Pogonomyrmecini and Solenopsidini are reconstructed as being Neotropical in origin,

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but they have subsequently colonized the Nearctic region (Pogonomyrmecini) and many parts of the Old World as well as the Nearctic region (Solenopsidini), respectively. The Stenammini have flourished primarily in the northern hemisphere, and are most likely of Nearctic origin, but selected lineages have dispersed to the northern Neotropics and the Paleotropics. Thus the evolutionary history of the Myrmicinae has played out on a global stage over the last 100 Ma, with no single region being the principal generator of species diversity.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:BB6829C4-DA79-45FE-979E-9749E237590E>.

## Introduction

Ants are one of evolution's great success stories, the most species-rich and ecologically dominant of all eusocial insects (Hölldobler & Wilson, 1990; Lach *et al.*, 2009), yet this success is far from evenly distributed among the major lineages of the group. There are 16 extant subfamilies of ants (Bolton, 2014; Brady *et al.*, 2014), but four of these – Dolichoderinae, Formicinae, Myrmicinae and Ponerinae – account for almost 90% of all known species (Bolton, 2014). Among these 'big four' the most biologically diverse and prolific is the subfamily Myrmicinae. With approximately 6475 described species – about half of all named ants – and many others awaiting discovery and description, the myrmicines are a hyperdiverse clade inhabiting most of the terrestrial surface of the Earth and encompassing a wide range of lifestyles including generalist and specialist predators, scavengers, omnivores, granivores and herbivores (Kugler, 1979; Brown, 2000).

Myrmicine ants have been subjects of intense investigation into colony organization, communication, demography and ecology (Davidson, 1977; Brian, 1983; Tschinkel, 2006). They contain a diverse array of socially parasitic species (Beibl *et al.*, 2005; Buschinger, 2009) and they furnish numerous examples of symbioses with other organisms (Davidson & McKey, 1993; Fiedler, 2006; Russell *et al.*, 2009), including the iconic mutualism between fungus-growing ants and their cultivars (Mueller *et al.*, 2001; Hölldobler & Wilson, 2011). Genomic studies have begun to probe the genetic architecture of prominent myrmicines in the genera *Solenopsis* (Wurm *et al.*, 2011), *Pogonomyrmex* (Smith *et al.*, 2011), *Acromyrmex* (Nygaard *et al.*, 2012) and *Atta* (Suen *et al.*, 2011).

Despite the attention that they have garnered, myrmicines present a number of taxonomic challenges. There are many difficult species complexes (Seifert, 2003; Schlick-Steiner *et al.*, 2006; Blaimer, 2012a), as well as multiple genera and tribes whose monophyly is doubtful (Brady *et al.*, 2006; Ward, 2011). The members of this subfamily have received only modest coverage in molecular phylogenetic studies of ants as a whole, and results have been inconsistent between studies (Brady *et al.*, 2006; Moreau *et al.*, 2006). Here we aim to address this problem by employing 11 nuclear genes and comprehensive taxon sampling across the entire subfamily. We combine phylogenetic inference with divergence dating and biogeographic analysis to

generate a robust picture of the evolutionary history of these remarkable ants. These results also provide the basis for a revised higher classification of the subfamily.

## Material and methods

### Taxon selection

We assembled a set of 234 species representing all 25 tribes of Myrmicinae and 128 of the 145 extant genera (taxonomy follows Bolton, 2014) (Table S1). One species could not be identified to genus. For genera with widespread distributions we attempted to sequence a species from each of the major biogeographic regions in which the genus occurs, to facilitate ancestral range estimation. We also sampled more intensively within several genera whose monophyly appeared to be questionable, including *Aphaenogaster*, *Monomorium*, *Pheidole*, *Solenopsis*, *Strumigenys* and *Tetramorium*. We included 17 outgroup taxa; these were drawn mostly from the other subfamilies of ants, but we also chose an aculeate hymenopteran wasp, *Apterogyna* (Braconidae), as the most distant outgroup to root the tree.

### Sequencing and sequence annotation

We sequenced fragments of 11 nuclear genes, including two ribosomal genes, 18S rDNA and 28S rDNA, and nine protein-coding genes: abdominal-A (*Abd-A*), elongation factor 1-alpha F1 copy (*EF1aF1*), elongation factor 1-alpha F2 copy (*EF1aF2*), long wavelength rhodopsin (*LWRh*), arginine kinase (*ArgK*), topoisomerase 1 (*Top1*), ultrabithorax (*Ubx*), wingless (*Wg*) and rudimentary (*CAD*). Protocols for extraction, amplification and sequencing follow Ward & Downie (2005), Brady *et al.* (2006), Ward *et al.* (2010), and Ward & Sumnicht (2012).

Sequences were collated in Sequencher v4.10.1 (Gene Codes Corporation, Ann Arbor, MI, U.S.A.), aligned with Clustal X v1.81 (Thompson *et al.*, 1997), and manually edited and concatenated with MacClade v4.08 (Maddison & Maddison, 2005). Alignment was straightforward for exons of protein-coding genes and for most 18S rDNA sequence. We excluded ambiguously aligned regions of 18S and 28S, introns of the protein-coding genes, and autapomorphic indels in exons

**Table 1.** Sequence characteristics of the 251-taxon data matrix (233 ingroup taxa).

Gene	No. of sites	VS	PS	VS, ingroup	PS, ingroup
<i>Abd-A</i>	600	262	221	246	206
<i>EF1aF2</i>	517	206	193	204	190
<i>LW Rh</i>	458	279	250	269	239
<i>ArgK</i>	673	332	297	309	285
<i>Top1</i>	880	477	424	464	419
<i>Ubx</i>	627	301	254	286	232
<i>Wg</i>	409	251	218	224	197
<i>EF1aF1</i>	359	141	129	138	128
<i>18S</i>	1850	224	106	184	85
<i>28S</i>	1653	480	271	425	223
<i>CAD</i>	961	605	532	592	519
All genes	8987	3558	2895	3341	2723

VS = variable sites; PS = parsimony-informative sites.

of *Abd-A*, *ArgK*, *CAD* and *Wg*. The resulting matrix that was used for all subsequent analyses contains 8987 bp (3558 variable sites, 2895 parsimony-informative sites). This matrix (251 taxa by 11 genes) contains no missing gene fragments. Of the 2761 fragments, 499 were previously published (Ward & Downie, 2005; Brady *et al.*, 2006; Ward, 2007a; Branstetter, 2009; Lucky & Sarnat, 2010; Ward *et al.*, 2010; Brady *et al.*, 2014); the remaining 2262 sequences were generated for this study (GenBank accession numbers KJ859686-KJ861947). Sequence characteristics of each gene are summarized in Table 1. The aligned data matrix has been deposited in TreeBase (study accession 15764).

### Phylogenetic analyses

#### Data partitions

We employed an iterative strategy to arrive at the partitioning scheme for analysing the 11-gene, concatenated dataset. In a first round of analyses we partitioned the data into 25 partitions based on the variability of codon-position sites within each gene. Four genes (*Abd-A*, *EF1aF1*, *EF1aF2*, *Ubx*) were each divided into two partitions consisting of (i) codon positions 1 and 2 and (ii) codon position 3, resulting in eight partitions; five genes (*LW Rh*, *ArgK*, *Top1*, *Wg*, *CAD*) were assigned site-specific models in which each codon position formed a separate partition, resulting in 15 partitions; and two nonprotein-coding genes (*18S*, *28S*) were each assigned a single partition, resulting in two partitions. The choice of nucleotide substitution model for each partition (Table S2) was determined using the Akaike Information Criterion (AIC) (Posada & Buckley, 2004) as implemented in JModelTest v2.0.2 (Posada, 2008). The tree resulting from a Bayesian analysis (MrBayes v3.2.1; Ronquist *et al.*, 2012) of these data employing these partitions and models was then submitted to PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) along with 29 predefined blocks, encompassing the first, second and third codon positions for each of the nine protein-coding genes and the two nonprotein-coding genes (*18S*, *28S*). Under the Bayesian Information Criterion (BIC), the 'greedy' algorithm, and 'models = all,' PartitionFinder identified 21 partitions

**Table 2.** The 21 partitions and models identified by PartitionFinder and used in the maximum likelihood and Bayesian analyses of the concatenated, unmodified 8987-bp dataset.

Partition	Blocks	Model
p1	Abd-A pos1, Ubx pos1	SYM+I+G
p2	Abd-A pos2, Ubx pos2	TVM+I+G
p3	Abd-A pos3	TIM+I+G
p4	EF1aF2 pos3, Top1 pos3	TrNef+I+G
p5	EF1aF2 pos1	GTR+I+G
p6	ArgK pos2, EF1aF2 pos2	TIMef+I+G
p7	LW Rh pos3, Ubx pos3	TrNef+I+G
p8	LW Rh pos1	TVM+I+G
p9	LW Rh pos2	GTR+I+G
p10	ArgK pos3	TrNef+I+G
p11	ArgK pos1	SYM+I+G
p12	Top1 pos1	SYM+I+G
p13	CAD pos2, Top1 pos2	GTR+I+G
p14	Wg pos3	GTR+I+G
p15	Wg pos1, Wg pos2	TrNef+I+G
p16	EF1aF1 pos2	JC
p17	EF1aF1 pos3	TIM+G
p18	18S, EF1aF1 pos1	TrNef+I+G
p19	28S	GTR+I+G
p20	CAD pos3	GTR+I+G
p21	CAD pos1	K80+I+G

(Table 2), which were then employed in intensive Bayesian and maximum-likelihood analyses. In cases where the model specified by PartitionFinder was not implemented in MrBayes, the next-most-complex available model was employed.

The choice of partitions for separate, single-gene Bayesian analyses of each of the nuclear genes followed an iterative scheme similar to that described above for the full concatenated dataset. An initial Bayesian analysis was conducted employing partitions based on variability of codon sites. The resulting tree was submitted to PartitionFinder using 'models = mrbayes,' 'model-Selection = BIC,' and 'search = all.' If PartitionFinder identified a partitioning scheme different from the one employed in the first analysis, a second Bayesian analysis was conducted employing the PartitionFinder scheme (Table S3).

#### Treatments addressing base frequency heterogeneity

For each of the three codon positions within each protein-coding gene, as well as for *18S* and *28S*, each treated as single partitions, we evaluated the homogeneity of base frequencies across taxa using PAUP\* 4.0a128 (Swofford, 2002), which indicated that nine partitions – the third positions of each protein-coding gene – contained significantly heterogeneous base frequencies (Table S4). In order to examine the effects of base frequency heterogeneity on phylogenetic results, we subjected each dataset to a number of treatments, including: (i) 'partial RY coding,' in which, for each gene, the subset of taxa (differing for each gene) with heterogeneous third positions deviating significantly from the observed averages were coded as RY and in which the remainder of third positions were coded normally (ACTG); (ii) 'complete RY coding' in which all third positions were coded as RY; (iii) exclusion of a minimum subset

of 324 characters (not necessarily third positions) deviating significantly from observed base-frequency averages based on the results of a likelihood-based method for filtering potential nonstationary sites, to be described elsewhere (D. Swofford, personal communication); and (iv) exclusion of 843 characters (not necessarily third positions), the 10% deviating the most from observed base-frequency averages, also based on the same filtering method. All analyses were carried out in MrBayes v3.2.1 and v3.2.2 (Ronquist *et al.*, 2012). For treatment i, 'partial RY,' decisions about whether to code a particular third-position site as ACTG or RY were made based on analyses of output from PAUP\* 4.0a128 (Swofford, 2002) (Table S4). Characters were recoded as RY in Mesquite v2.73 (Maddison & Maddison, 2010). Partitioning schemes for each of these treatments resulted from the same iterative strategy described in the *Data partitions* section above.

#### Treatments addressing possible 'wildcard' taxa

In order to explore the reasons for poor support in one region of the tree (Crematogastrini), particularly with respect to a number of unusually long-branched taxa in that region, we conducted analyses in which subsets of 11 taxa suspected of behaving as 'wildcards' were excluded (Nixon & Wheeler, 1992; Kearney, 2002). Unlike the most common type of wildcard taxa, however, none of the taxa in our analyses contained missing data. For this purpose we created and analysed two datasets consisting of: (i) 248 taxa, excluding *Acanthomyrmex ferox*, *Mayriella ebbei* and *Xenomyrmex floridanus*; and (ii) 243 taxa, excluding *Cardiocondyla mauritanica*, *Cardiocondyla MY01*, *Cardiocondyla thoracica*, *Liomyrmex gestroi*, *Melissotarsus insularis*, *Metapone madagascariensis*, *Metapone PG01* and *Ocymyrmex cf. fortior*.

