The evolution of social traits and biodiversity in the ants.

Thesis submitted by

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1 Abstract

Cooperation has shaped the evolution of life on Earth. The ants are the most numerically diverse of the eusocial Hymenoptera, and display wide variation in social complexity. This positions the ants as an ideal taxon in which to study social evolution in a comparative framework. Social evolution theory has generated many hypotheses that are testable in ants, however the lack of comprehensive or complete phylogenies, and the decentralised and scattered nature of trait data, has been an obstacle to these types of study.

In this thesis I construct a large species-level, and a complete genus-level, phylogeny of the ants, and draw together a large dataset of social traits from the literature in order to test hypotheses concerning the evolution of social traits in the ants. I find evidence that the earliest ant was large bodied, and lived in small highly related colonies. I show that group size is a significant trait in the evolution of sociality in ants, predicting the probability of a species having polymorphic workers, or of being polyandrous. I also show that the change in these traits is correlated between ancestral nodes on the phylogeny. Furthermore, in the Attini, colony size correlates closely with non-reproductive and reproductive division of labour. Together these results cement group size as a driving force of social evolution in the ants, and this has interesting implications for social evolution in general. Finally, I report the first evidence that intermediate colony sizes, the presence of discrete worker castes and polygyny are associated with increased diversification rates in ants. This thesis provides a valuable tool for the study of comparative hypotheses in the ants in the form of a complete genus-level phylogeny, and offers significant evidence to support several key hypotheses in social evolution. Furthermore, these results generate hypotheses regarding the evolution of social traits for future research.

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6 Declaration

This thesis involved collaboration with Andrew F G Bourke (AFB), Kate E Jones (KJ) and Seirian Sumner (SS).

Chapter 6

This work was supervised by AFB, KJ and SS, and I wrote the chapter.

Chapter 2

This work was supervised by AFB, KJ and SS. I constructed the supertree with essential advice and guidance from Olaf Bininda-Emonds, who also provided me with the necessary Perl scripts to implement the analysis. Elizabeth Rowse, Tracie Evans, William Miles and Alex Bower aided me with gathering and recording data from the literature.

Chapter 3

This work was supervised by AFB, KJ and SS. I carried out the analysis of the data.

Chapter 4

This work was supervised by AFB, KJ and SS. I carried out the analysis of the data.

Chapter 5

This work was supervised by AFB, KJ and SS. I carried out the analysis of the data and wrote the manuscript. This work has been published in Proceedings of the Royal Society B: Biological sciences and the text, figures and tables are reproduced here as published, with some minor formatting changes made for inclusion in the thesis. The electronic supplementary material from this publication has been integrated into the appendices.

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Chapter 6

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Chapter 7

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1 Introduction

1.1 The ants

The ants are arguably the most diverse, ecologically successful and ecologically dominant of the eusocial insects (Hölldobler & Wilson, 1990; Hölldobler & Wilson, 2009; Lach *et al.*, 2010). Eusociality is defined by a reproductive division of labour (the presence of a reproductive and a sterile worker caste), the overlap of generations within a nest or colony, and the cooperative care of brood (Michener, 1969; Crespi & Yanega, 1995). The 12,986 species of ant (Bolton, 2012) occur on every continent on Earth except Antarctica, and provide many important ecological services such as insect predation, seed dispersal, soil aeration, herbivory and detritivory (Lach *et al.*, 2010). (Michener, 1969; Crespi & Yanega, 1995).

All ants are eusocial, and they display startling variation in the development and complexity of their eusocial systems. Ants considered "primitively" eusocial live in simple societies, often consisting of only tens of workers, in which the characteristic division of labour is ill-defined (Bourke & Franks, 1995). Workers are able to become reproductive, workers are not readily distinguishable morphologically from queens, and colony tasks such as foraging and brood care are not highly organised (Bourke & Franks, 1995; Peeters, 1997). Worker reproduction in such societies often leads to overt conflict within the colony (Ratnieks, 1988; Ratnieks *et al.*, 2006). At the other end of the continuum of social organisation are "advanced" eusocial species. These species live in large colonies where the reproductive division of labour between queens and workers is manifest in pronounced queen-worker dimorphism – queens have specialised to be egg-layers and workers have specialised to work (Bourke, 1999; Bourke, 2011). Foraging is highly organised, with workers often using pheromone trails to coordinate large-scale foraging excursions, and the workforce may be divided into physical castes, allowing workers of different size-classes to specialise in different tasks (Oster & Wilson, 1978; Hölldobler & Wilson, 1990). Although overt conflict is not necessarily absent from such societies, sometimes workers have become so dedicated to working that the apparatus for mating (spermathecae and ovaries) has atrophied to the point of being almost undetectable, rendering them functionally sterile (Hölldobler & Wilson, 1990; Bourke & Franks, 1995; Crespi & Yanega, 1995).

How such a system might evolve has been a question of interest to evolutionary biologists since Darwin (Darwin, 1859). It is now understood that eusociality can evolve due to positive relatedness between the reproductive individual in a colony (the queen) and the workers. By helping to raise the offspring of the queen, workers pass copies of genes that they share with the queen on to the next generation, maximising their inclusive fitness (Hamilton, 1964). Positive relatedness is essential for, and high relatedness facilitates, the evolution of the extreme altruism observed in ants and the other eusocial insects (Hamilton, 1964; Boomsma, 2007; Boomsma, 2009; Boomsma, 2013).

1.2 The importance of social evolution

Eusociality is one of the major transitions in evolution, the name given to eight extremely significant events in the history of the evolution of life (Maynard-Smith & Szathmary, 1995). These transitions are characterised by the coming together of individual entities to form larger entities that can then evolve in their own right and so enter the next major transition (Maynard-Smith & Szathmary, 1995). For example, independent replicators have come together to form chromosomes, single celled organisms have come together to form multicellular organisms, and, in the case of eusociality, individuals have come together to form eusocial colonies (Maynard-Smith & Szathmary, 1995; Bourke, 2011). The major transitions are a key area of study in evolutionary biology, since they represent events that have entirely shaped the history of life on Earth. Furthermore they are among the most fundamental examples of the reconciliation of individual-level interests within a group, exemplifying the evolutionary puzzle of cooperation.

There are three steps in a major transition – social group formation (the coming together of individuals to form a social group), social group maintenance (the resolution of conflict within a social group) and social group transformation (the evolution of individuality) (Bourke, 2011). Most of the major transitions in evolution occurred in the distant history of life on earth. However, eusociality first evolved in the ants around 160-185 million years ago (Moreau & Bell, 2013). This positions the ants, and other eusocial groups, as key clades in which to study the predictions and processes of the major transitions in evolution, including social group transformation.

Theory predicts that eusociality evolved under conditions of positive relatedness and was facilitated by high relatedness (Hamilton, 1964). This suggests that queens at the origin of the ants headed colonies singly and mated only once, so generating high relatedness within a colony (Charnov, 1978; Boomsma, 2007; Hughes *et al.*, 2008b; Boomsma, 2009; Boomsma, 2013). Furthermore, theory regarding the evolution of multicellularity, another of the major transitions in evolution, has been extended to explain the evolutionary elaboration and increasing complexity of eusocial systems in the eusocial insects. It has been hypothesised that there is a causal relationship between the number of constituent cells and the number of functional cell types within a unitary organism, an association known as the "size-complexity rule" (Bonner, 1993; 2004). Particularly strong evidence for this relationship comes from the *Volvox*, a genus of algae in which extant species range from existing as individual cells to living in colonies of up to 50,000 cells in which there is a reproductive division of labour (Herron & Michod, 2008).

Unitary organisms display a reproductive division of labour between the germ line and the soma, and further divide non-reproductive labour within the soma through morphologically distinct cell types. In the ants, reproductive labour is divided between the queen and the workers and, sometimes, the workers further subdivide non-reproductive labour between physical worker castes. It has been recently hypothesised that, by analogy, the size-complexity rule for unitary organisms might also apply to the evolution of organisational complexity in eusocial insects and hence that, as colonies evolve to become larger, their greater size drives the evolution of more integrated and complex division of labour (Bourke, 1999; Bourke, 2011). If this is true, the study of the evolution of eusociality and social complexity in the social insects offers evolutionary biologists an opportunity to study the processes that underpin the major transitions in evolution, and social group transformation, in a system independent of the transition represented by the evolution of multicellularity (Bourke, 2011). The size-complexity hypothesis predicts that traits associated with advanced eusociality, such as a polymorphic worker caste, will be associated with large colonies. Since selection can only act to increase colony size after eusociality has first evolved, the hypothesis also predicts that the first ants lived in small colonies and that traits which reduce within-colony relatedness such as polygyny and polyandry will also be associated with large colonies. Further benefits of polygyny and polyandry stem from the increased within-colony genetic diversity that it brings. High genetic diversity has been associated with improved division of labour (Schwander *et al.*, 2005; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007) and increased disease resistance in ants (Hughes & Boomsma, 2004; Reber *et al.*, 2008) and bees (Baer & Schmid-Hempel, 2001; Seeley & Tarpy, 2007), and these factors may be more important in large, long-lived colonies than smaller ephemeral ones.

Finally, the evolution of eusociality may be the cause of the ecological and numerical success of the ants (Oster & Wilson, 1978). Moreover, it has been hypothesised that the larger colonies found in two ant subfamilies, the Dolichoderinae and the Formicinae, might be responsible for the high diversity found in these groups (Grimaldi & Engel, 2005). If the evolution of larger colonies drives the evolution of division of labour, it could be the case that the ecological benefits of more efficient and highly organised non-reproductive labour are the driving force behind the diversification of the ants.

There are three important questions relating to the evolution of eusociality that can be answered within a comparative framework using the ants as a study system. Firstly, the prediction of positive and possibly high relatedness at the origin of eusociality in the ants can be tested. Secondly, due to the diverse range of levels of social complexity found in the ants, the relationship between colony size and social complexity can be investigated. Finally, this variation in social complexity, in conjunction with the high species diversity in the ants, enables the investigation of the hypothesis that increases in the complexity of colony-level social traits are associated with higher diversification rates.

1.3 Phylogenies and comparative biology

Comparative questions require three key components to be tested: a phylogenetic hypothesis, trait data for extant species and realistic evolutionary models (Felsenstein, 1985). A phylogeny describes the relationships between species, or higher-level taxonomic units (e.g. genera), within a clade of organisms. When a phylogeny has branch lengths, i.e. a measure of the time between each branching event, it becomes a powerful tool for the investigation of evolutionary hypotheses in a comparative framework. If the value of one or more traits is known for each taxonomic unit at the tips of a phylogeny, the evolutionary process can be modelled, incorporating the branching structure of the phylogeny and the time since each branching event. In this way the ancestral states of a trait can be estimated and the evolutionary correlation between two or more traits can be quantified (Felsenstein, 1985; Grafen, 1989; Felsenstein, 2008). Furthermore a phylogeny can be used to model the rates of speciation and extinction to estimate diversification rates (Yule, 1925; Nee *et al.*, 1994; Pybus & Harvey, 2000) and to investigate how patterns of diversification might covary with trait evolution (FitzJohn, 2010; 2012).

A significant barrier to the comparative analysis of evolutionary questions in the ants is absence of a phylogeny that represents much of the extant diversity of the clade. Absent taxonomic units from a phylogeny may disrupt comparative analysis. For example, traits may be inferred to have evolved earlier than would be inferred if the tree was complete, and patterns of correlated evolution may be obscured or overestimated. Although phylogenies have been published that represent the full breadth of higher level ant diversity (i.e. subfamily level), none of these phylogenies includes more than 300 species (Moreau & Bell, 2013). In addition, trait data for the ants are scattered throughout a broad and diverse literature, meaning that collating these data for comparative analysis represents an essential and valuable task for the purposes of comparative analysis. As such, there is a need for a comprehensive phylogeny for the ants, and a corresponding database of data on key social traits. These tools will facilitate the investigation of macroevolutionary hypotheses concerning social traits, social complexity and biodiversity in the ants.

1.4 Thesis overview

The aim of this thesis is to combine modern phylogenetic techniques with rigorous comparative analytical techniques and a large-scale dataset to test three key hypotheses concerning the evolution of social traits and social complexity in the ants.

Chapter 2 describes the construction of a species-level phylogeny representing 12.6% of extant ant species, and a genus-level phylogeny featuring every extant genus of ant. These two phylogenies are constructed using supertree techniques. Supertree methodology uses the nodes shared between species present on phylogenies derived from the literature as character data which, in combination with molecular data derived from public databases, is used to generate a summary phylogeny. I also describe the design of a relational database in which I stored trait data gathered from the diverse ant primary literature. The process by which I gathered and processed data from the literature is also described. The supertrees and database presented in this chapter form the basis of the subsequent four data chapters in this thesis.

In Chapter 3 I employ ancestral state reconstruction methods applied to the genus-level supertree and data on mean worker head-width, colony size, the presence of discrete worker castes, gyny status and mating frequency to infer the phenotype of the ancestral ant. This chapter aims to provide evidence to help resolve the apparent conflicting evidence from the fossil record and molecular phylogenetics regarding the size of the ancestral ant, and to test hypotheses generated from inclusive fitness theory regarding the social phenotype of the ancestral ant. Specifically, I test the competing hypotheses that the ancestral ant was a large-bodied wasp-like ant similar to the fossil *Sphecomyrma* (Wilson *et al.*, 1967; Agosti *et al.*, 1998; Wilson & Hölldobler, 2005), or that the ancestral ant was a small-bodied and specialised subterranean ant, as inferred by recent molecular phylogenies (Brady *et al.*, 2006; Lucky *et al.*, 2013). I also test the hypotheses that the ancestral ant lived in small colonies, had monomorphic workers and was both monogynous and monandrous, as predicted by inclusive fitness theory (Hamilton, 1964; Bourke, 1999; Boomsma, 2007; Boomsma, 2009; Bourke, 2011; Boomsma, 2013).