#### Single-gene analyses

In order to assess the possibility of conflicting gene trees and to compare gene-specific support for clades, we conducted iterative analyses of each of the 11 genes as described above, using partitions and models identified by PartitionFinder v1.0.1 (Lanfear *et al.*, 2012), summarized in Table S3. All single-gene analyses were conducted under Bayesian criteria as described below and consisted of 10 million generations with a burn-in of 1 million generations.

#### Constraint analyses

One surprising result of several prior studies (Brady *et al.*, 2006; Moreau *et al.*, 2006; Rabeling *et al.*, 2008), that the species *Tatuidris tatusia* is a poneroid and as such only very distantly related to the Myrmicinae, has failed to significantly influence the posterior probabilities of some myrmecologists (e.g. Baroni Urbani & De Andrade, 2007; Keller, 2011). For this reason, we conducted a constraint analysis to explicitly quantify the difference in likelihoods between the unconstrained outcome, in which (*Tatuidris tatusia* + *Ankylomyrma coronacantha*) are poneroids, and the outcome in which they are constrained to be members of the Myrmicinae. The latter analysis was carried out in GARLI v2.0 as described below, using 100 search repetitions

and a minimally defined topological constraint. We included *Ankylomyrma* in this constraint because of a novel result (see below) placing it close to *Tatuidris*.

#### Bayesian analyses

We conducted Bayesian analyses using MrBayes v3.2.1 and 3.2.2 (Ronquist *et al.*, 2012) with `nucmodel = 4by4`, `nruns = 2`, `nchains = 8`, `samplefreq = 1000`, and either 20 million or 40 million generations and burn-ins of 2 and 4 million generations, respectively; single-gene analyses consisted of 10 million generations and burn-ins of 1 million generations. For partitioned analyses all parameters, including branch-length rate multipliers, were unlinked across partitions; the only exceptions were branch lengths and topology, which were linked. All analyses were carried out using parallel processing (one chain per CPU) on the Smithsonian NMNH LAB Topaz computing cluster (Apple computers with Intel processors). To address known problems with branch-length estimation in MrBayes (Marshall *et al.*, 2006; Brown *et al.*, 2010; Marshall, 2010; Ward *et al.*, 2010), we set `brlenspr = unconstrained:Exp(100)`. Burn-in, convergence and stationarity were assessed using Tracer v1.5 (Rambaut & Drummond, 2009), by examining PSRF values and .stat output files in MrBayes, and by using Bayes factor comparisons of harmonic-mean marginal likelihoods of pairs of runs with standard error estimated using 1000 bootstrap pseudoreplicates in Tracer 1.5 (Rambaut & Drummond, 2009), which employs the weighted likelihood bootstrap estimator of Newton & Raftery (1994) as modified by Suchard *et al.* (2001). For the full concatenated dataset, stationarity was regularly obtained within the first few million generations, even for the various base-frequency-heterogeneity treatments; single-gene analyses achieved stationarity within the first few hundred thousand generations. The results reported here are based on the combined post-burn-in data from both runs.

#### Maximum likelihood

ML analyses were carried out in GARLI v2.0 (Zwickl, 2006) using parallel processing on the Smithsonian Hydra supercomputer (Linux-based with AMD processors). Unconstrained and constrained ML best-tree analyses consisted of 200 and 100 replicate searches, respectively, and deviated from the default settings as follows: `topoweight = 0.01`; `brlenweight = 0.002`. ML bootstrap analyses consisted of 1000 pseudoreplicates and deviated from default settings as follows: `genthreshfortopoterm = 5000`; `scorethreshforterm = 0.10`; `startoptprec = 0.5`; `minoptprec = 0.01`; `numberofpre reductions = 1`; `treerejectionthreshold = 20.0`; `topoweight = 0.01`; `brlenweight = 0.002`. In all analyses the value for `modweight` was calculated as  $0.0005 \times (\#subsets + 1)$  (D. Zwickl, personal communication).

#### Divergence dating

We inferred divergence dates with BEAST v1.7.5 (Drummond *et al.*, 2012) under a parallel configuration using BEAGLE v1.0 on the aforementioned NMNH LAB Topaz cluster.

We employed an uncorrelated lognormal relaxed clock model (Drummond *et al.*, 2006). Data partitioning and nucleotide substitution models were determined using PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) in the same manner as for the MrBayes analyses described above, except that only models available in BEAST were evaluated. Substitution models were unlinked and clock and tree models were linked among partitions. The tree prior was a Yule process with a ML ultrametric starting tree. We provided *a priori* age distributions for 27 nodes from the fossil record (20 in Myrmicinae, 7 in the outgroups), based on stem-group membership (Table 3). We conducted BEAST runs each for 100 million generations with a burn-in of 25 million generations, saving trees and other parameter values every 10 000 generations. Stationarity and burn-in were determined by observing high ESS values and the consistency of likelihood values and other results among independent runs. We combined results from four independent runs, obtaining a total of 300 million post burn-in generations, and visualized the resulting topology and divergence times using FigTree v1.4.0.

#### Biogeographic inference

For the purpose of inferring the distributional history of Myrmicinae we adopted a coarse classification of six classic biogeographic areas: the Neotropical, Nearctic, Palearctic, Afrotropical, Indomalayan and Australasian regions (Cox, 2001), with Wallace's line (Wallace, 1876) as the boundary between the last two. To estimate ancestral areas we used the likelihood-based program LAGRANGE v20130526 (Ree *et al.*, 2005; Ree & Smith, 2008). This program implements a dispersal-extinction-cladogenesis (DEC) model and evaluates the likelihood of different range inheritance scenarios at the internal nodes of an ultrametric tree. The input for this analysis was (i) the post-burn-in consensus tree produced by BEAST (above), with branch lengths in units of time and outgroups removed, and (ii) a matrix of distribution ranges for all terminal taxa (Table S5). Maximum ancestral range size was set at three areas, because the overwhelming majority of contemporary species occupies only one biogeographic area, and none is found in more than three areas (Table S5). We also incorporated temporal and spatial constraints, such that dispersal was confined to adjacent areas and, in accordance with changing paleogeography (Scotese, 2010), different rates were used for the time periods 0–50 and 50–100 Ma (Table 4).

#### Taxonomic changes

We propose a number of changes to the higher-level taxonomy of the Myrmicinae that are impelled by the phylogenetic findings. The ultimate goal is a phylogenetic classification in which all higher taxa of a given rank (in this case, genus or tribe) are monophyletic and hence mutually exclusive (Ward, 2011). This goal cannot yet be fully realized, but the classification proposed here goes some distance towards this ideal

by substantially reducing the number of nonmonophyletic genera, and by ensuring that all tribes are monophyletic. In synonymizing or resurrecting genera we list all new or revived combinations for the affected species, and provide new names (if necessary) where secondary homonymy is created.

#### Phylogenetic results

The broad features of phylogenetic relationships within the Myrmicinae are stable and strongly supported across multiple methods of phylogenetic inference. Alternate Bayesian analyses, including RY coding for third positions, exclusion of some base frequency heterogeneous positions, and exclusion of 'wildcard' taxa, had little or no effect on overall tree topology or on support for the major clades (Fig. 1, Figure S1; Tables 5, S6). Single-gene trees were less well resolved, especially those with relatively few phylogenetically informative sites, but they did not yield strongly supported clades that conflicted with the results from concatenated analyses (Figure S2). In the discussion below the support values that are cited for any given node are (i) the Bayesian posterior probability (PP) based on the concatenated, partitioned MrBayes analysis, and (ii) the ML bootstrap percentage (BS) based on the concatenated, partitioned GARLI analysis with 1000 bootstrap pseudoreplicates.

We find that the ectaheteromorph clade, represented in our dataset by *Acanthoponera* and *Rhytidoponera*, is the sister group of Myrmicinae, to the exclusion of the Formicinae. This relationship has weak to moderate support (PP 0.91 BS 64) and mirrors the findings of a recent five-gene study of Formicidae as a whole (Moreau & Bell, 2013). The subfamily Myrmicinae is consistently recovered as monophyletic, with one caveat: the enigmatic ant genus *Ankylomyrma* (Bolton, 1973), hitherto placed in its own tribe within the Myrmicinae, is not a member of this subfamily, nor even of the more inclusive formicoid clade (Ward, 2007b). Rather, *Ankylomyrma* is sister to the genus *Tatuidris* (Agroecomyrmecinae), a poneroid ant that was also previously placed erroneously in the Myrmicinae (Bolton, 2003). The *Ankylomyrma*/*Tatuidris* clade has very strong support (PP 1.00 BS 100) and the results of the constraint analysis reveal that the most likely tree in which *Tatuidris* and *Ankylomyrma* are constrained to be members of the Myrmicinae has a likelihood that is lower than that of the unconstrained topology by a difference of 358.66 natural-log likelihood units, translating to a highly significant Bayes Factor of 717.32 (Nylander *et al.*, 2004). This is another striking case where worker ant morphology led to a mistaken inference about true affinities (Brady *et al.*, 2006; Moreau *et al.*, 2006; Ward, 2011; Brady *et al.*, 2014).

With *Ankylomyrma* excluded, the myrmicines are a robust monophyletic group (PP 1.00 BS 98) consisting of six major clades that emerge with strong support across all modes of analysis (Table 5), and in a consistent relationship to one another. These six clades form a pectinate series, here discussed in sequence.

**Table 3.** List of *a priori* age distributions applied to 27 fossil calibration points for BEAST divergence dating analysis.

Taxon (stem-group)	Offset	Median	95% quartile	Notes
<i>Acanthognathus</i>	15	40	73	<i>Acanthognathus poinari</i> in Dominican amber (Baroni Urbani & De Andrade, 1994). Upper bound is approximate estimated age of 'core Myrmicinae' (Brady <i>et al.</i> , 2006).
<i>Aphaenogaster occidentalis</i> + <i>Goniomma</i>	42	52	73	Three described <i>Aphaenogaster</i> species from Baltic amber are similar in form, size and sculpture to the extant species <i>A. subterranea</i> (Wheeler, 1915). Calibration follows Branstetter (2012).
<i>Apterostigma</i>	15	45	73	Two species of <i>Apterostigma</i> in Dominican amber (Schultz, 2007). Median age from Schultz & Brady (2008).
<i>Carebara</i>	42	52	73	<i>Carebara antiqua</i> in Baltic amber (Mayr, 1868; Wheeler, 1915). Upper bound is approximate estimated age of 'core Myrmicinae' (Brady <i>et al.</i> , 2006).
<i>Cataulacus</i>	30	45	73	Two species of <i>Cataulacus</i> described from Sicilian amber (Emery, 1891).
<i>Cephalotes atratus</i>	15	40	73	Twelve described species of <i>Cephalotes</i> in Dominican amber, assignable to extant species groups within the genus (De Andrade & Baroni Urbani, 1999). <i>Cephalotes atratus</i> group is sister to all other <i>Cephalotes</i> (Price <i>et al.</i> , 2014).
<i>Crematogaster acuta</i>	15	28	35	<i>Crematogaster crinosa</i> -group in Dominican amber (Blaimer, 2012b). The calibrated node represents crown <i>Crematogaster</i> ( <i>Orthocrema</i> ). Median age from Blaimer (2012b).
<i>Myrmica</i>	42	60	85	<i>Myrmica</i> species from Baltic and Saxonian ambers (Dlussky & Rasnitsyn, 2009), not definitely assignable to modern species groups, although similar to the plesiotypic <i>ritae</i> -group (Radchenko <i>et al.</i> , 2007).
<i>Nesomyrmex</i> ( <i>wilda</i> + <i>echatinodis</i> )	15	40	73	Two described species of <i>Nesomyrmex</i> from Dominican amber, similar to <i>N. wilda</i> and <i>N. echatinodis</i> , respectively (De Andrade <i>et al.</i> , 1999), here used conservatively to calibrate the node representing the most recent common ancestor (MRCA) of the New World and Old World species.
<i>Octostruma</i>	15	40	73	Undescribed <i>Octostruma</i> in Dominican amber (Wilson, 1988).
<i>Pheidole</i>	34	45	73	<i>Pheidole</i> from Florissant Formation (Carpenter, 1930).
<i>Pogonomyrmex</i> ( <i>striatinodis</i> + <i>subdentatus</i> )	34	50	73	<i>Pogonomyrmex fossilis</i> (worker) from the Florissant Formation (Carpenter, 1930) is presumably part of a Nearctic subclade of <i>Pogonomyrmex</i> , here used conservatively to calibrate the MRCA of <i>Pogonomyrmex</i> (excluding the southern Neotropical <i>P. angustus</i> ) and <i>Hylomyrma</i> .
<i>Pristomyrmex</i>	42	52	73	<i>Pristomyrmex</i> in late Eocene Danish amber (Dlussky & Radchenko, 2011).
<i>Solenopsis</i> ( <i>fugax</i> + <i>xyloni</i> )	15	40	73	Undescribed <i>Solenopsis</i> in Dominican amber (Wilson, 1988) ascribed to ' <i>Solenopsis</i> ( <i>Diplorhoptrum</i> )' and ' <i>Solenopsis</i> ( <i>Solenopsis</i> )', i.e. thief ants and fire ants, respectively. Here employed conservatively to calibrate the node representing the MRCA of <i>Solenopsis papuana</i> and <i>S. xyloni</i> (the latter is a <i>Solenopsis</i> in the fire ant group).
<i>Stenamma</i>	42	52	73	<i>Stenamma berendti</i> (male) in Baltic amber, not assignable to species groups within the genus (Branstetter, 2012). Calibration follows Branstetter (2012).
<i>Strumigenys ambatrix</i>	15	40	73	Four described species of <i>Strumigenys</i> from Dominican amber (Baroni Urbani & De Andrade, 1994, 2007), with two of these ( <i>S. electrina</i> and <i>S. poinari</i> ) evidently nested well within the genus, related to Nearctic taxa formerly placed in <i>Pyramica</i> . These are used conservatively to calibrate the node representing crown <i>Strumigenys</i> .
<i>Temnothorax</i>	42	52	73	Six described species of <i>Temnothorax</i> in Baltic amber (Dlussky & Rasnitsyn, 2009).
<i>Temnothorax poeyi</i>	15	40	73	<i>Temnothorax</i> of the ' <i>Macromischa</i> ' type from Dominican amber (De Andrade, 1992).
<i>Tetramorium</i>	42	52	73	Three undescribed species of <i>Tetramorium</i> in Baltic amber (Dlussky & Rasnitsyn, 2009).
<i>Trachymyrmex</i>	15	20	73	<i>Trachymyrmex</i> in Dominican amber (Baroni Urbani, 1980). Median age from Schultz & Brady (2008).
Outgroups				
Amblyoponinae	42	70	90	<i>Stigmatomma groehni</i> in Baltic amber (Dlussky, 2009). The divergence between two subclades of Amblyoponinae (one containing <i>Amblyopone</i> , and the other <i>Stigmatomma</i> ) is evidently quite old, based on high levels of genetic divergence.
Dolichoderomorphs	100	105	120	<i>Burmomyrma</i> , a putative aneuretine in Burmese amber (Dlussky, 1996). Aneuretinae may be paraphyletic relative to Dolichoderinae, so this fossil calibrates stem dolichoderomorphs.
Formicinae	92	95	120	<i>Kyromyrmex</i> in New Jersey amber (Grimaldi & Agosti, 2000).
<i>Lasius</i>	42	60	90	<i>Lasius</i> in Baltic amber (Dlussky, 2011).
Myrmeciinae	45	60	90	<i>Archimyrmex</i> (Myrmeciinae) in middle Eocene deposits of the United States, Argentina and Germany (Dlussky, 2012).
Ponerinae	42	60	90	<i>Platythyrea</i> in Baltic amber (Wheeler, 1915).
<i>Tatuidris</i>	42	60	90	<i>Agroecomyrmex duisburgi</i> (Agroecomyrmecinae) in Baltic amber (Wheeler, 1915; Dlussky & Rasnitsyn, 2009).

**Table 4.** Adjacency matrix used in LAGRANGE analysis, for the Neotropical (T), Nearctic (N), Palearctic (P), Afrotropical (E), Indomalayan (O) and Australasian regions (A). Dispersal rates for adjacent areas are given for the time periods 0–50 Ma (above diagonal) and 50–100 Ma (below diagonal). Rates are estimated to be lower (0.5) for adjacent regions separated by large water gaps, i.e. Neotropical/Afrotropical, Neotropical/Australian and Afrotropical/Australian in the first time period, and Indomalayan/Australian in the second time period, based on broad-scale reconstructions of tectonic history over these time periods (Scotese, 2010).

	T	N	P	E	O	A
T	–	1.0	0.0	0.5	0.0	0.5
N	1.0	–	1.0	0.0	0.0	0.0
P	0.0	1.0	–	1.0	1.0	0.0
E	1.0	0.0	1.0	–	1.0	0.5
O	0.0	0.0	1.0	1.0	–	1.0
A	1.0	0.0	0.0	1.0	0.5	–

#### Clade 1: Myrmicini

The reciprocally monophyletic genera *Manica* and *Myrmica* together form a clade (PP 1.00 BS 100) that is sister to all other Myrmicinae (PP 0.97 BS 78), a result that is consistent with the generalized morphology of these ants (Dlussky & Radchenko, 2009). We refer to this clade as the tribe Myrmicini, restricting its membership to these two extant genera, and excluding the other five genera currently placed in the tribe. Two of these, *Pogonomyrmex* and *Hylomyrma*, form a separate clade (Clade 2), whereas the other three (*Eutetramorium*, *Huberia* and *Secostruma*) belong to a large clade of predominantly Old World ants (Clade 6; see below). These results, and the relationships among the four *Myrmica* species that we sampled, are in agreement with other recent molecular phylogenetic analyses of Myrmicini (Jansen & Savolainen, 2010; Jansen *et al.*, 2010), but our study is the first to establish its position as sister to all other members of the subfamily.

In addition to their generalized morphology, *Myrmica* workers retain reproductive (haploid egg-laying) potential and are generalist predators and scavengers (Seifert, 1988; Elmes, 1991; Wardlaw & Elmes, 1998). Similar habits are thought to characterize the genus *Manica*, although less is known about the biology of these ants (Wheeler & Wheeler, 1970).

#### Clade 2: Pogonomyrmecini

The two genera *Pogonomyrmex* and *Hylomyrma* collectively constitute a well-supported clade (PP 1.00 BS 100) that is sister to all remaining myrmicines except Myrmicini (PP 1.00 BS 98). We apply the name Pogonomyrmecini, **trib.n.** to this clade (see Taxonomy section below). *Hylomyrma* is nested within *Pogonomyrmex*, but monophyly of the latter can be restored by creation of a new genus for *Pogonomyrmex angustus* and its close relatives. These form the *Pogonomyrmex angustus* complex, a monophyletic group that is sister to all other pogonomyrmecines (C. Moreau and R.A. Johnson, personal communication).

Most *Pogonomyrmex* species are noted for their granivory and preference for xeric environments (Cole, 1968; Taber, 1998; Johnson, 2001), but these are evidently derived traits within the Pogonomyrmecini. Species in the *Pogonomyrmex angustus* complex and in the genus *Hylomyrma* are found mostly in mesic habitats and are not specialist seed-harvesters (Kempf, 1973; Brown, 2000; P.S. Ward, personal observation).

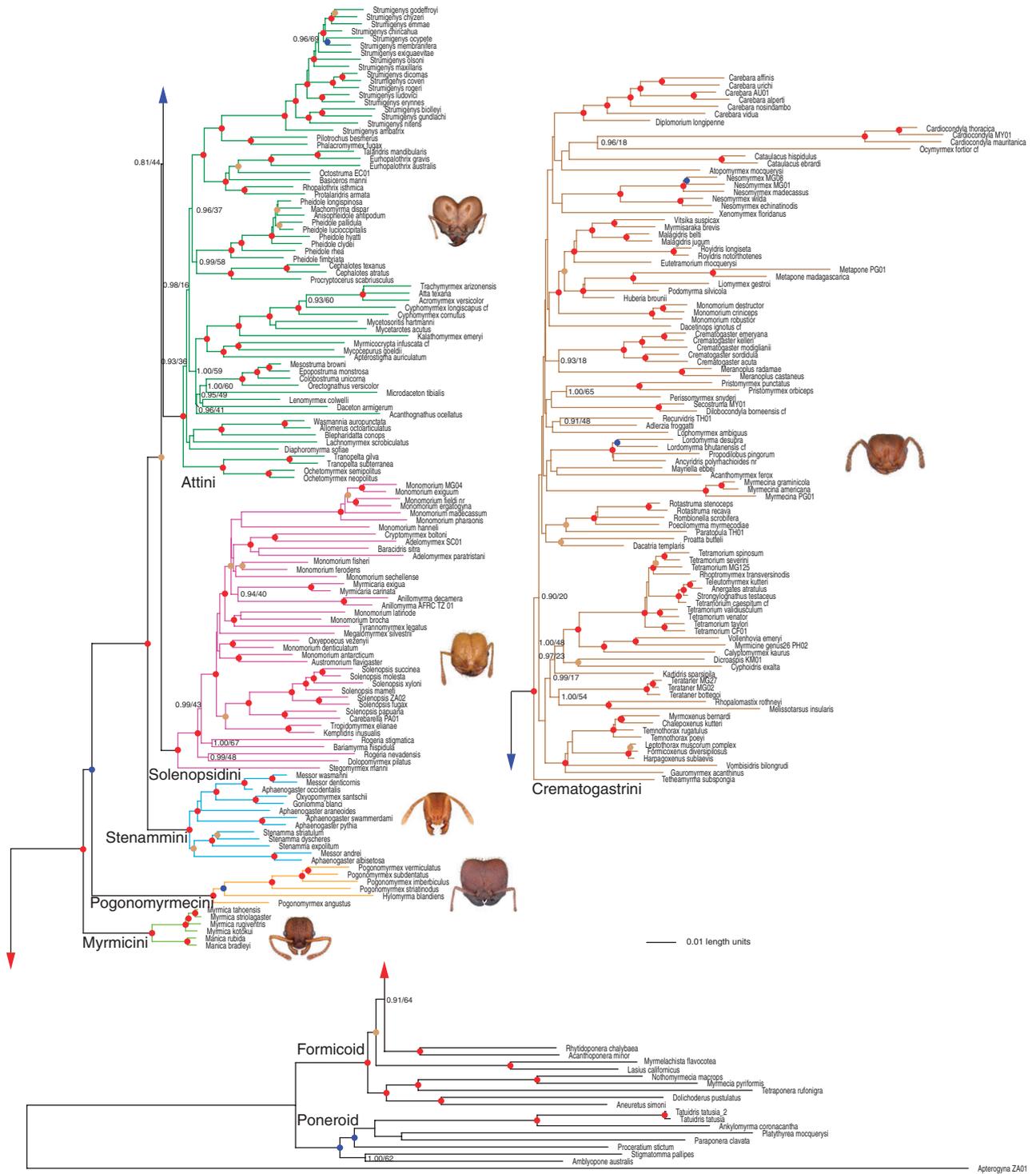
#### Clade 3: Stenammini

We recover, with strong support (PP 1.00 BS 100), a cluster of taxa comprising the genera *Stenamma*, *Messor*, *Aphaenogaster*, *Goniomma* and *Oxyopomyrmex*. This group, representing a modified circumscription of the tribe Stenammini (Branstetter, 2012), is sister to all myrmicines except Myrmicini and Pogonomyrmecini (PP 1.00 BS 76). Within Stenammini, *Messor* and *Aphaenogaster* are demonstrably nonmonophyletic: ants in the genus *Messor* consist of separate Old World and New World clades (see also Brady *et al.*, 2006), whereas those assigned to the genus *Aphaenogaster* represent at least four different lineages. The localized Mediterranean taxa, *Goniomma* and *Oxyopomyrmex*, are one another's closest relatives (see also Moreau *et al.*, 2006); and the species-rich genus *Stenamma* is recovered as sister to a New World clade composed of the erstwhile genera *Novomessor* (represented here by *Aphaenogaster albisetosa*) and *Veromessor* (represented by *Messor andrei*). We resurrect *Veromessor* from synonymy (see Taxonomy, below), but reclassification of the several *Aphaenogaster*-like lineages awaits a more comprehensive investigation of the phylogeny of the Stenammini, currently underway (M. Branstetter, personal communication).