In Chapter 4 the changes in colony size, discrete worker castes, gyny status and mating frequency are explored throughout the genus-level phylogeny, and I test several predicted evolutionary associations between these traits. Through ancestral state reconstructions I estimate the number of independent origins of discrete worker castes, polygyny and polyandry in the ant phylogeny, and discuss the implications of the ordering of these origins. I test a number of predicted correlations between colony size, the presence of discrete worker castes, polygyny and polyandry throughout the tree in two ways. Firstly, I test for the presence of a correlation between pairs of traits as they change between internal nodes of the tree (Revell, 2014). Secondly, I test correlations between trait values in extant species in both univariate and multivariate logistic regression models, controlling for phylogeny (Ives & Garland, 2010). The specific associations I test for are between discrete castes and colony size (Bourke, 1999; Bourke, 2011); discrete castes and polygyny (Oster & Wilson, 1978; Frumhoff & Ward, 1992); discrete castes and polyandry (Crozier & Page, 1985); polyandry and colony size (Cole, 1983; Boomsma & Ratnieks, 1996); and polyandry and polygyny (Keller & Reeve, 1994).

Chapter 5 describes a detailed examination of the relationship between colony size and aspects of non-reproductive and reproductive division of labour in a single tribe of ants, the Attini. In this tribe the available data for worker and queen head-widths enabled me to calculate continuous measures of worker size variation and queen-worker dimorphism. Measuring these traits as continuous variables allowed for a more detailed test of the hypotheses outlined in Bourke (2011), namely that larger colonies are positively associated with non-reproductive division of labour (worker size variation) and reproductive division of labour (queen-worker dimorphism).

Finally, in Chapter 6 I explore the relationship between diversification rates and key social traits in the ants (colony size, discrete worker castes, polygyny and polyandry). Eusociality has been suggested to be key to the ecological success of the ants (Hölldobler & Wilson, 1990; Lach *et al.*, 2010), and it has been hypothesised that large colonies are the cause of the high diversity within the subfamilies Formicidae and Dolichoderinae (Grimaldi & Engel, 2005). Furthermore, the evolution may confer a level of phenotypic plasticity at the colony level, which may facilitate diversification by allowing ants to rapidly adapt to new niches and environments (Passera *et al.*, 1996; Yang *et al.*, 2004; Rajakumar *et al.*, 2012). The hypothetical relationship between colony size and the presence of discrete worker castes (Bourke, 1999; Bourke, 2011), and colony level benefits associated with high genetic diversity achieved through polygyny and polyandry (Baer & Schmid-Hempel, 2001; Hughes & Boomsma, 2004; Schwander *et al.*, 2005; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007; Seeley & Tarpy, 2007; Reber *et al.*, 2008) predict that these traits may also be associated with diversification rates. I first use the complete genus-level phylogeny to model rates of diversification patterns in the ants and identify regions of the tree which have experienced significant increases or decreases in diversification rate. Then, by comparing models in which diversification rate is fixed, and models where diversification rate is allowed to covary with the value of a trait, I look for evidence that colony size, discrete worker castes, polygyny and polyandry are associated with higher or lower rates of diversification.

2 A supertree phylogeny and a trait database for the Formicidae

2.1 Abstract

Testing macroevolutionary hypotheses is essential to the understanding of the process of evolution. Studies addressing these problems require robust, complete phylogenies and comprehensive records of trait data. The ants are the most numerically diverse group of the eusocial Hymenoptera, and display a wide range of systems of social organisation. This positions them as an ideal taxon in which to test macroevolutionary hypotheses concerning the evolution of social traits, and the development of social complexity. Two obstacles to the goal of macroevolutionary studies using the ants as a focal taxon are the lack of a robust and comprehensive phylogeny, and the fact that available trait data is scattered throughout the literature. Here, I use supertree techniques to construct the largest species-level phylogeny to data and to construct a complete genus-level phylogeny for the Formicidae. In addition, I construct a database in which to store trait data, and populate it with data gathered from the wide primary literature of the ants. The supertrees and trait database are invaluable tools for the investigation of macroevolutionary hypotheses in the ants.

2.2 Introduction

2.2.1 The study of macroevolution

The study of macroevolution (the study of evolutionary change over long periods of time in large, or complete, clades) can answer questions concerning a range of historical processes such as the reconstruction of the trait values of extinct ancestors, change of traits over time, correlated evolution and patterns of diversification. Such analyses have been successfully applied to unravel macro-scale evolutionary and ecological patterns has been demonstrated in many clades, for example mammals (Stoner *et al.*, 2003; Jones *et al.*, 2005; Fritz *et al.*, 2009; Purvis *et al.*, 2011), spiny-rayed fish (Near *et al.*, 2012; Near *et al.*, 2013), grasses (Edwards & Smith, 2010) and hexapods (Davis *et al.*, 2010b). The study of macroevolutionary process is vital to the understanding of evolution in general, since these analyses allow the testing of hypotheses generated by evolutionary theory that are unobservable on human time scales. The study of macroevolution depends on the existence of robust phylogenies that describe the evolutionary relationships between the members of a clade of extant species. These phylogenies, in conjunction with information regarding the trait values of extant species, allow the testing of evolutionary hypotheses through the fitting of the evolutionary models that result from theoretical work.

2.2.2 Ant macroevolution

As well as being numerically diverse, the ants are extremely ecologically successful. They occur on every continent on Earth (except for Antarctica), fill a wide range of niches (including, but not limited to, detritivores, predators, and herbivores), and display a wide range of complexity in their social organisation and behaviours (Hölldobler & Wilson, 1990; Hölldobler & Wilson, 2009; Lach *et al.*, 2010). The diversity of the ants, both in terms of the number of species and the range of social behaviours, raises many macroevolutionary and comparative questions, such as; what was the first ant like; have social traits co-evolved; how do social traits evolve to become more complex; and what effects could sociality have on diversification? In addition, the study of the evolution of sociality and social complexity in eusocial insects may enhance our understanding of cooperative transitions in evolution in general (Maynard-Smith & Szathmary, 1995; Bourke, 2011). Limiting the power of researchers to answer these questions is the lack of a large-scale or complete phylogeny. Existing ant phylogenies do not offer the comprehensive taxonomic coverage desirable for macroevolutionary analysis. Phylogenies that focus on the relationships within a single genus or small genus-group may cover a large amount of the taxonomic diversity of that group, but exclude the wider diversity of the ants. Equally, phylogenies constructed to resolve deep relationships within the ants may include a small number of representative taxa from each subfamily, or other higher-level clade, but exclude a large amount of the variation within each of these clades. The taxonomic fragmentation of existing phylogenies means that no single phylogeny features a broad range of the extant diversity of the ants, making macroevolutionary inference difficult (but see Moreau and Bell (2013)). Finally, the history of investigation into the phylogenetic relationships within the ants leaves us with many morphological phylogenies, often examining the relationships within a genus or small clade, which have not been replaced by molecular analyses. As a result, much of the data that feeds our current understanding of ant phylogenetics is not present in public molecular databases. As a result, there is a need for a robust and comprehensive phylogeny for the ants.

2.2.3 The history of ant systematics and phylogenetics

Ants (Order Hymenoptera, Family Formicidae) are the most diverse eusocial insect lineage, comprising 12,986 species in 329 genera in 16 subfamilies (Table 2.2.1). Ants occur on all continents except Antarctica, where they dominate terrestrial ecosystems, both numerically and ecologically (Hölldobler & Wilson, 1990). Despite the position ants hold, quantitative phylogenetic analysis of the relationships within the family using modern only began just over two decades ago (Baroni Urbani *et al.*, 1992; Crozier, 2006; Ward, 2007).

The first explicitly quantitative study of the phylogenetic relationships within the Formicidae, based on morphology, was published in 1992 (Baroni Urbani *et al.*, 1992). This study established a fundamental split in the phylogeny of the ants between the Formicoids (the subfamilies Formicinae, Dolichoderinae, Aneuretinae, Myrmeciinae, Pseudomyrmecinae and Aneuratinae) and the Poneroids (subfamilies Ponerinae, Leptanillinae, and the army ants (Dorylinae, Ecitoninae, Aenictoninae, Cerapachyinae, Leptanilloidinae, and Aenictogitoninae). Subsequent phylogenetic analysis of ant morphology led to the seminal Bolton monograph (Bolton, 2003), where most notably, the subfamily Ponerinae was recognised as polyphyletic and split into morphologically coherent groups (Ponerinae, Amblyoponinae, Proceratiinae, Ectatomminae, Heteroponerinae, Paraponerinae, and Agroecomyrmecinae).

Since then, the rise of molecular phylogenetics has provided more information, sometimes contradictory, on the higher level relationships of the ants. In particular, the large formicoid clade was confirmed as monophyletic, as was Bolton's split (Bolton 2003) of the Ponerinae. The genus *Leptanilla* was thought to be sister to the subfamily Leptanilloidinae (Brady & Ward, 2005) (now part of the subfamily Dorylinae; Brady *et al*., 2014), until the publication of two molecular phylogenies in 2006 that suggested this genus was the sister group to the remainder of the ants (Brady *et al.*, 2006; Moreau *et al.*, 2006). Two years later, the discovery of the enigmatic, monotypic subfamily Martialinae (represented by the single species *Martialis heureka*) further advanced ant systematics (Rabeling *et al.*, 2008), albeit after a period of uncertainty (Kück *et al.*, 2011). The Martialinae were initially thought to be the sister group to all extant ants (Rabeling *et al.*, 2008), however more recent, and more conservative, analysis of the original data (Kück *et al.*, 2011) suggest that the Leptanillinae are the most basal extant lineage. This may be due to the fact that phylogenetic analyses under a Bayesian framework may overstate nodal support values (Suzuki *et al.*, 2002; Douady *et al.*, 2003; Erixon *et al.*, 2003). The position of the Leptanillinae was also supported in an analysis that combined the datasets of Brady *et al.* (2006) and Moreau *et al.* (2006) in a single analysis (Moreau & Bell, 2013).

Table 2.2.1 The number of genera and species within each subfamily of the Formicidae. Data from AntCat (Bolton 2012; http://www.antcat.org) (accessed July 2014), where incertae sedis are species that cannot be assigned to a subfamily.

Subfamily	**Number of genera**	**Number of species**
Agroecomyrmecinae	2	2
Amblyoponinae	13	125
Aneuretinae	1	1
Dolichoderinae	28	706
Dorylinae	18	678
Ectatomminae	4	265
Formicinae	51	3008
Heteroponerinae	3	24
Leptanillinae	6	58
Martialinae	1	1
Myrmeciinae	2	92
Myrmicinae	144	6502
Paraponerinae	1	1
Ponerinae	47	1154
Proceratiinae	3	137
Pseudomyrmecinae	3	230
incertae sedis	2	2
Total	329	12986

This growth in interest in the systematics and phylogeny of the ants since 1992 has resulted in 78 phylogenies of the ants being published (Web of Knowledge search, March 2012). The largest phylogeny to date, generated from the combined molecular datasets of two previously published phylogenies (Brady *et al.*, 2006; Moreau *et al.*, 2006) covers 295 species (Moreau & Bell, 2013). Although some of the higher-level relationships within the ants now seem clear, the four most recent large phylogenies (Brady *et al.*, 2006; Moreau *et al.*, 2006; Kück *et al.*, 2011; Moreau & Bell, 2013) show conflicting relationships (Figure 2.1). The structure of the most derived part of the tree, the clade incorporating Formicinae, Myrmicinae, Heteroponerinae and Ectatomminae, is different in each of the four most recent comprehensive (Figure 2.1, red box). The same can be said of the relationship between the Dolichoderinae and Aneuretinae (which are unambiguously allied) and the Myrmeciinae and Pseudomyrmecinae (which, when resolved, are also unambiguously allied), and the relationship of this clade to the remaining ants (Figure 2.1, blue box).

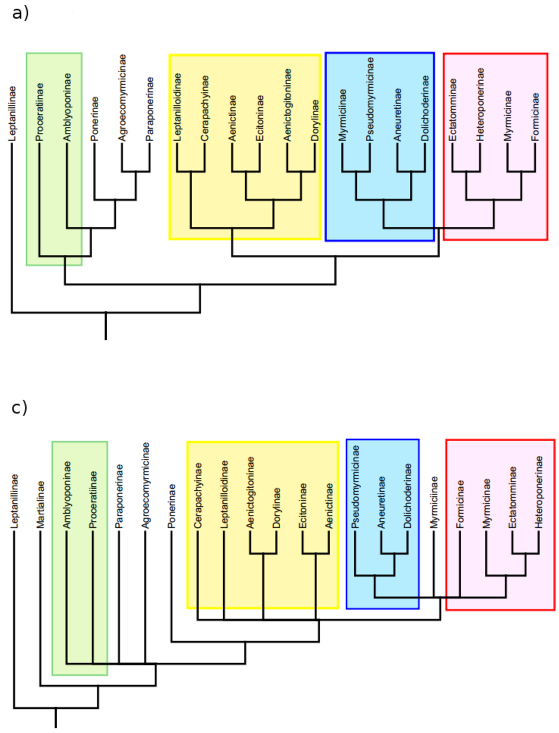


Figure 2.1 The four most recently published family-wide phylogenies of the ants, summarised to subfamily level. Coloured boxes indicate areas of topological conflict between each phylogeny. a) from Brady *et al.* (2006); b) from Moreau *et al.* (2006), c) from Kück *et al.* (2011) and d) from Moreau and Bell (2013).