#### Clade 4: Solenopsidini

This clade (PP 1.00 BS 99) is an amalgam of groups to which we assign the tribal name Solenopsidini, one of two oldest available names (the other is Myrmicariini). It includes the genera *Adelomyrmex*, *Anillomyrma*, *Austromorium*, *Baracidris*, *Bariamyrmex*, *Carebarella*, *Cryptomyrmex*, *Dolopomyrmex*, *Megalomyrmex*, *Monomorium*, *Myrmicaria*, *Oxyepoecus*, *Rogeria*, *Solenopsis*, *Stegomyrmex*, *Tropidomyrmex* and *Tyrannomyrmex*. The unsampled genus *Bondroitia* probably also belongs here (Bolton, 1987). The genus *Stegomyrmex* is sister to all other solenopsidines (PP 1.00 BS 100). According to our findings, *Rogeria*, *Adelomyrmex*, *Solenopsis* and *Monomorium* are not monophyletic. In the case of *Rogeria* and *Adelomyrmex* it appears that the Asian-Pacific species of these genera represent lineages separate from their Neotropical counterparts, but additional taxon sampling is required to confirm this. *Carebarella* is nested phylogenetically within *Solenopsis*; hence synonymization of the former under the latter (see Taxonomy, below) restores *Solenopsis* monophyly.

*Monomorium* presents a much more complicated situation – species assigned to this genus are scattered across the solenopsidine clade, and several are even positioned



**Fig. 1.** Maximum likelihood (ML) phylogeny of the ant subfamily Myrmicinae, including formicoid and poneroid outgroups, estimated with a partitioned ML analysis of a concatenated 11-gene dataset ( $-\ln L = 226\,779.1302$ ). Support values were generated in a separate partitioned ML bootstrap analysis with 1000 replicates, and a separate partitioned Bayesian analysis. Node support is indicated by the following colour scheme (PP, Bayesian posterior probability; BS, ML bootstrap percentage): red dots PP = 1.00, BS >90; brown dots PP = 1.00, BS = 70–90; blue dots PP = 0.95–0.99, BS  $\geq 70$ . For nodes of interest that do not fall into these three categories, we indicate actual support values as PP/BS.

**Table 5.** Support values under different modes of analysis, and crown age estimates from the BEAST analysis, for selected clades of Myrmicinae.

Clade <sup>a</sup>	BS	PP	PP (i)	PP (ii)	PP (iii)	PP (iv)	PP (BEAST)	Age (Ma)	95% HPD
Myrmicinae	98	1.00	1.00	1.00	1.00	1.00	1.00	98.6	87.9–109.6
Myrmicini	100	1.00	1.00	1.00	1.00	1.00	1.00	52.3	45.3–61.0
All myrmicines except Myrmicini	78	0.97	1.00	0.99	0.95	0.94	0.92	95.4	85.2–106.0
Pogonomyrmechini	100	1.00	1.00	1.00	1.00	1.00	1.00	54.3	43.7–66.1
Stenammini	100	1.00	1.00	1.00	1.00	1.00	1.00	52.9	48.1–58.6
Solenopsidini	99	1.00	1.00	1.00	1.00	1.00	1.00	71.1	62.4–79.7
Attini	100	1.00	1.00	1.00	1.00	1.00	1.00	67.0	59.2–75.4
Creinatogastrini	98	1.00	1.00	1.00	1.00	1.00	1.00	70.8	64.1–77.9
<i>Strumigenys</i> + <i>Phalacromyrmex</i> genus-group	100	1.00	1.00	1.00	1.00	1.00	1.00	48.4	40.4–56.5
<i>Strumigenys</i> + <i>Phalacro.</i> genus-group + <i>Basiceros</i> genus-group	98	1.00	1.00	1.00	1.00	1.00	1.00	55.9	48.3–63.6
<i>Daceton</i> genus-group	41	0.96	1.00	1.00	0.87	–	1.00	58.9	51.3–67.0
<i>Atta</i> genus-group	95	1.00	1.00	1.00	1.00	1.00	1.00	55.6	47.9–63.5
<i>Atta</i> genus-group + <i>Daceton</i> genus-group	59	1.00	0.69	0.63	0.86	–	1.00	59.9	52.3–67.8
<i>Pheidole</i> + <i>Cephalotes</i> genus-group	58	0.99	–	–	0.96	0.99	1.00	58.0	49.8–66.4
<i>Cardiocondyla</i> + <i>Ocymyrmex</i>	18	0.96	0.76	0.62	0.93	–	0.74	50.7	43.3–58.0
Core formicoxenines (including <i>Gauromyrmex</i> )	93	1.00	1.00	1.00	1.00	1.00	1.00	52.7	46.7–59.3
<i>Tetramorium</i> s.l.	100	1.00	1.00	1.00	1.00	1.00	1.00	20.1	15.4–24.8
<i>Eutetramorium</i> genus-group	92	1.00	–	–	1.00	1.00	1.00	46.4	37.8–55.5
' <i>Monomorium</i> ' <i>scabriceps</i> - and <i>destructor</i> -groups	100	1.00	1.00	1.00	1.00	1.00	1.00	16.2	9.3–23.8
<i>Lordomyrma</i> + <i>Ancyridris</i> + <i>Propodilobus</i>	100	1.00	1.00	1.00	1.00	1.00	1.00	28.9	18.9–39.8
<i>Paratopula</i> + <i>Poecilomyrma</i> + <i>Romblonella</i> + <i>Rotastruma</i>	70	1.00	1.00	1.00	1.00	1.00	1.00	50.8	39.2–62.0

<sup>a</sup>Tribal names are used in the new sense adopted in this paper. The *Phalacromyrmex*, *Basiceros*, *Daceton*, *Atta* and *Cephalotes* genus-groups refer to the erstwhile tribes Phalacromyrmecini, Basicerotini, Dacetini, Attini and Cephalotini, respectively.

BS = maximum likelihood bootstrap proportion from concatenated partitioned analysis of the full dataset; PP = Bayesian posterior probability from concatenated, partitioned Bayesian analysis of the full dataset; PP (i) to PP (iv) = Bayesian posterior probabilities from treatments (i) to (iv), respectively, addressing base frequency heterogeneity (see text); PP (BEAST) = Bayesian posterior probability from the BEAST analysis. PP values less than 0.50 are not recorded. Age is estimated crown-group age in millions of years; 95% HPD is 95% highest probability density.

outside it (see discussion of Clade 6 below). There are two pairs of austral clades, for example, comprising *Oxyepoecus* + '*Monomorium*' *denticulatum* (PP 1.00 BS 100) and *Austromorium* + '*Monomorium*' *antarcticum* (PP 1.00 BS 100). In the Palearctic '*Monomorium*' *brocha* and '*Monomorium*' *latinode* are sister to *Tyrannomyrmex* (PP 1.00 BS 94). There is, however, a core clade of *Monomorium* s.s., corresponding to the *monomorium*- and *salomonis*-groups of Bolton (1987), that is strongly supported as a monophyletic group (PP 1.00 BS 100). We also recover, with moderate support (PP 1.00 BS 72), a more inclusive clade that encompasses the *hanneli*-, *hildebrandti*-, *monomorium*- and *salomonis*-groups of *Monomorium* (Bolton, 1987; Heterick, 2006), but also includes the genera *Adelomyrmex*, *Anillomyrma*, *Baracidris*, *Cryptomyrmex* and *Myrmecaria*. We reinstate the genus *Syllophopsis* for the members of the *Monomorium hildebrandti*-group (see Taxonomy section below). Monophyly of the *hildebrandti*-group is only weakly supported in our analyses (PP 66, BS 43) but the group has distinctive morphological features (Heterick, 2006; B. Bolton, personal communication) that indicate monophyly.

Several genera currently placed in Solenopsidini do not belong in this clade: *Allomerus*, *Machomyrma* and *Tranopelta* are in Clade 5, whereas *Adlerzia*, *Carebara*, *Diplomorium* and *Mayriella* are in Clade 6 (Fig. 1). Based on the original description (Terayama, 2009) *Formosimyrmex*, which we did not sequence, is probably also a member of Clade 6.

#### Clade 5: Attini (new sense)

This well-supported clade (PP 1.00 BS 100) comprises a diverse selection of predominantly Neotropical taxa, for which the oldest available tribal name is Attini. This clade contains *Allomerus*, *Anisopheidole*, *Blepharidatta*, *Cephalotes*, *Diaphoromyrma*, *Lachnomyrmex*, *Lenomyrmex*, *Machomyrma*, *Ochetomyrmex*, *Pheidole*, *Procryptocerus*, *Tranopelta* and *Wasmannia*, as well as all the genera currently assigned to the tribes Attini (i.e. the fungus-growing ants), Basicerotini, Dacetini and Phalacromyrmecini. In the interests of establishing a stable, phylogenetic classification of the Myrmicinae, devoid of paraphyletic groups, we subsume these taxa under a single tribe, encompassing all members of Clade 5 (see Taxonomy section below). Although Attini is the oldest available name we recognize that within a large body of biological literature the noun 'Attini' and the adjective 'attine' refer exclusively to the fungus-growing ants. To avoid upsetting general usage by permanently expanding the definition of Attini, we are in the process of proposing to the International Commission on Zoological Nomenclature the substitution of the junior tribal synonym Pheidolini for Attini.

We uncover several intriguing relationships within this clade. The trap-jaw ants of the old tribe Dacetini are not monophyletic: species placed in *Strumigenys* form a separate clade that is sister to phalacromyrmecine ants, represented in our study by *Phalacromyrmex* and *Pilotrochus*. The phalacromyrmecines

and *Strumigenys* are in turn sister to basicerotine ants. This arrangement receives strong support (PP 1.00 BS 98–100) at the relevant nodes. Species of long-mandibulate *Strumigenys* with kinetic action are nested within groups of short-mandibulate species formerly assigned to the genus *Pyramica*. This justifies the synonymy of the latter under the former (Baroni Urbani & De Andrade, 2007), and supports the hypothesis (Bolton, 1999) that kinetic mandibles are a derived state in the genus.

The true dacetine ants (PP 96 BS 41) comprise all genera currently placed in this group except *Strumigenys*, but they also include the enigmatic genus *Lenomyrmex*, whose affinities were previously unclear (Fernández & Palacio, 1999). Dacetine ants are sister to the fungus-growing ants, hereafter referred to as the *Atta* genus-group (PP 1.00 BS 59 for the larger clade; PP 1.00 BS 95 for the *Atta* genus-group). Previous analyses (Schultz & Brady, 2008) also hinted at a relationship between the *Atta* genus-group and dacetine ants, but without significant support. Our results motivate a search for features in common between these two groups that might provide insight into the origins of specialized biology in both clades.

Elsewhere in the Attini (s.l.) we find that the large genus *Pheidole* is nonmonophyletic because two derivative genera, *Machomyrma* and *Anisopheidole*, are nested within it. Synonymy of these two under *Pheidole* (see Taxonomy section below) restores monophyly (PP 1.00 BS 100). The genus *Chimaeridris* (Wilson, 1989) is probably also nested within *Pheidole*, but we were unable to sequence this ant, so its status remains uncertain. The species of *Pheidole* that we sampled from the Old World, including *Pheidole pallidula*, form a clade (PP 1.00 BS 65) nested within a paraphyletic group of New World *Pheidole*, supporting the hypothesis of a New World origin of the genus and a single dispersal event to the Old World (cf. Moreau, 2008), although the recent report of *Pheidole* in Baltic amber (Dubovikoff, 2011) suggests the possibility of another earlier colonization, possibly by a stem *Pheidole*. The sister group of *Pheidole* appears to be the turtle ants, or *Cephalotes* genus-group (PP 0.99 BS 58 for the more inclusive clade, PP 1.00 BS 100 for the *Cephalotes* genus-group), a rather surprising finding in view of the morphological discrepancy between these two groups.

#### Clade 6: *Crematogastrini* (new sense)

The sixth clade (PP 1.00 BS 98) is also a highly diverse assemblage, centred primarily in the Old World tropics. We apply one of the two oldest tribal names, *Crematogastrini*, to this group (the other available name is *Formicoxenini*). It contains all the remaining myrmicine genera, including *Cardiocondyla*, *Carebara*, *Cataulacus*, *Crematogaster*, *Leptothorax*, *Lordomyrma*, *Meranoplus*, *Myrmecina*, *Nesomyrmex*, *Podomyrma*, *Temnothorax*, *Tetramorium*, *Vollenhovia* and about 50 other genera.

Relationships are not well resolved at the base of this clade, suggesting a period of rapid diversification early in its history. An additional challenge is posed by the long-branched taxa *Ocymyrmex* and *Cardiocondyla* (Fig. 1), whose positions are unstable across different analytical treatments. In the Bayesian

analysis of the full dataset these two are sister taxa (PP 0.96 BS 18). However, in treatment (iv), the Bayesian analysis addressing base frequency heterogeneity in which the 10% of characters deviating most strongly from observed average base frequencies were removed, the two genera are well separated: *Cardiocondyla* is in a weakly supported clade (PP 0.81) containing *Tetramorium* and several other genera, whereas *Ocymyrmex* appears in a moderately well supported clade (PP 0.94) with *Meranoplus* and *Nesomyrmex*. We focus in this discussion on other subgroups within Clade 6 that we recover more consistently and with more robust support.

One of these is a clade of core formicoxenines (PP 1.00 BS 93) comprising *Gauromyrmex*, *Vombisidris*, *Harpagoxenus*, *Formicoxenus*, *Leptothorax*, *Temnothorax*, *Chalepoxenus* and *Myrmoxenus*, with the last two nested within *Temnothorax*. Based on mtDNA sequence data (Beibl *et al.*, 2005) *Protomognathus* also falls within *Temnothorax*. Most of the other genera currently placed in Formicoxenini, including *Atopomyrmex*, *Dilobocondyla*, *Ochetomyrmex*, *Nesomyrmex*, *Podomyrma* and *Terataner*, show no close relationship to this group (Fig. 1). Because we cannot reliably place *Cardiocondyla*, the question of its possible relationship to the core formicoxenines remains unresolved.

The tetramoriine ants are a very strongly supported group (PP 1.00, BS 100), comprising *Tetramorium* and derivative ‘satellite genera’ that are nested within it: *Rhoptromyrmex*, *Anergates*, *Teleutomymex* and *Strongylognathus*. These are social parasites whose divergent morphology caused them to be placed in their own genera. We identify a clade (PP 1.00 BS 100) composed of *Calypatomyrmex*, *Vollenhovia* and an undescribed genus from the Philippines, as sister to the tetramoriines, with moderate support (PP 1.00 BS 86).

Three groups of species assigned, or recently assigned, to *Monomorium* also appear in *Crematogastrini*. The genus *Royidris* (PP 1.00 BS 100), formerly the ‘*Monomorium*’ *shuckardi*-group (Heterick, 2006), is part of a well-supported clade (PP 1.00 BS 92) of morphologically disparate genera all endemic to Madagascar, the *Eutetramorium* genus-group (Bolton & Fisher, 2014). The ‘*Monomorium*’ *scabriceps*- and *destructor*-groups form their own clade (PP 1.00 BS 100) that is part of a larger group (PP 1.00 BS 92) comprising two other clades: *Huberia* + *Podomyrma* + *Liomyrmex* + *Metapone* (PP 1.00 BS 99) and the aforementioned *Eutetramorium* cluster. We resurrect the genus *Trichomyrmex* to contain the *scabriceps*- and *destructor*-groups (see below).

*Lordomyrma* + *Ancyridris* + *Propodilobus* form a very strongly supported clade (PP 1.00 BS 100), with very short branches separating these three genera. The sister group of this diverse Australasian clade (Lucky & Sarnat, 2010) is not confidently identified in our analyses, although we can reject some candidate taxa, namely *Bariamyrma*, *Lachnomyrmex* and *Rogeria* (cf. Taylor, 2009), because these are in distant clades. We do not find evidence of a close relationship of the *Lordomyrma* clade to the genera *Cyphoidris* or *Dacatinops* within the *Crematogastrini*, but attention should be focused on *Indomyrma* (Brown, 1986) and *Lasiomyrma* (Terayama & Yamane, 2000), two taxa that we were unable to sequence.

The Indo-Pacific genera *Paratopula*, *Poecilomyrma*, *Romblonella* and *Rotastruma* constitute a clade (PP 1.00 BS 70) in which *Paratopula* is sister to the other three (PP 1.00 BS 99). Among other findings, we also recover the following sister-group relationships in Crematogastrini: *Melissotarsus* + *Rhopalomastix* (PP 1.00 BS 100), *Cyphoidris* + *Dicroaspis* (PP 1.00 BS 75), *Dacatria* + *Proatta* (PP 1.00 BS 75), *Dilobocondyla* + *Secostruma* (PP 1.00 BS 100) and *Diplomorium* + *Carebara* (PP 1.00 BS 99). *Carebara affinis*, a representative of the erstwhile genus *Pheidologeton*, is nested well within *Carebara* (Fig. 1), justifying synonymy of the former under the latter (Fischer *et al.*, 2014).

The affinities of the large and diverse genus *Crematogaster* are uncertain (Blaimer, 2012b). We obtain weak evidence (PP 93 BS 18) that its sister group is the Paleotropical genus *Meranoplus* and that *Recurvidris*, previously hypothesized to be the closest relative of *Crematogaster* (Bolton, 2003), is sister to *Adlerzia* (PP 91 BS 48).

There is also modest support for a *Perisomyrmex* + *Pristomyrmex* sister pair (PP 1.00 BS 65), but surprisingly we do not recover a more inclusive clade containing these two plus *Myrmecina* and *Acanthomyrmex*: the erstwhile tribe Myrmecini (Ogata & Okido, 2007). Nevertheless, we cannot confidently reject this putative clade, because *Myrmecina* and *Acanthomyrmex* are isolated taxa of uncertain position in our tree, emerging from the bushy base of Crematogastrini. Other apparently isolated genera, not strongly associated with particular taxa, include *Dacatinops*, *Kartidris*, *Lophomyrmex*, *Mayriella*, *Nesomyrmex*, *Tetheamyrmex* and *Xenomyrmex*. There is a weak indication that *Tetheamyrmex* is sister to all other Crematogastrini (PP 90 BS 20), but confirmation of this and other relationships within Crematogastrini requires improved taxon sampling and, more critically, a much larger sampling of genes.

### Divergence dating and biogeographic history

The chronogram derived from a BEAST analysis (Fig. 2) recovers a crown-group age for the Myrmicinae of 98.6 Ma [95% highest posterior density (HPD) 87.9–109.6 Ma]. The major clades within the subfamily are considerably younger, with estimated crown ages of 52.3 Ma for Myrmecini, 54.3 Ma for Pogonomyrmecini, 52.9 Ma for Stenammini, 71.1 Ma for Solenopsidini, 67.0 Ma for Attini and 70.8 Ma for Crematogastrini (Table 5). It is striking that the ‘basal’ (i.e. earliest branching) lineages of myrmicines (Myrmecini, Pogonomyrmecini, Stenammini) have younger crown ages than the other major clades, attesting to substantial pruning of the stem lineages of these three groups.

Our inferred crown age of ~100 Ma for Myrmicinae is somewhat older than estimates from other studies, which are in the range of 75–90 Ma (Brady *et al.*, 2006; Moreau & Bell, 2013; Schmidt, 2013), although the 95% HPD values overlap with those of most estimates in Moreau & Bell (2013). The fossil record does not include any definitive Myrmicinae from the Cretaceous. *Afromyrma petrosa*, described from a Turonian mudstone imprint from Orapa, Botswana (91 Ma), was

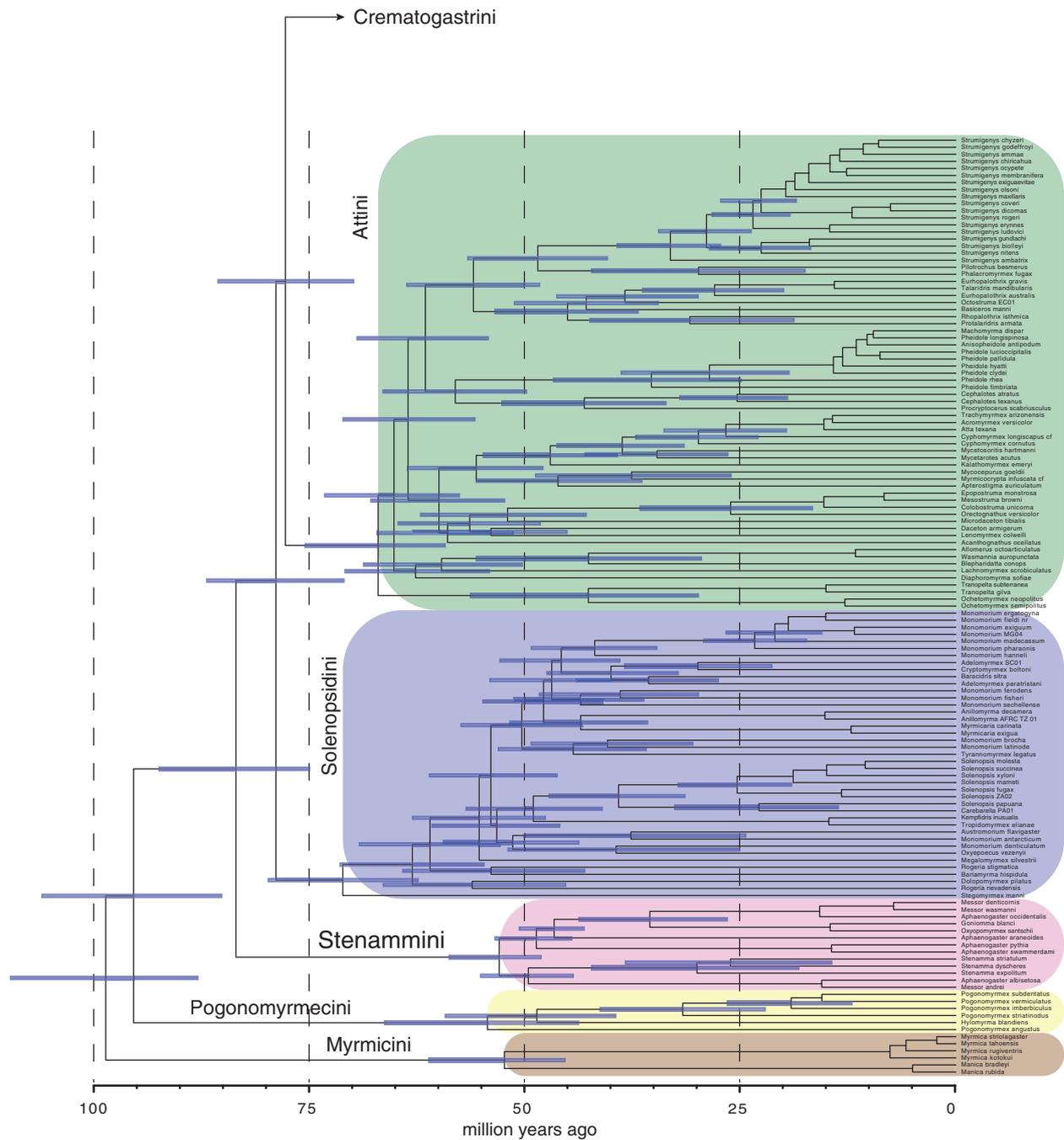
attributed to this subfamily by Dlussky *et al.* (2004), but this has been questioned by others (Wilson & Hölldobler, 2005; Archibald *et al.*, 2006) and thus *Afromyrma* was not used as an *a priori* calibration in our dating analysis. Otherwise the first myrmicine ants are not reported until early Eocene (50–55 Ma) amber deposits from China (Hong, 2002), India (Rust *et al.*, 2010) and France (Aria *et al.*, 2011). These await detailed study – or re-evaluation in the case of the Chinese amber inclusions (LaPolla *et al.*, 2013) – but they reveal considerable taxonomic diversity, consistent with our inference that the major lineages of Myrmicinae had already originated by this time.