There is similar disagreement in the relationships between the Dorylomorphs (Figure 2.1, yellow box) and between Amblyoponinae and Proceratiinae (Figure 2.1, green box). The trees of Brady *et al.* (2006) and Moreau *et al.* (2006) are produced using Bayesian methods, the tree of Kuck *et al.* (2011) is a reanalysis of Brady *et al.*'s (2006) data, with the inclusion of data for *Martialis heureka* (Rabeling *et al.*, 2008), using a more conservative maximum likelihood method and the tree of Moreau and Bell (2013) is produced from the combined datasets of Brady *et al.* (including *Martialis heureka* (Rabeling *et al.*, 2008)) and Moreau *et al.* (2006) analysed with maximum likelihood methods. This shows that the subfamily level relationships within the Formicidae, whilst broadly identified, are difficult to resolve, and vary depending on the quantity of data and mode of analysis.

2.2.4 Building large or complete phylogenies

There are many methods available for constructing complete, or very large, phylogenies from both primary data, and from secondary data. These methods vary in their reliance on certain data types, level of robustness/conservativeness and sensitivity to missing data. The two best-established methods are supermatrix (Kluge, 1989) and supertree (Bininda-Emonds, 2004). More recently the mega-phylogeny approach (Smith *et al.*, 2009) and PASTIS have emerged (Jetz *et al.*, 2012; Thomas *et al.*, 2013). Here I will outline the advantages and disadvantages of each approach, and assess how appropriate they are for the problem of constructing a tree for the Formicidae.

(a) Supermatrix methods

The supermatrix approach combines primary molecular data from many different genes into a single 'supermatrix' (Kluge, 1989; de Queiroz & Gatesy, 2007). This approach relies solely on the available molecular data, and the resulting data matrix is characterised by its high level of missing data (Sanderson *et al.*, 1998; Bininda-Emonds, 2004) (i.e., any given gene is typically missing data for many species). Since such a data matrix is constructed from many different genes, applying a single model of nucleotide evolution over the whole matrix can be problematic. For this reason a super matrix is best analysed with a method which allows for a different model of nucleotide evolution for each gene (e.g., MrBayes; Ronquist, 2004, , or BEAST; Drummond *et al*., 2012). Branch lengths can be estimated from the primary data by fitting molecular clock models, and then calibrated using fossil or geological calibration points. Supermatrices are widely used to reconstruct phylogenies when molecular data is available (e.g., primates; Springer *et al*., 2012, big cats; Davis *et al*., 2010, or fungi; Gaya *et al*., 2012), and have been used to resolve phylogenies constructed from genomic data (phylogenomics) with success (e.g., Fernández *et al.* (2014)). This method attempts to produce and analyse the data matrix with as many taxa as possible from a database of sequences. The reliance of this method on purely molecular data presents a problem for the present problem, since only 9.7% of ant species are represented in public databases, and furthermore many of these specimens are not identified to species level.

(b) Supertree methods

Supertree methods make use of the topologies of published trees generated from primary character data as opposed to using character data directly (Sanderson *et al.*, 1998; Bininda-Emonds, 2004). These data are combined with a hierarchical reference taxonomy, which acts as a backbone for the analysis, to create an undated phylogeny more comprehensive than any of the individual source trees. Branch lengths can then be inferred for this tree by calibrating a molecular clock derived from available sequence data with fossil calibration points on the tree(Bininda-Emonds, 2004; Nyakatura & Bininda-Emonds, 2012). Phylogenetic supertrees are controversial (Gatesy & Springer, 2004) due to the detachment of the supertree from primary character data, problems with assessing the independence of source phylogenies, difficulties in weighting input data (such that more well supported nodes in source trees carry more weight in the final analysis than less well supported nodes) and the rare tendency for supertree analyses to generate novel clades (Bininda-Emonds, 2003; Gatesy & Springer, 2004). Due to these problems supertree methods are often seen as a way to summarise existing phylogenetic information into a single large phylogeny rather than as a method to generate new phylogenetic hypotheses (Gatesy & Springer, 2004). There are a number of ways to analyse the data matrix of topology-derived data, the most widely accepted of which is matrix representation with parsimony (MRP). This method returns supertrees with as well as supported as those derived from competing methods under real life (i.e. non-simulation) conditions (Gaubert *et al.*, 2009; Davis *et al.*, 2010b; Nguyen *et al.*, 2012). More recent developments in protocols for the creation of phylogenetic supertrees allow for the inclusion of primary molecular data, have reduced the problem of assessing the independence of source phylogenies, and feature improved protocols for weighting input data (e.g., Nyakatura and Bininda-Emonds, 2010).

(c) Megaphylogeny method

The megaphylogeny method is a modification of the supermatrix approach designed to produce less data-poor data matrices by restricting the analysis to only the most informative regions of each gene, and using hierarchical taxonomic information to produce within-clade alignments rather than attempting to align long sequences across a large number of potentially divergent clades. This method differs from the supermatrix approach by producing denser matrices through the specification of regions of interest (Smith *et al.*, 2009). This not only reduces the problem of how to handle missing data, but also decreases computation time (Smith *et al.*, 2009). The downside of this method is the reliance solely on molecular data, and specifically the necessity of at least one gene that covers most of the target species (Smith *et al.*, 2009). The megaphylogeny method was used to analyse the phylogeny of the green plants derived from a single gene for 13,533 taxa, and a 4954-tipped phylogeny of the Asterales derived from 6 genes (Smith *et al.*, 2009).

(d) PASTIS method

PASTIS is functionally similar to both the supermatrix and megaphylogeny approach, in that the bulk of its data is derived from molecular information of identified species. When species are missing from the molecular dataset they are assigned to genus groups based on taxonomy, morphology and/or behaviour. This method produced a phylogeny of all 9,993 extant bird species (Jetz *et al.*, 2012), which although widely used (175 citations as of August 2014, Google Scholar search), has been criticised due to the fact that approximately one third of the species present on the tree were constrained in their placement by existing taxonomic paradigms (Ricklefs & Pagel, 2012). In addition, this method cannot incorporate data from sources other than primary database-derived molecular data.

2.2.5 Trait data

The second requisite to the study of macroevolutionary questions concerning trait evolution is a database of trait values for the trait or traits of interest. The importance of a collated database of trait data is such that a number of databases have been constructed and made publicly accessible, for example the PanTHERIA database contains life-history data for most extant mammals (Jones *et al.*, 2009), and the TRY database brings together diverse and specialist plant trait databases from across the literature into a single resource (Kattge *et al.*, 2011a). The literature is rich in studies describing the behaviour, ecology, and social structure of ant species, however these data are scattered between individual primary publications. Extracting these data from the literature and storing them in a database is a necessary and valuable task.

This chapter attempts to address two obstacles to macroevolutionary analysis in the ants: the lack of a robust and complete/large scale phylogeny and the lack of collated trait data. In this chapter I construct of the largest possible dated species level phylogeny, for the ants. In order to account for the fact that due to the very high diversity of the ants, and the relative lack of phylogenetic information for much of this diversity I also construct a complete genus-level phylogeny to provide a phylogenetic hypothesis for the entire family. To accompany these phylogenetic tools I also construct a trait database, and populate it with trait data gathered from the literature.

2.3 Methods

2.3.1 Phylogenetic reconstruction

Of the four methods available for the construction of very large or complete phylogenies, two of them (supermatrix and mega-phylogeny) rely entirely on molecular data. When it comes to the ants, 9.7% of all extant species have sequence data for at least one gene in public databases (GenBank; Benson *et al*., 2010, accessed March 2012). Since the goal of this study is to produce a phylogeny with as much taxonomic coverage as possible to facilitate comparative analysis, this precludes the use of supermatrix and mega-phylogeny approaches. Although the PASTIS method makes up for absent molecular data by using taxonomy, a criticism of this method is that these species are placed on the phylogeny based on taxonomy, and in the case of the ants this would mean 90.3% of a phylogeny generated through the use of PASTIS would be no more informative or useful than the current taxonomy. The supertree method, however, provides a tool that enables me to draw together the taxonomically fragmented phylogenies previously published, as well as the molecular data from public databases, to produce a summary of the state of understanding of ant phylogenetics. Recent improvements in the supertree method have ameliorated (but not eliminated) many of the problems for which supertree methods were initially criticised (Gatesy & Springer, 2004), and so I followed the most up-to-date of these protocols, that of Nyakatura and Bininda-Emonds (2012).

2.3.1.1 Source tree collection

I searched online databases for phylogenetic trees of ants, morphological, molecular or otherwise, from 1992 onwards. I selected 1992 as the starting date for the search as this was when Baroni Urbani and colleagues published the first quantitative phylogeny for the ants (Baroni Urbani *et al.*, 1992). I searched Thomson-Reuter's Web of Knowledge, Google Scholar and Scopus using the terms phylogeny* or taxonom* or systemat* or cladisti* or clado* or classify* or morphology*. These terms were all used in combination with Formicidae or any of the ant subfamilies, following the Bolton (2012) taxonomy. The abstracts of all resulting hits were read to initially discard papers that would contain no phylogenetic information (e.g. myrmecological inventories) and the remaining papers were downloaded and stored locally in an EndNote database for further inspection.

Papers were excluded that were published prior to 1992 (before the onset of robust phylogenetic construction for the ants); that were unclear or did not provide their data source; that featured trees that were built from existing data with no additions; and that featured trees with no formal analysis (Bininda-Emonds, 2004; Nyakatura & Bininda-Emonds, 2012). These exclusions were in order to make sure that every source contributing data to the final supertree contained reliable and robust phylogenetic estimates.

Once source trees were downloaded and uninformative trees were rejected the remaining trees were assessed for non-independence. In the instance of two trees having identical taxon sets, they were considered independent if they had non-identical data sets. Trees constructed from data sets containing multiple genes or morphological characters were considered independent of trees constructed from a subset of those characters (Nyakatura & Bininda-Emonds, 2012). In the case of non-independent trees, each of these trees was included in the analyses and down-weighted accordingly at a later stage of the analysis. The topology of these trees was then reproduced in a NEXUS file (Maddison *et al.*, 1997) ready for encoding into a data matrix.

In order to incorporate as much data as possible, including available sequence data, I collected data from GenBank (Benson *et al.*, 2010) for all available species, retaining the species names as they were recorded in GenBank for subsequent synonomysation and constructed single-gene trees for each of the genes *cytochrome oxidase I* (COI), *cytochrome oxidase II* (COII), *elongation factor 1-α F1* and *F2* (EF1aF1 and EF1aF2), *wingless* (wg) and *long-wavelength rhodopsin* (lwrh). I selected these genes due to the fact they are widely used in existing phylogenetic analyses (e.g. Brady *et al*., 2006; Moreau *et al*., 2006; Moreau and Bell 2013), and as such cover a wide range of species. Sequences were aligned using CLUSTAL Omega (Sievers *et al.*, 2011), MUSCLE (Edgar, 2004), Kalign (Lassmann & Sonnhammer, 2005) and MAFFT (Katoh *et al.*, 2002), and then the alignments were checked using MUMSA (Lassmann & Sonnhammer, 2006). MUMSA compares multiple alignments and calculates a multiple overlap score (MOS) for each alignment and an average overlap score (AOS) for the entire alignment set. A higher AOS score indicates a better alignment. When scores were low the alignments were checked by eye, and if necessary split into smaller units to allow for better alignment. This resulted in *COI* being split into three pieces, *EF1aF1* into two pieces and *lwrh* into two pieces. When the AOS for each alignment was over 95, the alignment with the highest MOS was taken as the best alignment. The alignments were then cleaned up using the Perl script seqCleaner.pl (Bininda-Emonds, 2012c), which ensures that all sequences overlap with each other by at least 100 base pairs and automatically removes any ragged ends of the alignments. These alignments were then used to construct a tree for each gene or gene section using RaxML (Stamatakis, 2006) implemented on the XSEDE server of the CiPRES phylogenetic gateway (Miller *et al.*, 2010). The optimal model of nucleotide substitution for each gene was determined using jModelTEST (Darriba *et al.*, 2012).

The Bolton (2012) taxonomy was used to create a hierarchical reference taxonomy tree to act as a backbone for the analysis. This was made by grouping subfamilies into a single polytomy, genera within subfamilies into a polytomy for each subfamily, and species within genera into a polytomy for each genus. This reference taxonomy tree is, by default, badly resolved. This bad resolution will bleed across into the final supertree. As an example, in a situation where a genus has 5 species, but the dataset only confers information about the phylogenetic relationships of 3 of them the remaining 2 species can cluster equally well with any of the other three. This means the consensus of the whole genus is an unresolved polytomy. The more species present in the taxonomy and not the dataset, the worse this problem becomes. In the present situation there are 12,986 species in the taxonomy and 1656 in the dataset, which means that it is highly likely that the majority of clades will emerge as unresolved polytomies. For this reason the taxonomic tree was pruned so that the species on it matched exactly the species in the dataset, allowing it to function as a backbone tree to guide the analysis without obfuscating the phylogenetic signal present in the dataset.

2.3.1.2 Constructing the data matrix

The literature-derived, molecular and taxonomic source trees were coded into a single data matrix using Mesquite (Maddison & Maddison, 2011) and the Perl script SuperMRP.pl (Bininda-Emonds, 2012e). The final matrix consisted of one row per species, and one column per node from a source phylogeny. When a species is descended from a node on a source tree, a "1" is recorded in the column for that node, and if the species is not descended from that node, but present on the source tree a "0" is recorded (Bininda-Emonds, 2004). If a species is not present on a source tree a "?" is recorded (Bininda-Emonds, 2004). For the species-level tree the names of each taxonomic unit (species) in this matrix were synonymised according to the most up-to-date taxonomy of the ants (Bolton, 2012). If only a genus name was given in a source and the text gave no indication of which species the data was sampled from, the type-species of that genus was used. If the genus was suspected to be non-monophyletic (i.e. a previously published phylogeny had identified it as paraphyletic) then the species was excluded from the analysis. If a species was identified with a cf., e.g. *Formica cf. moki*, it was considered to be the named species (i.e., in this case, *Formica moki*). This decision was made for because it was desirable to maximise the taxonomic coverage of the tree. Species designated nr. or aff. were dropped, as these designations refer to a specimen that appears similar to a described species, but that the author is quite sure is different (Bengtson, 1988). Species that were not named but assigned a location code (e.g. *Myrmica sp.* MADAGASCAR) were excluded, since assigning the type species would not be appropriate if the type species does not occur in the location specified, and it is not clear how best to assign a species that does occur in that locality.