Our divergence date estimates indicate that the early and mid-Eocene (55–40 Ma) was an important period of diversification for myrmicine ants (Table 5). Among taxa with estimated crown origins at about this time are the three aforementioned tribes (Myrmecini, Pogonomyrmecini, Stenammini), and numerous other suprageneric taxa including the following (ages in Ma, with 95% HPD): *Daceton* genus-group (58.9; 51.3–67.0), *Atta* genus-group (55.6; 47.9–63.5), *Cephalotes* genus-group (43.0; 33.6–52.6), *Basiceros* genus-group (45.0; 36.8–53.4) and ‘core formicoxenines’, as defined above (52.7; 46.7–59.3). Our age inferences for the fungus-growing ants (*Atta* genus-group) are comparable to those of a previous Bayesian dating analysis of the group (Schultz & Brady, 2008; 52 Ma, 95% HPD 44–59).

Nevertheless we find that some of the most prominent contemporary genera in the Myrmicinae have relatively recent crown-group origins. Examples include (ages in Ma, with 95% HPD) *Solenopsis* (39.1; 31.4–47.1), *Pheidole* (35.2; 24.9–46.6), *Cephalotes* (25.3; 19.5–31.9), *Strumigenys* (33.1; 27.2–39.2), *Crematogaster* (34.7; 28.1–42.4) and *Tetramorium* (20.1; 15.4–24.8). These are highly successful, species-rich genera that appear to have undergone intense diversification since the Eocene. Our estimates of the crown ages of *Pheidole* and *Cephalotes* are considerably younger than those of other recent studies (*Pheidole*: 58.4–61.2 Ma, Moreau, 2008; *Cephalotes*: 46 Ma, 95% HPD 37–56 Ma, Price *et al.*, 2014), suggesting a more compressed history of diversification in these groups than inferred by those investigators.

Results of the LAGRANGE analysis show that the two largest clades of Myrmicinae, the sister taxa Attini and Crematogastrini, originated and diversified largely in the Neotropics and Paleotropics, respectively (Fig. 3, Table S7). Some Crematogastrini lineages subsequently spread into the Palearctic region and Australia, and a few (such as the genera *Nesomyrmex*, *Temnothorax*, *Carebara* and *Crematogaster*) colonized the New World. Conversely, the early evolution of Attini was centred in the New World tropics, with subsequent dispersal events, in the late Eocene, to the Afrotropics (*Strumigenys*) and Australia (*Daceton* genus-group, *Eurhopalothrix*). Dispersal to the Old World by *Pheidole* is estimated to have occurred more recently, in the middle Miocene (Fig. 3).

The Solenopsidini is another clade which is inferred to have had a Neotropical origin (Table S7). In contrast to the Attini, however, there appears to have been an early colonization of the Paleotropics about 50 Ma, which led to substantial diversification there. There was also an independent dispersal of solenopsidines from the Neotropics to Australia, presumably



**Fig. 2.** (a, b) Chronogram of Myrmicinae, from a BEAST analysis, with outgroups not shown. Blue bars depict the 95% HPD (highest probability density), and are given for all nodes for which the 95% HPD function encompasses an estimate of 25 Ma or older.

via Antarctica, about 40–50 Ma (Fig. 3). The latter event was followed by a large radiation of *Monomorium*-like species in Australia (Ettershank, 1966; Heterick, 2001). The genus *Solenopsis* itself is of Neotropical origin but has come to occupy all the major biogeographic regions; in this case dispersal outside the Neotropics occurred more recently, within the last 25–30 Ma (Fig. 3).

Of the three earliest diverging (‘basal’) lineages of Myrmicinae, the Stenammini are most abundant in the northern hemisphere and are most likely of Nearctic origin, although selected lineages have dispersed to the northern Neotropics and the Paleotropics; the Pogonomymecini arose in the Neotropics and subsequently colonized the Nearctic region; and the Myrmicini are reconstructed as having a Nearctic

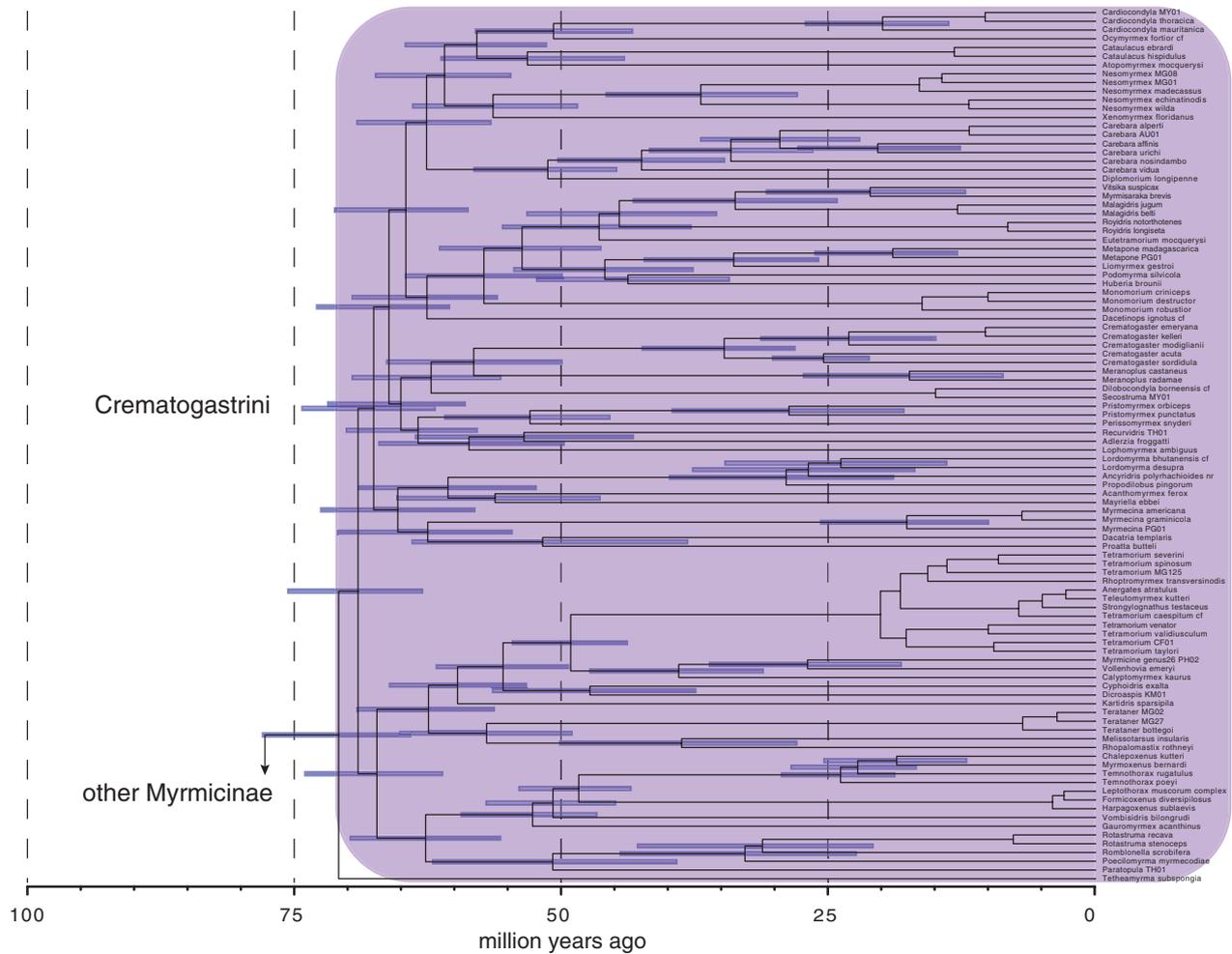


Fig. 2. Continued.

origin, with multiple dispersals to the Palearctic region (Fig. 3, Table S7).

The two descendant branches of crown Myrmicinae, leading to (i) Myrmicini and (ii) all other myrmicines, are reconstructed as most likely inheriting a Nearctic and Neotropical distribution, respectively (Table S7). The evolution of the 'all other myrmicines' clade in the Late Cretaceous and early Tertiary appears, on the one hand, to have been concentrated in the Neotropics (Fig. 3), attesting to the importance of this region for early ant evolution (Moreau & Bell, 2013). On the other hand, dispersal to other regions and diversification therein – starting as early as 70 Ma for the Crematogastrini – has also been an integral part of the myrmicine success story.

## Taxonomy

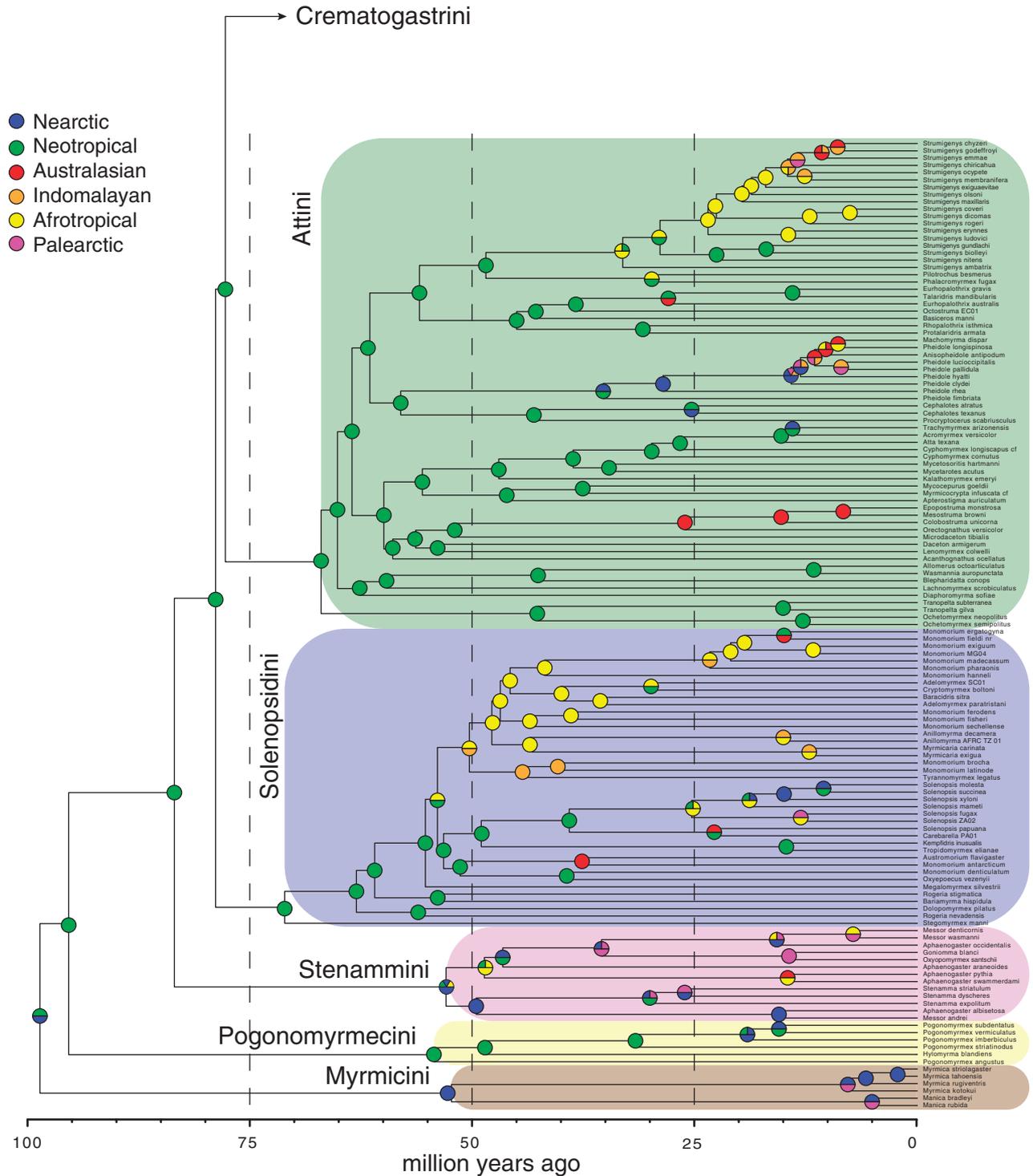
### Generic changes

The following generic changes are instituted, primarily to eliminate obvious cases of nonmonophyly. New and revived

combinations implicitly include the junior synonyms of the species names listed below. Author and year of publication for all genus and species names can be found in AntCat (<http://antcat.org>).

*Veromessor* **stat.r.** is resurrected from synonymy under *Messor*, generating the following **revived combinations** in *Veromessor*: *andrei*, *chamberlini*, *chicoensis*, *julianus*, *lariversi*, *lobognathus*, *pergandei*, *smithi* and *stoddardi*.

*Syllophopsis* **stat.r.** is resurrected from synonymy under *Monomorium*, to contain the *Monomorium* species in the *hildebrandti*-group (*sensu* Heterick, 2006; this includes the *fossulatum*-group of Bolton, 1987). *Ireneidris* is removed from synonymy under *Monomorium*, and newly synonymized (**syn.n.**) under *Syllophopsis*. This creates the following **new combinations** in *Syllophopsis*: *adiastolon*, *aureorugosa*, *australica*, *dentata*, *ferodens*, *fisheri*, *gongromos*, *hildebrandti*, *infusca*, *kondratieffi*, *malamixta*, *sechellensis*, *sersalata*, *subcoeca*, *thrascolepta* and *vitensis*; and the following **revived combinations** in *Syllophopsis*: *arnoldi* (= *jonesi*, unnecessary replacement name), *cryptobia*, *elgonensis* and *modesta*.



**Fig. 3.** (a, b) Biogeographical history of Myrmicinae as inferred from an analysis with LAGRANGE, using a DEC (dispersal-extinction-cladogenesis) model. The ancestral range inheritance scenario with the highest relative probability is indicated for the two descending branches of each node. The lower half of each sphere pertains to the lower descending branch; the upper half to the upper descending branch. Most (60%) of the relative probabilities are greater than 0.70, but for some nodes the most probable scenario has weak support and there are alternative scenarios of only slightly lower relative probability. See Table S7 for a more detailed account of range inheritance scenarios for the major lineages.

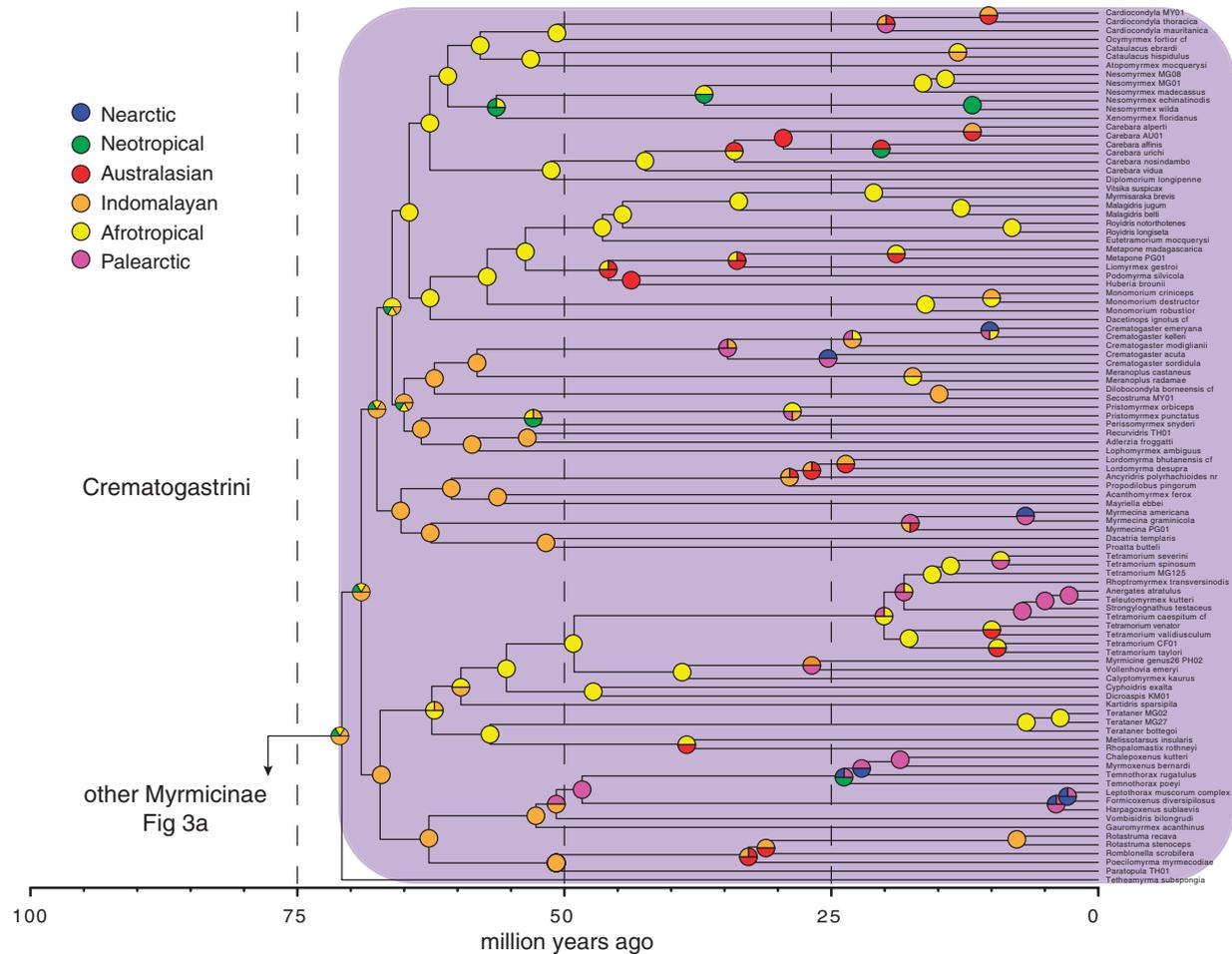


Fig. 3. Continued.

The genus *Epelysidris* **stat.r.** is resurrected from synonymy under *Monomorium* to contain the single known species *E. brocha* (**comb.r.**). Its putative sister species '*Monomorium* *latinode*' is very different morphologically and a new genus will be erected for it in a forthcoming publication (B. Bolton, personal communication).

We support the synonymy of *Carebarella* under *Solenopsis*, generating the following **new combinations** in *Solenopsis*: *alvarengai*, *condei*. The type species of *Carebarella* (*bicolor*) was already combined with *Solenopsis* by Pacheco & Mackay (2013). Although they declined to propose new generic synonymy, their new combination effectively did this, although it left the other two names orphaned.

*Anisopheidole* is synonymized (**syn.n.**) under *Pheidole*, generating the following **revived combination** in *Pheidole*: *antipodum*.

*Machomyrma* is synonymized (**syn.n.**) under *Pheidole*, generating the following **new combination** in *Pheidole*: *dispar*.

*Chalepoxenus* is synonymized (**syn.n.**) under *Temnothorax*, generating the following **new combinations** in *Temnothorax*: *brunneus*, *hyrcanus*, *kutteri*, *muellerianus*, *spinosus*, *tarbinskii*,

*tauricus*, *tramieri* and *zabelini*. Two of these new combinations become secondary junior homonyms, *T. spinosus* (Arnoldi) and *T. tauricus* (Radchenko), which are here replaced (**nom.n.**) with *T. sentosus* and *T. inquilinus*, respectively.

*Myrmoxenus* is synonymized (**syn.n.**) under *Temnothorax*, generating the following **new combinations** in *Temnothorax*: *adlerzi*, *africana*, *algeriana*, *bernardi*, *birgitae*, *corsica*, *gordiagini*, *kraussei*, *ravouxi*, *stumperi*, *tamarae*, and *zaleskyi*. Two of these new combinations, *T. kraussei* (Emery) and *T. tamarae* (Arnoldi), create secondary junior homonyms among two species already in *Temnothorax*, *T. kraussei* (Emery) and *T. tamarae* (Radchenko), which are here replaced (**nom. n.**) with *T. mediterraneus* and *T. georgicus*, respectively.

*Protomognathus* is synonymized (**syn. n.**) under *Temnothorax*, generating the following **new combination** in *Temnothorax*: *americanus*.

*Rhopotromyrmex* is synonymized (**syn.n.**) under *Tetramorium*, generating the following **new combinations** (unless otherwise noted) in *Tetramorium*: *caritum*, *critchleyi*, *globulinodis*, *mayri*, *melleum* (**comb.r.**), *opacum*, *rawlinsoni*, *schmitzi*, *transversinodis* and *wroughtonii*. One of these, *T. mayri* Forel, creates a

secondary junior homonym of a species already in *Tetramorium*, *T. mayri* (Mann), which is here replaced (**nom.n.**) with *T. solomonensis*. The new combination *T. transversinodis* (Mayr) is a secondary senior homonym of an invalid name, *T. transversinodis* (Enzmann), which therefore does not require a replacement name.

*Anergates* is synonymized (**syn.n.**) under *Tetramorium*, generating the following **new combination** in *Tetramorium*: *atratum*.

*Teleutomyrmex* is synonymized (**syn.n.**) under *Tetramorium*, generating the following **new combinations** in *Tetramorium*: *kutteri*, *schneideri*. *Tetramorium schneideri* (Kutter) becomes a secondary junior homonym, here replaced with *T. inquilinum* (**nom.n.**).

*Strongylognathus* Mayr is also a synonym of *Tetramorium* Mayr, but it has priority over *Tetramorium*. Transfer of the hundreds of valid *Tetramorium* species names to *Strongylognathus*, with consequent changes in spelling to many of them, would create considerable confusion. In this instance a ruling by the International Commission on Zoological Nomenclature would be required to validate a reversal of precedence (ICZN Article 23.9.3). In the interim we maintain current usage and refrain from synonymizing the two genera.

*Trichomyrmex* **stat.r.** is resurrected from synonymy under *Monomorium*, to contain the *Monomorium* species in the *scabriceps*- and *destructor*-groups (*sensu* Bolton, 1987; see also Radchenko, 1997). *Holcomyrmex* and *Parholcomyrmex* are removed from synonymy under *Monomorium*, and newly synonymized (**syn.n.**) under *Trichomyrmex*. These actions generate the following **new combinations** in *Trichomyrmex*: *aberrans*, *abyssinicus*, *chobauti*, *chobauti ajjer*, *criniceps*, *destructor*, *emeryi*, *emeryi laevior*, *epinotale*, *glaber*, *lameerei*, *mayri*, *muticus*, *oscaris*, *perplexus*, *robustior*, *santschii* (= *santschianum*, unnecessary replacement name) and *scabriceps*; and the following **revived combinations** in *Trichomyrmex*: *rogeri* and *wroughtoni* (= *wroughtonianum*, unnecessary replacement name).

#### Tribal classification

We propose the recognition of six tribes within Myrmicinae. These correspond to the six major (and mutually exclusive) clades that we recover with overwhelming support in all phylogenetic analyses. This represents a considerable reduction from the 25 tribes currently recognized, but most of those tribes are nonmonophyletic or – more often – their recognition leaves behind a residue of nonmonophyletic taxa. It is this latter problem that is often overlooked. In the same way that monophyletic ‘satellite genera’ render the genera within which they arise paraphyletic (see above), the recognition of small well-defined monophyletic tribes, such as Adelomyrmecini, Basicerotini, Lenomyrmecini, Melissotarsini and Myrmicariini, similarly ignores the rump of nonmonophyletic tribes in which these more derived taxa evolved.

In the scheme below, genera known only from fossils are signified by a dagger (†). In many instances their placement

requires further study. Sixteen extant genera that we did not sequence in this study are indicated with an asterisk (\*); they have been placed provisionally in tribes on the basis of close morphological or genetic similarity to sequenced taxa. We cite the author and year of publication of each tribe name; equivalent information for genus names is available in AntCat (<http://antcat.org/>).

#### Tribe Myrmicini Lepelletier de Saint-Fargeau 1835

*Constituent genera.* *Manica*, *Myrmica*, †*Plesiomyrmex* and †*Protomyrmica*.