For the genus-level tree I used the same taxonomy (Bolton, 2012) to synonymise the source trees (literature-derived, molecular and taxonomic) to genus level. An added complication of synonymisation for a genus-level tree is the presence of 15 paraphyletic genera (table 2.3.2). Supertree methods cannot preserve paraphyly in a taxon, and instead will place all pieces of the taxon together in the final tree. This means information will be lost in the final tree. In order to circumvent this problem I retained the species names of the members of each paraphyletic genus in the source trees. In this way the divergent pieces of each paraphyletic genus are recognised as separate, and grouped accordingly in the final analysis. After a supertree is obtained, each of these pieces can be collapsed to a single tip, and the paraphyly of the 15 paraphyletic genera is preserved in the final tree. This synonymisation process resulted in a series of trees with species names replaced by genus names, often including monophyletic clades with each tip bearing the same genus name. I reduced each of these clades to a single tip, resulting in a data matrix describing genus-level relationships within the ants. Beyond this point the genus-level matrix was treated in exactly the same way as the species-level one.

Table 2.3.1 A list of known paraphyletic genera within the ants.

Genus	Reference
Acromyrmex	Sumner *et al*., 2004; Schultz & Brady, 2008
Amblyopone	Saux *et al*., 2004
Aphaenogaster	Brady *et al.,* 2006
Camponotus	Johnson *et al*., 2003
Cerapachys	Moreau *et al.,* 2006
Cyphomyrmex	Schultz & Brady 2008
Leptothorax	Baur *et al.,* 1996
Messor	Brady et al., 2006
Mycetophylax	Schultz & Meier, 1995; Schultz & Brady, 2008
Mycetosoritis	Schultz & Brady, 2008
Myrmicocrypta	Schultz & Meier, 1995
Odontomachus	Ouellette *et al.,* 2006
Pachycondyla	Schmidt, 2013
Prenolepis	La Polla *et al.,* 2010
Trachymyrmex	Schultz & Meier, 1995; Brandão & Mayhé-Nunes, 2007; Schultz & Brady 2008

2.3.1.3 Weighting the data matrix

In order to ensure that non-independent trees were not over-represented, and that trees derived from different data sources were equally represented, characters in the final matrix were weighted in a three step process in the final supertree analysis. First, all nodes coming from the RaxML generated gene-trees were weighted according to their bootstrap support values, and all nodes without this data (i.e. nodes coming from literature-derived source trees and taxonomy) were weighted according to the mean bootstrap score over all gene-trees (Nyakatura & Bininda-Emonds, 2012). Secondly, nodes from trees generated with equivalent data-types were down-weighted so that each data-type was weighted equally in the final analysis. Finally, non-independent trees (e.g. the different permutations of trees with paraphyletic taxa in them, or equally likely topologies presented in the same source) were down-weighted so that the weight per-tree for the appropriate data partition was shared equally between each non-independent tree. For example, in a situation where there are 10 morphological trees, and the mean bootstrap value is 50 each node from each morphological tree receives a weighting of 5. If one of these trees then has 5 non-independent permutations, each of those permutations is then given the weight of 1. This weighting scheme is in accordance with the weighting scheme used by Nyakatura and Bininda-Emonds (2012). This process was applied to both the species-level and genus-level matrices.

2.3.1.4 Phylogenetic estimation

Tree searches on the final weighted data matrix were performed using PAUP*Swofford 2010). Searches were performed using the parsimony ratchet (Nixon, 1999). This method was used as it samples from more 'tree islands' (groups of equally parsimonious trees), and is considerably faster, than traditional parsimony methods (Nixon, 1999). For both the species-level and genus-level matrices, each iteration of the ratchet performed 50 independent batches of 200 reweighting iterations. Each of these batches stored each tree produced, resulting in a pool of 10,000 trees which were fed into a heuristic search using a tree bisection and reconnection search algorithm. Each iteration of this process could produce a maximum of 20,000 equally parsimonious trees, and so the resultant supertree was taken as the consensus tree of all these equally parsimonious trees from 50 iterations of this process. This entire process was directed using the Perl script perlRat.pl (Bininda-Emonds, 2012a).

2.3.1.5 Calculating nodal support values

Supertrees cannot utilise the familiar nodal support values of molecular or morphological phylogenies due to the disparate nature of the data that goes into the analysis. Instead the relative quantitative support (rQS) index is used (Bininda-Emonds, 2003; Price *et al.*, 2005). This algorithm takes the consensus supertree topology, and one of the source trees, and prunes the supertree to confer upon it the exact same taxon set as the source tree. It then checks each node to see if it is in agreement or conflict with the source tree, and scores the node a 1 for agreement and a -1 for conflict. This process is repeated for each source tree, and then each node is given a score corresponding to the mean of all of the scores it received throughout the process. In this way each node receives a score between 1 (indicating that the existence of that node is agreed upon in every source tree in which it may appear) and -1 (indicating complete conflict between the supertree and all source trees in which that node may appear). A score of 0 indicates equivocal support for the node. Positive node values indicate general support for the node, and a positive value for the mean rQS score of the entire supertree indicates positive support for the whole tree (Bininda-Emonds, 2003; Price *et al.*, 2005). This algorithm was applied to both the species-level and genus-level supertrees.

2.3.1.6 Dating the tree

Branch lengths enable inferences concerning correlated evolution and diversification patterns to be more accurate. For this reason it is important that the resultant supertrees are time calibrated. In order to confer branch lengths upon the supertree I fitted each of the ten sets of molecular data derived from GenBank and used in the data matrix to the topology of the supertree under the optimal model of evolution as determined by the software jModelTest2 (Darriba *et al.*, 2012). This generates relative branch lengths for the branches on the supertree that are described by the species in each set of molecular data. Once these relative branch lengths are known they can be calibrated to points of known age in the tree derived from fossil information to calculate relative absolute branch lengths. This process was implemented individually for each gene, using either the median age of the genetic data and fossil data, or the youngest fossil estimate should it be younger than the genetic data indicated Nyakatura and Bininda-Emonds (2012). The whole process was directed by the Perl script relDate.pl v2.3 (Bininda-Emonds, 2012d). Ages for nodes missing age values from the previous calculations were calculated according to a pure-birth model based on the relative sizes of subtending clades (Purvis, 1995). 42 fossil calibration points were used (Appendix 1, table A1.1), chosen due to their unambiguous membership of extant clades and robust age estimates. This process was applied to both the species- and genus-level supertrees.

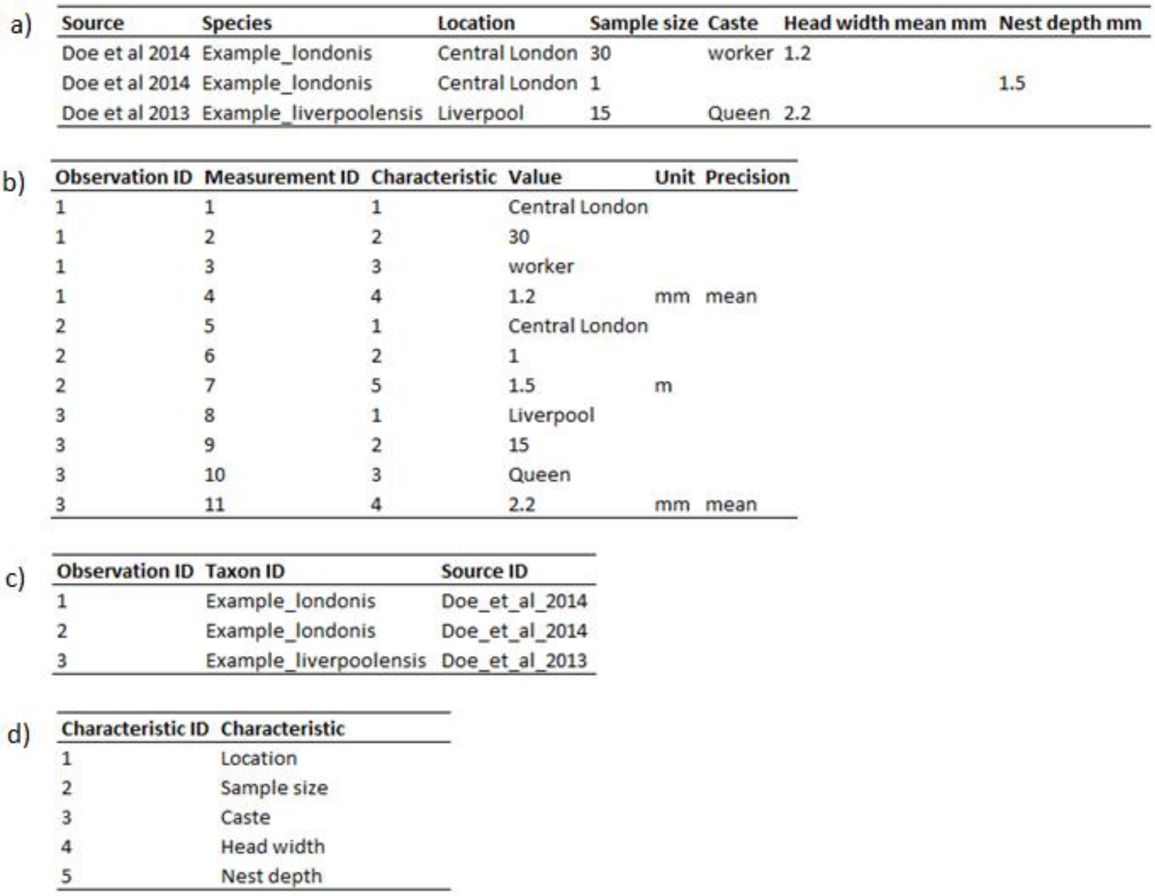
2.3.2 Trait database

2.3.2.1 Database design

Because no cross-species comprehensive databases existed for ant traits at the time of writing, I constructed and populated my own. The database needed to be capable of containing varied data about myriad different traits, and also have the flexibility to incorporate the same data but reported in different formats. For example, polyandry might be presented as the number of mates that sire offspring, the number of males a female has mated with, the number of males that own sperm stored in the spermatheca or the proportion of eggs each male has sired. Although these are all measures of polyandry, the units are very different. For this reason, I decided to modify the design of the TRY database (Kattge *et al.*, 2011a), as it allows for more or less infinite flexibility in the recording of traits. The trade-off is that the database is less intuitive and straight forward to populate than other popular database designs, e.g. YouTHERIA (Jones *et al.*, 2009).

The database works by separating the data point and the core ancillary information (the name of the trait in question, the unit, the precision and the value) into measurements, and then grouping measurements from the same entity, in the same place, at the same time, into observations. For example, the observation of the head widths of 30 worker ants from a colony might consist of 5 measurements: 1. the species being studied; 2; the location of the colony being studied; 3. the size of the sample of ants; 4. the caste of the sample of ants; and 5. the mean head width in mm (Figure 2.2). If in this same example, the depth of the nest was measured this would constitute a second observation (Figure 2.2a). Measurements and core ancillary information (units, and precision) are stored in one table and grouped by observation

(Figure 2.2b), which relates to a second table detailing the data concerning the observation (Figure 2.2c). A final table stores the name of the traits or characteristics linked to each observation (Figure 2.2d).



a)

Source	Species	Location	Sample size	Caste	Head width mean mm	Nest depth mm
Doe et al 2014	Example_londonis	Central London	30	worker	1.2	
Doe et al 2014	Example_londonis	Central London	1			1.5
Doe et al 2013	Example_liverpoolensis	Liverpool	15	Queen	2.2	

b)

Observation ID	Measurement ID	Characteristic	Value	Unit	Precision
1	1	1	Central London		
1	2	2	30		
1	3	3	worker		
1	4	4	1.2	mm	mean
2	5	1	Central London		
2	6	2	1		
2	7	5	1.5	m	
3	8	1	Liverpool		
3	9	2	15		
3	10	3	Queen		
3	11	4	2.2	mm	mean

c)

Observation ID	Taxon ID	Source ID
1	Example_londonis	Doe_et_al_2014
2	Example_londonis	Doe_et_al_2014
3	Example_liverpoolensis	Doe_et_al_2013

d)

Characteristic ID	Characteristic
1	Location
2	Sample size
3	Caste
4	Head width
5	Nest depth

Figure 2.2 An illustration of organisation of the trait database. a) Data are collected from the literature in spreadsheets, with each row describing an observation (data from a single object, at a single point in time and space) and each column describing a measurement of that observation, including units and precision where relevant. These data are stored in the database between three tables, b) the table of measurements lists each measurement along with relevant units and precision and groups them by observation ID. b) the observation table contains the data that concerns each unique observation; the species and the source of the data. c) contains the characteristics that correspond to the characteristic ID in table d).

The database was populated with data from the literature. Google Scholar, Web of Knowledge and Scopus were searched by genus names, one genus at a time. The resulting hits were scanned through and irrelevant papers rejected immediately. Remaining papers were downloaded, and the abstracts scanned through. Papers that clearly would contain no data were discarded and papers that contained only large-grain location data (e.g. regional checklists) were put to one side for later use if required (e.g. if a particular genus had scant locational data and these large-grain studies would help). The remaining papers were read through and all data were recorded as given in the paper. All data were labelled as primary or secondary depending on their provenance. Data were recorded into spreadsheets in Microsoft Excel 2010, with each row representing an observation, and each column measurements within that observation. Character names were identified in the headers of each column, and followed by the units and precision where relevant. An R script was used to take the data supplied in the spread sheet and transform it into a format ready for upload into the database. The database was constructed and stored in Microsoft Access 2010.

2.3.2.2 Data collection

Data were recorded for colony size, head-width, the presence or absence of discrete worker castes, polygyny and polyandry. Colony size was recorded as number of workers at maturity, and if a source made it clear that a measured colony was still developing, the measurement was not recorded. When individual measurements from a sample were presented these were favoured, and if the mean of a sample was presented I recorded the mean, and all other descriptive statistics for the sample presented (e.g. median, standard deviation etc.). Head-width was recorded in mm, and the caste of the individual or individuals measured was also recorded. Discrete worker castes were recorded as present or absent according to any description in the source. When a number of discrete castes was reported this was also recorded. Polygyny was recorded as the number of dealate (wingless) queens found in a colony, unless the source presented a measure of functional polygyny (e.g. what proportion of queens laid eggs, the effective number of queens measured from the relatedness of workers), in which case the more accurate functional polygyny was recorded. In the case of a source that cites a species as polygynous without presenting quantitative data, that datum was not recorded. Polyandry was recorded as the number of mates per queen, unless a more accurate measure of functional polyandry was presented (e.g. effective mating frequency measured from genotyping eggs/workers, number of mates measured from spermatheca contents rather than mating observations) in which case the more accurate measure was recorded. In the case of a source that cited a species as polyandrous without presenting quantitative data, that datum was ignored. For all traits sample sizes were recorded where applicable, and in cases where sample size was not reported or was otherwise unclear, it was assumed to be one.

2.3.2.3 Measures of central tendency and division of labour

I calculated per-species mean values for colony size, worker head-width, queen head-width, polygyny and polyandry by averaging the mean value of each observation weighted by the sample size of the observation. I used the following equation:

$$\bar{x}\ mean\ trait\ value = \frac{\sum(x_s n_s)}{\sum n_s}$$

where x_s is the mean of the observation, n_s is the observation sample size, and Σn_s is the sum of all sample sizes of the observations contributing to the per-species mean for each trait. When a species occurred in a unicolonial form I did not include estimates of the size of the 'supercolony', and instead used only estimates for non-unicolonial populations or of the cryptic, discrete single-colony sub-populations of the unicolony if this data was reported. I excluded social parasites from colony size calculations, and in the case of slave-making species I took the number of slave-making workers as the colony size rather than the number of slaves. Species with physical worker castes may express those castes at different relative frequencies, with large soldier castes often being rare in a population (Oster & Wilson, 1978). When this occurs, the mean worker head-width, as calculated here, may be overestimated. Since reliable data on the relative frequency of caste expression is absent from the literature for the majority of polymorphic species, this cannot currently be corrected for. However, estimating mean worker head-width in this way still represents the mean of possible head-widths for a species, and is calculated in the same way for each species, I believe this will not make a significant difference to the main conclusions of this thesis. Socially parasitic species were excluded from these calculations due to either the absence of a worker caste.

In order to calculate a second measure of non-reproductive division of labour (in addition to the presence of physical worker castes), I calculated the coefficient of variation in worker head-width. This measure of non-reproductive division of labour is also able to quantify non-reproductive division of labour in species that have a size-based polyethism with a continuous distribution of worker sizes (Beshers & Traniello, 1996; Arnan *et al.*, 2011). Head-width correlates closely with body size in ants (Hölldobler & Wilson, 1990; Kaspari, 1993; Vainio *et al.*, 2004; Weiser & Kaspari, 2006) and coefficient of variation in measures of body size have been used previously to quantify variation in worker size (Fjerdingstad & Crozier, 2006). I calculated the coefficient of variation in worker head-width using the following formula:

$$Worker\ size\ variation = 100\left(\frac{\sigma\ worker\ head\ width}{\bar{x}\ worker\ head\ width}\right)$$

where $\bar{x}$ = mean, σ = standard deviation. Standard deviation of worker head width was calculated as the standard deviation of all mean worker head width observations contributing to each per-species value, and $\bar{x}$ worker head width was calculated by averaging the mean value from each observation weighted by its sample size.

In order to quantify reproductive division of labour I calculated the percentage difference between the species-level weighted mean queen head-widths and the species-level weighted mean worker head-widths using the following formula:

$$Queen - worker\ dimorphism = 100\left(\frac{2(\bar{x}\ queen\ head\ width - \ \bar{x}\ worker\ head\ width)}{\bar{x}\ queen\ head\ width + \ \bar{x}\ worker\ head\ width}\right)$$

If a source reported the presence of discrete worker castes I defined the species as positive for discrete worker castes. I was not able to use the number of physical castes since for many species the data regarding physical worker castes was descriptive, and maximising the number of species in the dataset was desirable.

For polygyny I calculated the mean number of queens per species from the data. Due to the divergent methods by which polygyny is estimated I could not accurately weight the data from the sample sizes reported by the sources. For polyandry I calculated the mean number of mates per queen per species from the data. As for polygyny, the divergent and incompatible ways in which polyandry was measured meant that I could not use the sample sizes of the sources to weight the data. For both polygyny and polyandry I elected to define a species as monogynous or polygynous, and as either monandrous or polyandrous. I made this decision in order to make use of the data from studies that report evidence of multiple queens or multiple matings (for example, relatedness data) without reporting an estimate of queen number or mating frequency, and data from studies that report a minimum number of queens or of matings. This enabled me to maximise the potential number of species present in an analysis, at the cost of increasing the coarseness of the data. I defined a species as polygynous if the mean number of queens for the species was higher than one. I defined a species as polyandrous if the mean number of mates per queens was higher than one. Polygyny and polyandry are recorded and measured in many different, and often incompatible, ways (Jaffé, 2014), and this approach allows for the use of the largest amount of data for the largest amount of species.

Genus-level data for continuous traits were calculated by taking the mean of each trait for each species within a genus. For the discrete traits a genus was defined as having evolved discrete worker castes, polygyny and/or polyandry if at least one species within that genus was positive for the trait in question.

2.3.2.4 Data checking

In order to ensure that the raw species-level data were not influenced by sample size I fitted a linear model to each trait using the trait value as the response variable, and using sample size as the predictor variable. I also included study effort (measured as the number of hits from a Web of Knowledge search for the genus name) as a predictor variable in order to control for fact that species with larger colonies or more polymorphic workers may be more intensively studied. I controlled for phylogeny in these models, and used the phylogenetic generalised least squares (PGLS) model as implemented in the R package ape (Paradis *et al.*, 2004).

Due to the nature of the data on discrete worker castes sample size is not applicable, and so it was not possible to assess the possible bias of sample size. Due to the varied ways that polygyny and polyandry data are reported, these variables are recorded as binary variables in the database. Also due to the varied and incompatible ways of measuring these traits estimating the sample sizes of the data contributing to the polygyny/polyandry status for each species is problematic. For this reason I used the number of sources contributing to each species-level estimate of gyny status or mating frequency as a measure of sample size to assess bias. To assess the possibility of bias due to sample sizes in these data, for each trait, I fitted a logistic regression model using presence/absence of the trait at species level as the response variable and the total number of sources contributing to that trait as the predictor variable. I also controlled for study effort in these models. I implemented these models using the R package mcmcGLMM (Hadfield, 2010), which uses MCMC to sample from the posterior distribution of parameter estimates whilst allowing me to control for phylogeny. For each model I used uninformative priors with a low degree of belief for all parameters. I ran each model for 80,000,000 generations, sampling every 16,000 generations to give a pre-burnin posterior sample size of 5000 samples, the first 20% of which were discarded as burnin leaving a post-burnin posterior sample size of 4000. I ensured the convergence of each model by visually inspecting the trace of the MCMC chain or each parameter, checking for the absence of autocorrelation and ensuring the effective sample size for each parameter was over 200.

2.4 Results

2.4.1 Phylogenetic reconstruction

2.4.1.1 Supertree – Data availability

The final supertree contained 1656 terminal taxa (Figure 2.3). Although this represents only 12.8% of extant ant species, it is the biggest tree of the Formicidae to date by a factor of over 5. The low percentage of present species in the dataset precluded the construction of a full species-level supertree, and meant I had to reduce the source taxonomy to only the species present in the dataset. Including the 10 gene trees the final MRP matrix had data from 78 trees from 67 sources (Appendix 1, table A1.2).

2.4.1.2 Supertree resolution and support.

a) Species-level supertree

The final consensus supertree is 100% resolved (Figure 2.3). Typically supertrees have two sources of uncertainty that contribute to lack of resolution – species that are present only in the source taxonomy and conflict between source trees (Bininda-Emonds, 2004; Nyakatura & Bininda-Emonds, 2012). Since I reduced the source taxonomy to only species for which I had other sources of data that eliminates the taxonomy as a source of uncertainty from this supertree. The fact that the resultant tree was 100% resolved indicates that three were no hard mismatches (i.e. total contradictions) between input phylogenies. This is reflected by the rQS scores for the supertree. The mean rQS index value for the entire tree was 0.023 (Appendix 1, table A1.3, figure A1.1). That this number is positive shows that the topology of the supertree is in reasonable agreement with the 68 literature-derived source trees and 10 gene trees, and most nodes were supported by more trees than they were contradicted by. No nodes had an rQS value of 1, indicating the absence of nodes that were unequivocal in their position, and no nodes had an rQS value of -1, indicating the absence of any nodes that were were completely unsupported (i.e. a hard mismatch).

Figure 2.3 A species-level supertree of 1,656 species of ant (12.6% of extant species). Subfamily divisions are marked around the outside. Internal red circles mark 50 million year internals.

b) Genus-level supertree

The final consensus genus-level supertree is 82.5% resolved (Figure 2.4). The mean rQS score of the genus-level tree was 0.02 (Appendix 1, table A1.4). This is a positive number, indicating good support for the topology of this supertree. There were no nodes with an rQS score of -1, which indicates complete conflict in the source trees, and two nodes had an rQS score of 1, indicating complete agreement between the source trees and the final supertree (Appendix 1, table A1.4, figure A1.2).

Figure 2.4 A complete genus-level supertree of the ants. Subfamily divisions are marked around the outside. Internal red circles mark 50 million year intervals.

2.4.1.3 Subfamily-level relationships

a) Species-level supertree

At the subfamily level in the species-level tree there were some relationships that have not been shown on previous estimates of the subfamily level relationships within the Formicidae, but all occur in regions of the tree where relationships have been known to be fluid (figure 2.1). Furthermore, none of these relationships were novel, either in the sense that they are contradicted by all source trees (rQS = -1), or the sense that they were supported by no source trees.

In the species-level supertree the sister group to the ants emerged as *Martialis heureka*, rather than a member of the Leptanillinae as more recent trees might have suggested (Moreau & Bell, 2013). This is not a wholly new relationship, however, as various previously published phylogenies have presented both hypotheses (Rabeling *et al.*, 2008; Kück *et al.*, 2011; Moreau & Bell, 2013; Schmidt, 2013).

The most significant deviation from previous work is the absence of the Heteroponerinae from the relationship with the Myrmicinae and Formicinae. In all major previous work the Ectatomminae has been sister to the Heteroponerinae (Brady *et al.*, 2006; Moreau *et al.*, 2006; Kück *et al.*, 2011; Moreau & Bell, 2013) and then that group was either sister to the Formicinae and Myrmicinae (Brady *et al.*, 2006; Moreau *et al.*, 2006), or sister to the Myrmicinae (Kück *et al.*, 2011; Moreau & Bell, 2013), showing uncertainty in its placement (Figure 2.1). In the present supertree we find the Ectatomminae as sister to the Heteroponerinae, and this group to be sister to a larger clade containing the Myrmicinae, Formicinae, Dolichoderinae, Aneuretinae, Myrmeciinae and Pseudomyrmecinae. The Ectatomminae and Heteroponerinae are grouped together, conforming to previous work (Brady *et al.*, 2006; Moreau *et al.*, 2006; Kück *et al.*, 2011; Moreau & Bell, 2013). The placement of this clade, however, differs from previous work. It has been presented as sister to the Formicinae + Myrmicinae (Brady *et al.*, 2006; Moreau *et al.*, 2006), and sister to the Myrmicinae (Kück *et al.*, 2011; Moreau & Bell, 2013). This relationship has an rQS score of 0.626, suggesting strong agreement between sources in its accuracy. This relationship is found in the gene trees used in the analysis, specifically the trees for *CAD*, *elongation factor 1-α F1*, and *long-wavelength rhodopsin*, and this may have contributed to the observed topology. Another possibility is that Myrmiciinae + Pseudomyrmecinae and Aneuretinae + Dolichoderinae (two pairs of sister relationships that appear consistently in all previous work) grouping closely with Myrmicinae and Formicinae disrupted the sister relationship between Ectatomminae + Heteroponerinae and Myrmicinae + Formicinae.

b) Genus-level supertree

Subfamily-level relationships were the same as in the species-level tree with one important exception: the sister-pair of Ectaomminae and Heteroponerinae appeared as sister to the Formicinae and Myrmicinae, as in previous studies (Brady *et al.*, 2006; Moreau *et al.*, 2006). This node was supported by an rQS score of 0.624.