*Note.* *Eutetramorium*, *Huberia*, *Hylomyrma*, *Pogonomyrmex* and *Secostruma* are excluded from Myrmicini.

#### Tribe Pogonomyrmecini trib.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:BD404053-2C51-412B-9291-4A7E9D323A95>.

*Type genus.* *Pogonomyrmex*

*Worker diagnosis.* Myrmicine ants of moderate to large size (head width 0.73–2.90 mm, head length 0.78–2.50 mm); mandible elongate to subtriangular, with 5–8 teeth on masticatory margin; psammophore present or absent; antenna with 12 segments, the last 4–5 segments forming a weakly expanded club; palp formula (number of maxillary palp segments, followed by number of labial palp segments) 5,4 or 4,3; mesosoma lacking distinct promesonotal suture or metanotal groove; propodeum usually with a pair of spines, but lacking in some species; propodeal lobes usually prominent, and rounded or spiniform; metasternum with a deep V-shaped or U-shaped median emargination running forward from the posterior border and terminating at or near the metasternal pit, well in front of the metacoxal cavities (Bolton, 1994); metasternal process large and comprising two prominent teeth; mesotibia and metatibia each with a single apical spur, usually finely barbate or pectinate; petiole elongate, with prominent anterior peduncle; sting well developed and functional; integument sculpture usually conspicuous on head, mesosoma, petiole, and postpetiole, typically striate, costate, or rugulose; striae often extending onto fourth abdominal tergum (first tergum of gaster).

*Constituent genera.* *Hylomyrma* and *Pogonomyrmex*.

*Note.* As currently circumscribed *Pogonomyrmex* is non-monophyletic, but this can be rectified by assignment of a new genus name to the ‘*Pogonomyrmex*’ *angustus*-complex. We refrain from this action because a detailed phylogenetic analysis of Pogonomyrmecini is currently underway (C. Moreau and R.A. Johnson, personal communication)

#### Tribe Stenammini Ashmead 1905

= Aphaenogastrini Enzmann 1947 **syn.n.**

*Constituent genera.* *Aphaenogaster*, *Goniomma*, *Oxyopomyrmex*, *Messor*, †*Paraphaenogaster*, *Stenammina* and *Veromessor*.

*Note.* *Veromessor* is resurrected from synonymy (above). The reclassification of ‘*Aphaenogaster*’ awaits more detailed phylogenetic analysis of lineage diversity within *Stenammini*.

#### Tribe Solenopsidini Forel 1893

= Myrmicariini Forel 1893 **syn.n.**  
 = Monomoriini Emery 1914  
 = Megalomyrmechini Dlussky & Fedoseeva 1988  
 = Stegomyrmechini Wheeler 1922 **syn.n.**  
 = Adelomyrmecini Fernández 2004 **syn.n.**

*Constituent genera.* *Adelomyrmex*, *Anillomyrma*, *Austromorium*, *Baracidris*, *Bariamyrma*, \**Bondroitia*, *Cryptomyrmex*, *Dolopomyrmex*, *Epelysidris*, *Kempfidris*, *Megalomyrmex*, *Monomorium*, *Myrmicaria*, *Oxyepoecus*, *Rogeria*, *Solenopsis*, *Stegomyrmex*, *Syllophopsis*, *Tropidomyrmex* and *Tyrannomyrmex*.

*Note.* *Carebarella* is considered a synonym of *Solenopsis* (above). *Monomorium* remains a heterogeneous, nonmonophyletic group. Extant genera excluded from Solenopsidini include *Adlerzia*, *Allomerus*, *Carebara*, *Diplomorium*, *Mayriella* and *Tranopelta*.

#### Tribe Attini F. Smith 1858

= Pheidolini Emery 1877 (= Anergatidini Emery 1922) **syn.n.**  
 = Dacetini Forel 1892 (= Epopostrumina Brown 1952  
 = Orectognathina Brown 1952 = Strumigenina Brown 1952)  
**syn. n.**  
 = Ochetomyrmecini Emery 1914 **syn.n.**  
 = Cephalotini M. R. Smith 1949 (= Cryptoceridae F. Smith 1853) **syn.n.**  
 = Basicerotini Brown 1949 **syn.n.**  
 = Phalacromyrmechini Dlussky & Fedoseeva 1988 **syn.n.**  
 = Blepharidattini Wheeler & Wheeler 1991 **syn.n.**  
 = Lenomyrmecini Bolton 2003 **syn.n.**

*Constituent genera.* *Acanthognathus*, *Acromyrme*, *Allomerus*, *Apterostigma*, *Atta*, †*Attaichnus*, *Basiceros*, *Blepharidatta*, *Cephalotes*, \**Chimaeridris*, *Colobostruma*, \**Cyatta*, *Cyphomyrmex*, *Daceton*, *Diaphoromyrma*, *Epopostruma*, *Eurhopalothrix*, \**Ishakidris*, *Kalathomyrmex*, *Lachnomyrmex*, *Lenomyrmex*, *Mesostruma*, *Microdaceton*, \**Mycetagroicus*, *Mycetarotes*, \**Mycetophylax*, *Mycetosoritis*, *Myocepurus*, *Myrmicocrypta*, *Ochetomyrmex*, *Octostruma*, *Orectognathus*, \**Paramycetophylax*, *Phalacromyrme*, *Pheidole*, *Pilotrochus*, *Procryptocerus*, *Protalaridris*, \**Pseudoatta*, *Rhopalothrix*, \**Sericomyrmex*, *Strumigenys*, *Talaridris*, *Trachymyrme*, *Tranopelta* and *Wasmannia*.

#### Tribe Crematogastrini Forel 1893

= Formicoxenini Forel 1893 (= Cardiocondyliini Emery 1914 = Leptothoracini Emery 1914 = Stereomyrmecini Emery 1914 = Podomyrmini Emery 1924 = Solenomyrmini Donisthorpe 1943) **syn.n.**  
 = Cataulacini Emery 1895 **syn.n.**  
 = Tetramoriini Emery 1895 (= Anergatini Emery 1914 = Teleutomyrmecini Kutter 1950) **syn.n.**  
 = Melissotarsini Emery 1901 **syn.n.**  
 = Myrmeciniini Ashmead 1905 **syn.n.**  
 = Metaponini Forel 1911 **syn.n.**  
 = Lophomyrmecini Emery 1914 **syn.n.**  
 = Meranoplini Emery 1914 **syn.n.**  
 = Ocymyrmechini Emery 1914 **syn.n.**  
 = Pheidologetonini Emery 1914 **syn.n.**  
 = Proattini Forel 1917 **syn.n.**  
 = Hypopomyrmecina Brown 1952 **syn.n.**  
 = Calyptomyrmecini Dlussky & Fedoseeva 1988 **syn.n.**  
 = Liomyrmecini Bolton 2003 **syn.n.**  
 = Paratopulini Bolton 2003 **syn.n.**

*Constituent genera.* *Acanthomyrmex*, *Adlerzia*, *Ancyridris*, *Atopomyrmex*, *Calyptomyrmex*, *Cardiocondyla*, *Carebara*, *Cataulacus*, *Crematogaster*, *Cyphoidris*, *Dacatria*, *Dacetinops*, *Dicroaspis*, *Dilobocondyla*, *Diplomorium*, †*Enneamerus*, †*Eocenomyrma*, *Eutetramorium*, *Formicoxenus*, \**Formosimyrmex*, *Gauromyrme*, \**Goaligongidris*, *Harpagoxenus*, *Huberia*, †*Hypopomyrmex*, \**Indomyrma*, *Kartidris*, \**Lasiomyrma*, *Leptothorax*, *Liomyrmex*, †*Lonchomyrmex*, *Lophomyrmex*, *Lordomyrma*, *Malagidris*, *Mayriella*, *Melissotarsus*, *Meranoplus*, *Metapone*, *Myrmecina*, *Myrmisaraka*, *Nesomyrmex*, *Ocymyrme*, †*Oxyidris*, †*Parameranoplus*, *Paratopula*, *Perissomyrmex*, \**Peronomyrmex*, *Podomyrma*, *Poecilomyrma*, *Pristomyrmex*, *Proatta*, *Propodilobus*, *Recurvidris*, *Rhopalomastix*, *Romblonella*, \**Rostromyrmex*, *Rotastruma*, *Royidris*, *Secostruma*, \**Stereomyrmex*, †*Stigomyrmex*, †*Stiphomyrmex*, *Strongylognathus*, *Temnothorax*, *Terataner*, *Tetheamyrma*, *Tetramorium*, *Trichomyrmex*, *Vitsika*, *Vollenhovia*, *Vombisidris* and *Xenomyrmex*.

#### Fossil taxa unplaced to tribe

†*Afromyrma*, †*Attopsis*, †*Bilobomyrma*, †*Boltonidris*, †*Brachytarsites*, †*Cephalomyrmex*, †*Clavipetiola*, †*Electromyrme*, †*Eocenidris*, †*Eomyrmex*, †*Fallomyrma*, †*Fushunomyrmex*, †*Ilemomyrmex*, †*Miosolenopsis*, †*Myrmecites*, †*Orbigastrula*, †*Quadrulicapito*, †*Quineangulicapito*, †*Sinomyrmex*, †*Solenopsites*, †*Sphaerogasterites*, †*Wumyrme* and †*Zhangidris*.

#### Excluded from Myrmicinae

The tribe Ankylomyrmini Bolton and its sole genus, *Ankylomyrma* Bolton, are hereby transferred to the subfamily

Agroecomyrmecinae, in accordance with our finding that *Ankylomyrma* is sister to *Tatuidris* (Fig. 1).

### Concluding remarks

With respect to taxonomic diversity, geographical distribution and ecological breadth, myrmicine ants are the most successful of all ant subfamilies. Our results indicate that the diversification of crown-group Myrmicinae began about 100 Ma, and was initially concentrated in the New World tropics. Repeated dispersal to, and radiation in, other biogeographic regions was a key feature of myrmicine evolution. The subfamily now comprises more than 6000 described species – the actual number of species could well be twice this – and occupies all major terrestrial ecoregions. Analysis of our 251-taxon 11-gene dataset, in conjunction with 27 fossil calibration points, reveals the broad outlines of the evolutionary history of this group, including the existence of six large, mutually exclusive clades. Nevertheless considerable challenges remain in myrmicine systematics, including resolution of the basal polytomy in the Crematogastriini clade, reclassification of nonmonophyletic taxa such as *Aphaenogaster* and *Monomorium*, and better incorporation of fossil taxa into the phylogenetic scaffold. Much more attention also needs to be directed towards the neglected species-level taxonomy of many myrmicine genera.

### Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12090

**Figure S1.** Majority-rule consensus trees from partitioned, concatenated Bayesian analyses of datasets with ‘wildcard’ taxon exclusions.

**Figure S2.** Majority-rule consensus trees resulting from Bayesian analyses of single-gene fragments, under the partitions and models described in Table S3(b).

**Table S1.** List of taxa sampled, voucher specimen codes, and GenBank accession numbers.

**Table S2.** The subjective partitions used in initial Bayesian analyses of the concatenated dataset.

**Table S3.** The subjective partitions used in initial, separate Bayesian analyses of each of the 11 genes (a) and the more objective partitions and models used in the final, separate Bayesian analyses of each of these genes (b).

**Table S4.** Summary of rate heterogeneity values for third-position partitions of protein-coding genes, which informed the ‘partial RY coding’ and ‘complete RY coding’ analyses. AA = *Abd-A*, F2 = *EF1aF2*, LR = *LW Rh*, AK = *ArgK*, TP = *Top1*, UB = *Ubx*, WG = *Wg*, F1 = *EF1aF1*, CD = *CAD*.

**Table S5.** Species distribution matrix, based on six biogeographic areas: Neotropical (T), Nearctic (N), Palearctic (P), Afrotropical (E), Indomalayan (O) and Australasian regions (A).

**Table S6.** Support values from various modes of analysis for selected clades of interest. These include maximum-likelihood analysis of the full dataset, Bayesian analysis of the full dataset and treatments designed to address base frequency heterogeneity.

**Table S7.** Range inheritance inferences for major clades of Myrmicinae, based on LAGRANGE analysis.

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