2.4.1.4 Genus-level relationships

a) Species-level supertree

Several genera emerged as paraphyletic. These are *Ponera*, *Discothyrea*, *Pachycondyla*, *Simopone*, *Dolichoderus*, *Dorymyrmex*, *Cataglyphis*, *Camponotus*, *Calomyrmex*, *Oecophylla*, *Messor*, *Aphaenogaster*, *Temnothorax*, *Monomorium*, *Myrmicocrypta*, *Polyrhachis*, *Brachymyrmex*, *Cerapachys*, *Leptomyrmex*, *Technomyrmex*, *Crematogaster, Tetramorium*, and *Solenopsis*. Of these, fifteen of these were previously known to be paraphyletic (table 2.3.1). Of the remaining genera some appear anomalous. Lucky (2011) found the genus *Leptomyrmex* to be monophyletic, however in this supertree it appears paraphyletic with respect to *Cerapachys cribrinodis*, a species from an ostensibly distantly related subfamily. This species is represented by a single molecular sequence of the *cytochrome oxidase 1* gene, and the taxonomy. Since the taxonomy is only a guide or a seed in the analysis, in situations such as this the only information regarding the placement of the taxon in question comes from a single source, and in the absence of further data to correctly place the taxon it ends up erroneously placed. Other genera that show paraphyly driven by this process (data from a single source) include *Solenopsis* (*S. mameti* clusters with the genus *Mayriella*, informed solely from the *cytochrome oxidase 1* gene tree), *Cyphomyrmex* (*C. lectus* clusters with *Leptothorax*, a relationship that isn't supported in any source tree), *Azteca* (*A. longiceps* appears as a sister species to the genus *Leptomyrmex*) and *Myrmecocystus* (*M. pyramicus* is shown as a sister species to *Brachymyrmex depilis*, however this relationship has an rQS support value of 0, indicating equivocal support, and the remainder of the *Myrmecocystus* species are shown as a monophyletic sister group to this pair, again with an equivocal rQS value of 0.

An alternative reason for unexpected paraphyly in the supertree is that the combination of species from a given genus have not appeared together in a prior study before. In such a case the relationships on the supertree represent the summary of the phylogenetic signal from all sources, and the members of the genus are grouped accordingly. In this situation there is no *a priori* reason to suspect monophyly of the genus. Paraphyletic genera for which this appears to be the case are *Ponera, Monomorium* (although one of these placements, *M.latinode* as sister to *Pheidole rhea* has an rQS score of 0), *Tetramorium, Creamtogaster, Dolichoderus, Brachymyrmex, Rossomyrmex, Discothyrea, Polyrhachis* and *Cataglyphis*.

b) Genus-level supertree

Since the data were reduced to genus-level for the construction of a genus-level phylogeny it was methodologically impossible to find a genus to be paraphyletic unless there was an *a priori* reason to allow that genus to be split in the analysis. For this reason there is no unexpected paraphyly in the genus-level supertree. The fifteen genera that were allowed to be split due to existing evidence of paraphyly were all recovered as paraphyletic (none of the pieces of those genera clustered together).

2.4.2 Trait data

2.4.2.1 General patterns

The database contained data on at least one of: colony size, worked head-width, queen head-width, polygyny, polyandry and discrete worker castes, from 903 sources (Appendix 1, table A1.5). The mean number of observations per source (across all traits) was 9.73 (SD = 18.34), the mean number of species per source was 5.21 (SD = 13.57) and the mean number of genera per source was 2.11 (SD = 3.74). The mean number of observations per trait per source ranged from 0.38-2.89 across all sources, and ranged from 2.63-6.26 considering only sources that data for the trait (Table 2.3).

2.4.2.2 Species coverage

The database had data on at least one trait for 1957 species, 521 of which appear on the species-level supertree (Table 2.4.1). 513 species had colony size data (253 on the phylogeny, sample sizes ranged from 1-2404), 1364 had worker head-width data (271 on the phylogeny, sample sizes ranged from 1-5821), 406 had queen head-width data (132 on the phylogeny, sample sizes ranged from 1-431), 532 had polygyny data (263 on the phylogeny, sample sizes ranged from 1-5374), 94 had polyandry data (67 on the phylogeny, sample sizes ranged from 1-2404), and 262 had data on discrete worker castes (87 on the phylogeny, Table 2.4.2). The mean number of observations per species per trait ranged from 0.09-0.68 across all sources, and ranged from 1.36-5.36 considering only sources that had data for the trait (Table 2.4.1).

Table 2.4.1 Descriptive statistics of morphological and social data collected from 903 sources. For each trait in the database, the mean, median and standard deviation of the number of observations per species, genus and source are reported. These measures were calculated across all sources (all data) and just those for which data were present (present data only).

	Mean obs. per species		**Median obs. per species**		**SD obs. per species**	
Trait	**All data**	**Present data only**	**All data**	**Present data only**	**All data**	**Present data only**
Colony size	0.68	5.35	0	1	4.4	11.35
Worker head-width	0.56	1.68	0	1	1.16	1.45
Queen head-width	0.14	1.36	0	1	0.61	1.42
Polygyny	0.7	5.36	1	2	4.09	10.16
Polyandry	0.11	4.61	0	1	1.68	10.12
Discrete castes	0.09	1.37	0	1	0.41	0.94
	Mean obs. per genus		**Median obs. per genus**		**SD obs. per genus**	
Trait	**All data**	**Present data only**	**All data**	**Present data only**	**All data**	**Present data only**
Colony size	10.12	20.47	0	5	29.91	40.04
Worker head-width	8.46	15.39	1	4	23.29	29.71
Queen head-width	2.04	5.87	0	2.5	5.85	8.74
Polygyny	10.52	22.1	0	5	32.29	44.06
Polyandry	1.6	10.31	0	3.5	7.79	17.55
Discrete castes	1.32	4.92	0	2	5.13	8.99
	Mean obs. per source		**Median obs. per source**		**SD obs. per source**	
Trait	**All data**	**Present data only**	**All data**	**Present data only**	**All data**	**Present data only**
Colony size	2.89	6.26	0	2	8.89	12.25
Worker head-width	2.42	6.02	0	2	7.46	10.83
Queen head-width	0.58	2.63	0	1	1.85	3.19
Polygyny	3	5.78	1	2	8.21	10.68
Polyandry	0.46	5.41	0	2	3.47	10.81
Discrete castes	0.38	3	0	1	2.32	5.83

2.4.2.3 Genera coverage

The database had data on at least one trait for 208 genera, all of which appear on the genus-level phylogeny. 134 genera had colony size data, 149 genera had worker head-width data, 94 genera had queen head-width data, 129 genera had polygyny data, 42 genera had polyandry data and 73 genera had data on discrete worker castes (table 2.4.2). The number of observations per trait per genus ranged from 1.6-10.52 across all sources, and from 4.92-20.47 considering only sources that had data for the trait (table 2.4.1).

Table 2.4.2 The number of observations per trait in the database at both the species and genus level, and the amount of overlap between the taxa present in the database and on both the species- and genus-level supertrees.

	Genera			**Species**		
Trait	**In database**	**Overlap - genus tree**	**Sample size range**	**In database**	**Overlap - species tree**	**Sample size range**
Colony size	134	134	1-3525	513	253	1-2404
Worker head-width	149	149	1-6730	1364	271	1-5821
Queen head-width	94	94	1-1049	406	132	1-431
Polygyny	129	129	1-49	532	263	1-12
Polyandry	42	42	1-9	94	67	1-7
Discrete worker castes	73	73	1-16	262	87	1-6
Total	208	208	n/a	1957	521	n/a

2.4.2.4 Effect of sample size

There were no significant effects of sample size on colony size, worker head-width or queen head-width (table 2.4.3). There was a weak but significant positive relationship between colony size and study effort, and no significant relationship between either worker head-width or queen head-width and study effort (table 2.4.3).

Table 2.4.3 Results from phylogenetic least squares (PGLS) models examining the relationship between species-level trait means of colony size, worker head-width and queen head-width with sample size and study effort (number of hits from a web of knowledge search).

Trait	Variable	β	Standard error	t-value	p-value
Colony size	Sample size	-9.00E-05	1.00E-03	-0.67	0.94
	Study effort	4.00E-04	1.00E-04	3.4	<0.001
Worker head-width	Sample size	2.86E-04	2.70E-04	1.06	0.29
	Study effort	6.05E-05	5.92E-05	1.02	0.31
Queen head-width	Sample size	-4.32E-04	6.28E-04	-0.69	0.49
	Study effort	5.92E-05	6.91E-05	0.56	0.4

There was a weak and significant relationship between polygyny and sample size, such that species that have been sampled more had a higher probability of being polygynous in the database (Table 2.6), and no significant relationship between polyandry and sample size. Neither polygyny nor polyandry had a significant relationship with study effort (Table 2.6).

Table 2.4.4 Results from phylogenetic logistic regression models examining the relationship between polygyny and polyandry with sample size (number of contributing sources) and study effort (defined as number of web of knowledge hits). Posterior mean is the mean value of the posterior distribution of the expected change in log-odds of being either polygynous or polyandrous with one unit increase in the relevant variable. Effective sample size is the number of independent iterations the MCMC chain sampled. pMCMC is a Bayesian p-value.

Trait	Variable	Posterior mean	CI_{95}	Effective sample size	pMCMC
Polygyny	Sample size	7.99E-01	1.20E+00	246.5	0.048
	Study effort	1.91E-02	5.00E-02	201	0.06
Polyandry	Sample size	1.00E-01	2.40E-01	259	0.241
	Study effort	1.56E-02	8.00E-02	364.9	0.429

2.5 Discussion

2.5.1 Phylogenetic reconstruction

The two supertrees presented in this chapter are derived from 78 published phylogenies and 10 gene trees. By comparison, a recent supertree of the Carnivora contained 114 literature-derived source trees and 74 gene trees (Nyakatura & Bininda-Emonds, 2012), and a recent supertree of the Bromeliaceae contained 26 source trees and 7 gene trees (Escobedo-Sarti *et al.*, 2013). I recovered a species-level supertree of 1656 species. This supertree had reasonable support, and is 5.6 times bigger than the previous largest phylogeny (Moreau & Bell, 2013). In general the topology of the phylogeny is in agreement with previous work. However, there was one seemingly odd relationship – Ectatomminae + Heteroponerinae appeared as sister to Myrmeciinae, Pseudomyrmecinae, Dolichoderinae, Formicinae and Myrmicinae, rather than as sister to Formicinae + Myrmicinae (Brady *et al.*, 2006; Moreau *et al.*, 2006), or derived from Myrmicinae (Kück *et al.*, 2011; Moreau & Bell, 2013). The relationship between these seven subfamilies (Ectatomminae, Heteroponerinae, Myrmeciinae, Pseudomyrmecinae, Dolichoderinae, Formicinae and Myrmicinae) is not unambiguously resolved in the literature (figure 2.1), and so the relationship found in this analysis represents the most parsimonious placement of these subfamilies, considering the input data from studies where many variations of these relationships exist. Furthermore, existing phylogenies that do not show this relationship are constructed from concatenated alignments of more than one gene, whereas the support for this relationship in the supertree comes from three single-gene trees. Since gene trees and species trees are not necessarily congruent (Maddison, 1997), the dependence of this relationship on these three single-gene trees might explain the absence of this relationship in previously published work.

Several genera also appeared paraphyletic, with a single rogue species placed a long way from the remainder of is congeners. In all cases, these placements were also informed by single gene trees. The erroneous placement of these species may be due to missing data in the source gene trees, or even an incorrect labelling of the sequence contributing to the gene tree.

The genus-level tree had a topology much more in agreement with previous work regarding positioning of Ectatomminae + Heteroponerinae. Reducing the source trees to genus level means that any conflicting relationships at species-level and any single species that may be misidentified in the genetic dataset are not present in the analysis, which perhaps explains why this version of the phylogeny does not present unexpected relationships. In addition, I was able to include the full genus-level taxonomy due to a larger proportion of genera being present in the dataset. This meant that the genus-level phylogeny is complete to genus level. In general I believe the genus-level tree to be a more useful tool for comparative analysis than the species-level tree. Although the species-level tree represents a realistic summary of all currently available phylogenetic data for the ants, a large amount of extant diversity is missing from it, and it is not free from problems caused by rare data, or the absence of data. For example, species that are represented only by sequence data for a single gene might be erroneously placed, especially when the gene-tree on which they appear is not congruent with the true species-tree. Equally, problems can occur when a species appears on only one source tree, and that source tree represents a sparse cross-section of ants. For example, if a species appears on one tree as sister to a clade it is in fact distant from, due to the absence of any more closely related species in the tree, the only data contributing to the placement of that species says that it belongs as sister to the distantly related group. The genus-level tree, by contrast, is complete. Furthermore by reducing the dataset to the genus level the amount of data per tip (genus) is higher, and so the problems encountered by rarely sampled species in small or sparse trees is absent.

2.5.2 Database

At the species-level there was, on average, less than one observation per species for each trait when every source was considered (Table 2.4.1). This reflects the fact that many sources contained data on only one or two traits, and this is further highlighted by the fact that, across all sources, the median number of observations per source is 0 for all traits but polygyny (Table 2.4.1). One problem with the data at species level was that of the 1957 species in the database, only 521 of them appeared on the species-level supertree meaning that just under three quarters of the species in the dataset are not useable in any comparative analysis. The inverse implication of this is that of the 1656 species on the supertree only 521 have useable data. This highlights a problem of phylogenetic comparative analysis in general – that there is often a lack of overlap between sources of trait data and sources of phylogenetic data. Summarising the data to the genus-level increases the number of observations per genus, and since the genus-level supertree is complete also improves overlap with the relevant phylogenetic hypothesis. Another advantage to utilising data at the genus level is that much of the data for species that do not appear on the supertree at species level can contribute to data at the genus level, improving the quality of genus-level trait estimates.

At species level, and at genus level, all continuous traits were represented by sample sizes of one (either due to the sample size being one, or being assumed to be one when a source did not report sample size) at least once. For discrete traits the same pattern was true – at species and at genus level there were instances of polygyny, polyandry and discrete worker castes being inferred from only a single source. Pooling data to genus-level reduced this problem by increasing the mean sample size of each continuous trait and increasing the mean number of sources for each discrete trait, as well as increasing mean number of observations per trait per genus. Despite the fact that for some species and genera sample size was low, there appears to be no statistical relationship between sample size and any of the traits measured other than polygyny. This suggests that the data are relatively robust to small sample sizes, increasing the confidence with which the data can be used. Although there is a significant relationship between polygyny and sample size, namely that higher sample sizes correspond to an increasing probability that a species is identified as polygynous, this relationship appears to be weak.

The construction of a species-level supertree provides a summary of the current state of ant phylogenetics, but more importantly it highlights some of the problems that may face the pursuit of phylogenetic comparative questions in large, diverse insect clades such as the ants, namely the lack of data to facilitate the construction of complete or near-complete species-level phylogenies.

The construction of a complete genus-level phylogeny, however, provides a useful tool for the analysis of comparative datasets across the entire ant family.

Large, close to complete, species-level phylogenies of other clades such as the mammals (Bininda-Emonds *et al.*, 2007) and the birds (Jetz *et al.*, 2012) have revolutionised the study of macroevolutionary and macroecological questions in these clades. However these clades are also considerably smaller than a group such as the ants. In addition, a large proportion of the extant diversity of the ants remains known only from museum specimens, unrepresented in genetic databases, and biologically understudied. The size of the Formicidae, and the lack of data for the majority of the species in the family, meant that a complete species-level supertree was unattainable. A complete genus-level supertree and compiled data to the genus level greatly facilitates the investigation of comparative questions in the ants, however. As more comprehensive phylogenies of under-studied parts of the ant tree of life emerge the capacity for supertree methods to recover a complete phylogeny for the ants will grow. Furthermore, as the price of sequencing falls and the ability to recover useable sequence data from museum specimens grows, the possibility of a complete species-level phylogeny for the ants becomes even more realistic.

3 The phenotype of the ancestral ant

3.1 Abstract

It is widely assumed that the earliest ants lived in small colonies of monomorphic workers, headed by one, singly-mated queen, but these hypotheses concerning the ancestral colony size, level of worker polymorphism have never been tested. The earliest ant fossils belong to the genus *Sphecomyrma*, and suggest that the first ants were relatively large-bodied, terrestrial insects. Conversely, molecular analysis of ant phylogenetic relationships find that the genus *Leptanilla* to be the sister-group to the remaining ants, suggesting that the earliest ants were very small, subterranean, highly-specialised predators. Here, using a genus-level supertree of the ants, a large database of trait data, and model-based ancestral state reconstruction methods I estimate the worker head-width, colony size, level of worker polymorphism, gyny status and mating frequency of the ancestral ant. I find very little support for a small-bodied ancestor as expected if *Leptanilla* was representative of the ancestral ant. In addition, analysis of rates of phenotypic evolution suggest that *Leptanilla* have not experienced a slower rate of worker head-width evolution compared to the rest of the ants, implying that they are not a relict taxa displaying plesiomorphic characteristics. By contrast, I find support for an ancestral ant of comparable size to *Sphecomyrma*. The ancestral colony size of the ants was estimated small (around 40), and I find strong support for the hypotheses that the ancestral worker ant was monomorphic and lived in monogynous, monandrous colonies. This study helps to clarify the phenotype of the ancestral ant and to unite ostensibly contradictory evidence from the fossil record and molecular phylogenetic studies.

3.2 Introduction

Despite intensive consideration of the topic (Schultz, 2000; Wilson & Hölldobler, 2005; Crozier, 2006), very little is known concerning the nature of the earliest ants. This problem is compounded by the incongruent implications regarding the ancestral ant from the fossil record and molecular phylogenetic evidence, and the fact that social traits do not fossilise. The traditional view is that the ancestral ant was a large-bodied, wasp-like terrestrial predator, reflecting its divergence from a Scoliid wasp ancestor (Johnson *et al.*, 2013) approximately 139-148 million years ago (Moreau & Bell, 2013). The fossil record supports this view because the oldest known stem-group (a group more closely related to the ants than any other extant group, from which the ants may have originated) ant fossils (approximately 100 million years old (LaPolla *et al.*, 2013)) are of the genus *Sphecomyrma* (subfamily Sphecomyrmicinae), which appear to be large-bodied, large-eyed, wasp-like, active predators (Wilson *et al.*, 1967; Agosti *et al.*, 1998; Wilson & Hölldobler, 2005). The large eyes of *Sphecomyrma* are consistent with the "dynastic succession" hypothesis of early ant evolution, which posits that the earliest ants foraged in the leaf litter of tropical forests before diversifying into other habitats and lifestyles (Wilson & Hölldobler, 2005). The '*Sphecomyrma*-like ancestor hypothesis' therefore predicts that the earliest ants were large-bodied, visual predators in the leaf litter (figure 3.1).

In contrast, recent molecular phylogenetic analysis suggests that the subfamilies Leptanillinae (Brady *et al.*, 2006; Moreau *et al.*, 2006; Kück *et al.*, 2011; Moreau & Bell, 2013) or Martialinae (Rabeling *et al.*, 2008) are sister groups to the rest of the extant ants, which appear to have diverged 100-150 million years ago (Moreau & Bell, 2013). Both the Leptanillinae and the Martialinae are subfamilies of small, cryptic, nearly eye-less ants (Bolton, 1990; Masuko, 1990; Rabeling *et al.*, 2008). Very little is known of the biology of these species, but they appear to be highly specialised predators that forage in subterranean habitats (in the case of the Leptanillinae,(Bolton, 1990; Masuko, 1990)) or in leaf litter (in the case of the Martialinae (Rabeling *et al.*, 2008)). The Leptanillinae and the Martialinae could be relict taxa presenting plesiomorphic (ancestral or primitive) characters and being protected from extinction by their stable subterranean nesting habitat (Rabeling *et al.*, 2008). They are absent from the fossil record, and this absence could stem from low chances of fossilisation associated with their subterranean lifestyle (most ant fossils are known from amber (LaPolla *et al.*, 2013)). The Leptanillinae appear to be monogynous (having one queen per colony), and to have small colonies of around 100 workers (Masuko, 1990). Specialisations of the Leptanillines include dichthatdiiform queens (i.e. permanently wingless, queens with an unusually enlarged gaster specialised for egg laying) and queens that feed exclusively on haemolymph exuded from the larvae (Masuko, 1990). The '*Leptanilla*-like ancestor hypothesis' therefore predicts the earliest ants to have been small, blind, specialised and subterranean (Figure 3.1).

The *Sphecomyrma*-like ancestor hypothesis implies that the Leptanillinae and the Martialinae represent early specialisations in the ant tree of life, derived from the ancestral phenotype, and that they are not representative of the ancestral ant despite their current basal position. By contrast, if the *Leptanilla*-like ancestor hypothesis is correct, later ants must have secondarily acquired larger eyes for diurnal vision and the habit of above-ground foraging as seen in their earlier Scoliid-like ancestors. In addition, a recent ancestral state reconstruction suggests that soil is the ancestral habitat of the ants (Lucky *et al.*, 2013). This provides evidence that supports both hypotheses. It is reasonable to assume that the earliest ants nested underground since the Scoliid wasps they are hypothesised to have evolved from parasitized subterranean coleopteran larvae (O'Neill, 2001). This does not, however, necessarily imply that the earliest ant lineages were entirely subterranean, like the Leptanillines (Masuko, 1990). Indeed many extant ponerine species nest underground but forage terrestrially in the leaf litter (Lucky *et al.*, 2013).

The *Sphecomyrma*-like and *Leptanilla*-like ancestor hypotheses make differing predictions regarding worker size in the ancestral ant. In ants, head-width correlates closely with body size (Hölldobler & Wilson, 1990; Kaspari, 1993; Vainio *et al.*, 2004; Weiser & Kaspari, 2006), and so reconstructing the head-width of the workers of the ancestral ant permits the two hypotheses to be discriminated. In the genus *Sphecomyrma*, mean worker head-width is 1.20 mm (Wilson *et al.*, 1967; Wilson, 1985; Engel & Grimaldi, 2005), whereas in the genera *Leptanilla* + *Martialis* it is 0.46 mm (Bolton, 1990; Masuko, 1990; Rabeling *et al.*, 2008), less than half that of *Sphecomyrma*. This comparison uses a mean head-width for *Leptanilla* + *Martialis* combined due to the ambiguity over which of these ancient genera is truly the sister group to the rest of the ants (Brady *et al.*, 2006; Moreau *et al.*, 2006; Kück *et al.*, 2011; Moreau & Bell, 2013). Hence the two hypotheses predict differing head-widths in workers of the ancestral ant, i.e. large and small, respectively.

If the hypothesis that the basal lineages *Martialis* and *Leptanilla* are relict taxa displaying plesiomorphic characters (Brady *et al.*, 2006; Rabeling *et al.*, 2008; Lucky *et al.*, 2013) is correct , I would expect, as just discussed, to see evidence that the ancestral ant was of similar body size to these ants. In addition, analysis of the rates of phenotypic evolution of body size should show a very slow rate of evolution in these lineages, with, furthermore, a pattern of trait evolution distinct from the rest of the tree. This would reflect the evolutionary 'stasis' of these taxa hypothesized to follow from their relict status (Rabeling *et al.*, 2008).

Inferring the ancestral state for key social traits such as colony size, the presence of discrete worker castes, gyny status (number of queens) and queen mating-frequency is much more difficult since these traits do not fossilise. As a result hypotheses regarding the ancestral value of these traits are driven by theoretical work. It is important to test these hypotheses quantitatively since traits such as colony size, discrete worker castes, gyny status and mating frequency could have profound impacts of the social evolution of the ants, and on their ecological success. It is thought that evolutionary increases in colony size may have driven increases in the degree of non-reproductive division of labour characteristic of the ants (Bourke, 1999; Bonner, 2004; Bourke, 2011), which is manifest in, variously, the occurrence in workers of discrete physical castes, temporal division of labour and task partitioning (in which different groups of workers specialise in separate sub-tasks). Since advanced division of labour, including the presence of physical worker castes, appears to be a derived feature within the ants, it is thought that eusocial societies originate as small colonies.

In addition to colony size, the gyny status (monogynous or polygynous) and mating frequency (monandrous or polyandrous) of a colony can affect the social structure of ant colonies. For this

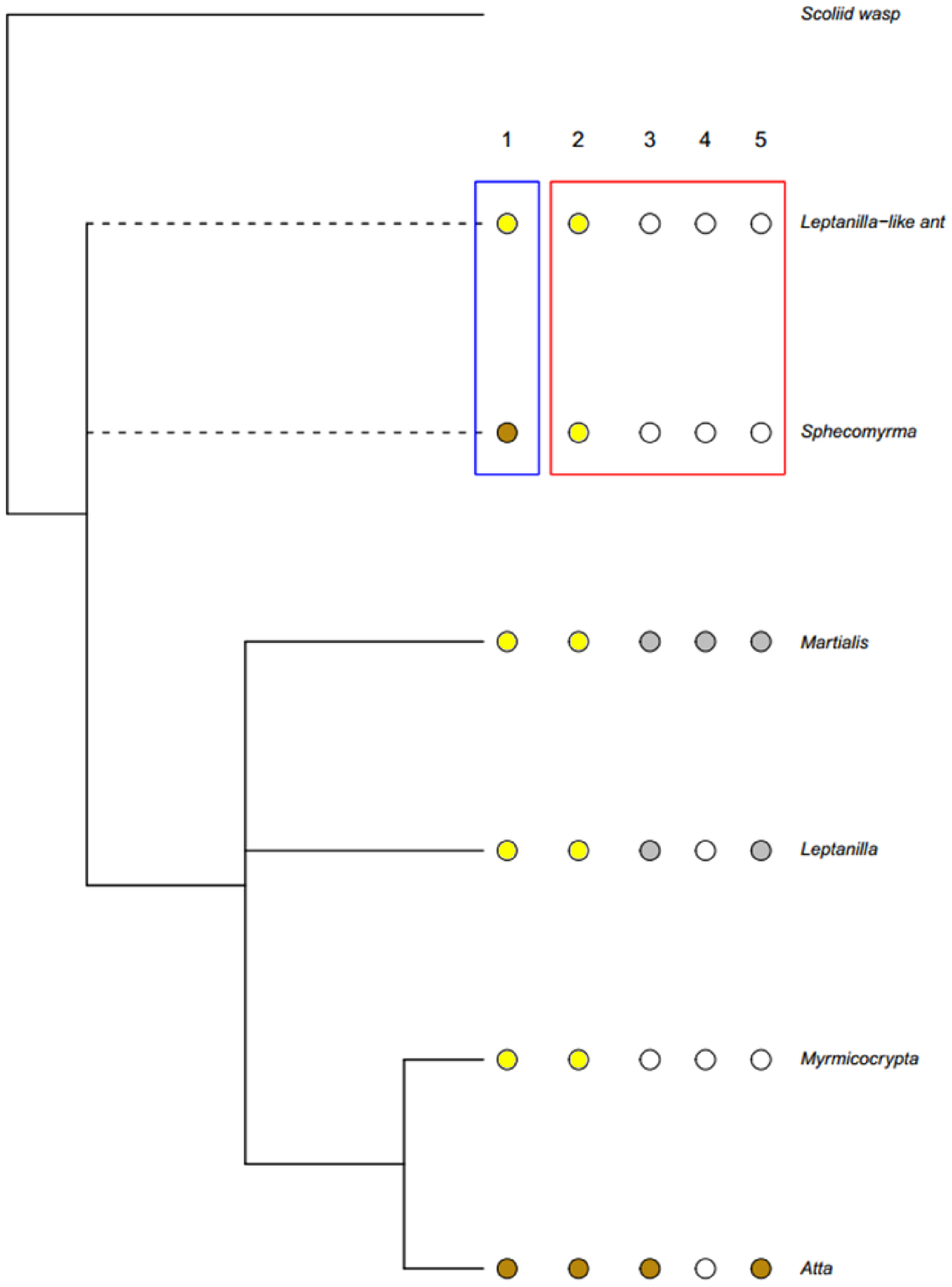


Figure 3.1 Alternative hypotheses for an ancestral phenotype within the context of ant evolutionary history. Circles at the tips represent taxon trait values where 1 represents mean worker head width 2, colony size 3, discrete worker castes, 4, polygyny and 5, polyandry. For 1 and 2 bright yellow indicates small, and dark yellow indicates large and for 2, 3 and 4 dark yellow indicates the presence of a trait, white the absence of a trait and grey indicates a lack of data. Dotted lines indicate potential ancestors. The blue box indicates hypotheses derived from the fossil record and molecular phylogenetic reconstruction. The red box indicates hypotheses derived from theoretical work. The extant genera the tree are selected to show a sample of extant trait values.

reason, understanding the patterns of the evolution of these traits, including their ancestral states, is important to the study of social evolution in the ants, and in general. According to current evidence, eusociality evolves due to the indirect fitness benefits of altruism, which are maximised in populations or colonies of highly related individuals (Hamilton, 1964). As more matrilines (as polygyny increases) and patrilines (as polyandry increases) occur in a colony, the mean within-colony relatedness between the workers falls (Hamilton, 1964), weakening the selective forces that originally favoured eusociality. It has long been hypothesised that monogyny and monandry are ancestral to the ants (Charnov, 1978; Boomsma, 2007; Hughes *et al.*, 2008b; Boomsma, 2009; Boomsma, 2013). In an ancestral state reconstruction of mating frequency across 267 species of eusocial Hymenoptera, including 148 species of ant (from 56 genera), it was shown that monandry and monogyny were the ancestral states at the root of the ants, and each other origin of eusociality (Hughes *et al.*, 2008b).

Polygyny and polyandry are frequent throughout the Formicidae (Bourke & Franks, 1995; Boomsma & Ratnieks, 1996; Boomsma *et al.*, 1999; Wiernasz *et al.*, 2004; Ratnieks *et al.*, 2006; Kronauer *et al.*, 2007), suggesting a potential adaptive reason for the evolution of multiple queens and multiple mating. Once an obligate worker caste has evolved (i.e. workers with a worker-like adult morphology) polygyny or polyandry may be selected for in order to increase within-colony genetic diversity (Hamilton, 1987; Sherman *et al.*, 1988; Schmid-Hempel, 1998; Hughes *et al.*, 2008b; Boomsma *et al.*, 2014). High genetic diversity within social insect colonies has been linked to increased parasite resistance in ants (Hughes & Boomsma, 2004; Reber *et al.*, 2008) and bees (Baer & Schmid-Hempel, 2001; Seeley & Tarpy, 2007), more efficient division of labour within colony workforces (Schwander *et al.*, 2005; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007) and higher rates of colony growth and reproductive rates (Cole & Wiernasz, 1999; Wiernasz *et al.*, 2004) (although this seems to vary between species, e.g. Rosset *et al.* (2005)). The consequences of increased within-colony genetic diversity are wide-ranging (Ratnieks *et al.*, 2006). For example, models predict that, as colonies become more polygynous worker reproduction should increase (Wenseleers *et al.*, 2004), whereas under increasing polyandry worker policing can evolve (Ratnieks, 1988). There is also a reduction in the potential for conflict between queens and workers over sex allocation (Ratnieks, 1988; Ratnieks *et al.*, 2006). There is a negative relationship between polygyny and polyandry across the eusocial Hymenoptera (Hughes *et al.*, 2008a), implying that different selection pressures have led to the evolution of high genetic diversity in different lineages. This may reflect between-lineage variation in the importance of the various advantages high genetic diversity offers, or different environmental pressures leading to the evolution of these traits (for example, polygyny may evolve primarily due to environmental constraints and pressures (Bourke & Franks, 1995; Keller, 1995), and secondarily generate benefits associated with high genetic diversity).

Ancestral state reconstruction methods are widely applied to questions regarding the origins and evolution of many traits and features of living organisms. By using a phylogeny and a dataset for extant species at the tips, these methods are able to infer the likely traits of past organisms. For example, ancestral state reconstruction has been used to infer the number and the approximate timing of origins of carotenoid pigmentation in birds (Thomas *et al.*, 2014); the ancestral mechanism of seed dormancy in the spermatophytes (seed plants, Willis *et al*., 2014); the ancestral body size in the Carniformia (Finarelli & Flynn, 2006); the evolution of orb webs in spiders (Blackledge *et al.*, 2009); the number of origins of compound eyes in arthropods (Oakley & Cunningham, 2002); and the evolution of microhabitat and prey specialisation in assassin bugs (Hwang & Weirauch, 2012).

Recent methods of ancestral state reconstruction explicitly model the evolution of a continuous trait along the branches of a tree, either under a Brownian motion (random walk) or Ornstein-Uhulenbeck (random walk with a central tendency) model (Butler & King, 2004). These methods are more flexible and biologically realistic than previous parsimony-based methods (Swofford & Maddison, 1987; Collins *et al.*, 1994), which do not utilise branch-length information and do not explicitly model trait evolution (Royer-Carenzi *et al.*, 2013). Furthermore, by adopting a Bayesian approach to parameter estimation, these methods can facilitate the comparison of different hypotheses. By sampling trait value estimates from the posterior distribution a probability distribution of possible trait values can be obtained, rather than a single point estimate of a trait value as returned by maximum-likelihood parameter estimation. This allows the probability of a given range of ancestral states to be calculated by integrating under the applicable section of the probability distribution.

Equally, recent methodological developments have improved the reconstruction of discrete traits. The "threshold model" assumes that changes in a discrete trait are underpinned by cumulative genetic and environmental changes, and models these changes as an unobserved trait termed "liability" (Felsenstein, 2005; 2012; Revell, 2014). When the value of the liability crosses a certain threshold, the state of the trait is assumed to have changed. Liabilities, and values for liability thresholds, are sampled from the joint posterior probability distribution using a Bayesian MCMC method (Revell, 2014). This method is more biologically realistic than previous methods based on Markovian processes (which assume instantaneous trait changes between time steps, and are widely agreed to be biologically unrealistic (Revell, 2014)).

New developments in estimating rates of phenotypic evolution enable me to test the hypothesis that basal genera like *Leptanilla* and *Martialis* are relict taxa (Rabeling *et al.*, 2008). Bayesian

Analysis of Macroevolutionary Mixtures (BAMM) (Rabosky, 2014) is a newly developed method that enables researchers to identify shifts in evolutionary rates without an *a priori* hypothesis. The method estimates per-branch evolutionary rates and then identifies areas of the tree with significantly different rates (Rabosky *et al.*, 2013; Rabosky, 2014). In doing so, the method is able to sample from a huge range of different models, and output a range of credible shift configurations with associated probabilities. These candidate models can then be summarised into a maximum credibility model which takes into account the full range of likely rate regimes (Rabosky, 2014; Rabosky *et al.*, 2014). This method outperforms other methods of inferring evolutionary rates. For example, independent contrast-based approaches cannot cope with non-Brownian motion traits (Garland, 1992; O'Meara *et al.*, 2006) and AUTEUR assumes constant rates within each rate regime, and is susceptible to over-fitting problems (Eastman *et al.*, 2011).

Here I use a complete genus-level phylogeny and trait data on worker head-width to infer, by ancestral state reconstruction, the mean worker head-width of the ancestral ant. I then compare this value to the mean head-widths of known *Sphecomyrma* fossils and the extant *Leptanilla* + *Martialis* in order to discriminate between the *Sphecomyrma*-like ancestor hypothesis and *Leptanilla*-like ancestor hypothesis. By examining the rates of phenotypic evolution of worker head-width I also test the hypothesis that *Leptanilla* and *Martialis* are relict taxa, representing early specialisation in the evolution of the ants. Finally, using data on mean colony size, the presence of physical worker castes, gyny status and mating frequency, and again using ancestral state reconstruction methods, I infer the social phenotype of the ancestral ant in order to confirm the long-standing hypotheses that the ancestral ant lived in small colonies, and did not have physical worker castes – two hypotheses that have never been quantitatively tested. I also reconstruct the ancestral mating system (gyny status and mating frequency) using a more complete phylogeny and more biologically realistic methods than previous studies have employed.

3.3 Method

3.3.1 Trait Data

I collected data on worker head width (mm) (1364 species, 145 genera, 3039 populations), colony size (number of workers at maturity) (512 species, 125 genera, 2428 populations), presence or absence of physical worker castes (245 species, 80 genera, 361 populations), gyny status (531 species, 123 genera, 2854 populations), and mating frequency (94 species, 43 genera, 434 populations) from the primary literature. The full description of this data can be found in Chapter 2.

3.3.2 Supertree construction

I used a complete, dated genus-level supertree of the ants as constructed in Chapter 2. I used the genus-level tree rather than the species-level tree in order to preserve as much of the structure of the full phylogeny as possible. For example, an analysis of data on 94/325 genera would incorporate 28.9% of the structure of the ant phylogeny, but an analysis of 300/12,980 species would incorporate only 2.3% of the structure of the phylogeny. Since ancestral state reconstruction is sensitive to the topology of the phylogeny (Schultz *et al.*, 1996; Li *et al.*, 2008), it follows that as much of the overall structure of the phylogeny as possible should be included to generate robust results.

3.3.3 Ancestral state reconstruction

Prior to analysis I removed any species in the dataset that were not present on the supertree, and removed any branches of the supertree that were not represented in the trait dataset. When a genus was paraphyletic on the supertree, I assigned the same trait value to all parts of the genus. I did this for each trait separately, resulting in one, trait-specific tree for each ancestral trait analysis. This resulted in separate trees of 165 tips for worker head width data, 147 tips for colony size data, 97 tips for discrete worker castes, 144 tips for polygyny and 58 tips for polyandry (counting each part of a paraphyletic genus separately, in all cases). In addition I added hypothetical species with a colony size of one to the dataset for the reconstruction of colony size, corresponding to the solitary Scoliid wasp ancestor of the ants (Johnson *et al.*, 2013).

a) Continuous trait reconstruction

By adopting a model-based approach to the reconstruction of the body size of the ancestral ant under a Bayesian framework, I was able to generate a posterior distribution for the body size of the ancestor to the ants. I was then able to use this to find the probabilities that the ancestor was *Sphecomyrma*-like or *Leptanilla*-like. The same methods enabled me to estimate the ancestral colony size for the ants, which has traditionally been assumed to be small, but has never been tested quantitatively before, and to test the hypothesis that the ancestral ant did not have physical worker castes, and was monogynous and monandrous. This method samples from the posterior distribution of trait values (head-width or colony size) at each internal node of the tree (Revell, 2012). The model assumes that the trait evolves according to a Brownian motion (BM) model, and that data at the tips have a normal distribution. I first tested this assumption by fitting both a BM and an Ornstein-Uhlenbeck (OU) model to the data (using the function fitContinuous in the R package Geiger (Harmon *et al.*, 2008)) and I then compared the model fits using a log-likelihood ratio test. When an OU model is a better fit than a BM model, it is possible to transform the tree according to the parameters of the OU model, resulting in a tree and dataset that conform to the BM assumptions of the model. In all cases a BM model fitted the data better than an OU model according to a log-likelihood ratio test ($p=0.63$ for worker head-width, $p=0.98$ for colony size).

In order to ensure realistic priors for each model, I fitted a maximum-likelihood model of ancestral state reconstruction to the tree and the data using the anc.ML function from the R package phytools (Revell, 2012). I then used the point estimates of the trait value at each node as the starting point for the MCMC analysis. In addition I used the drift parameter (σ^2) from the BM models as the starting point for this parameter in the MCMC analysis.

I ran 4 chains each of 10,000,000 generations for each trait, sampling from the chain every 2,000 generations to give 5,000 samples. I discarded the first 20% of these samples as burnin for each chain and then combined the samples from each chain to give a total of 16,000 samples for each trait. I used the R package coda (Plummer *et al.*, 2006) to assess the convergence of each analysis by visually inspecting the trace of each chain to ensure it covered the full range of parameter space, ensuring that effective sample sizes were over 200 for each parameter, and checking for the absence of autocorrelation within each chain. In all cases the run of 10,000,000 generations proved adequate to ensure convergence of each chain and to provide a reliable pool of samples from the posterior distribution of each parameter.

To calculate the probabilities of a *Sphecomyrma*-like ancestor and a *Leptanilla*-like ancestor from the posterior distribution, I integrated the area under the probability distribution that unambiguously supported each hypothesis (i.e. the area where the ancestral worker head-width is larger than the mean worker head-width of *Sphecomyrma* and smaller than the mean worker head-width for *Leptanilla*, respectively). The worker head-width dataset included data for the genus *Martialis*. This genus is considered to be extremely basal in the Formicidae (Rabeling *et al.*, 2008; Kück *et al.*, 2011), and therefore informative with regard to the present analysis. However, *Martialis* has been discovered only recently (Rabeling *et al.*, 2008) and is very rare, so only one head-width measurement is available for it, making the estimate potentially unrepresentative of the genus. Rather than excluding this potentially informative genus from the analysis, I instead fitted two models to worker head-width, one with *Martialis* included and one with it excluded, in order to investigate the effects of this genus on the reconstructions. *Martialis* was only present in the worker head-width data.

b) Discrete trait reconstruction

In order to reconstruct discrete traits (discrete worker castes, gyny status and mating frequency), I used the threshold model (Revell, 2014). For each trait I ran 3 chains of 100,000,000 generations, sampling each chain every 20,000 generations to give a pre-burnin sample of 5000. I discarded the first 20% of these samples to give a post-burnin sample of 4000. After combining the 3 chains, I had 12,000 samples for each trait. In the absence of any concrete information on ancestral trait values for any of the discrete traits I used an uninformative prior distribution for the liability at each node (Revell, 2014). I used the R package coda (Plummer *et al.*, 2006) to check each chain for proper convergence by visually examining the trace to ensure it covered the full range of parameter space, ensuring the effective sample size for each parameter was above 200, and checking for the absence of autocorrelation within each chain. In all cases the run of 100,000,000 generations was adequate to ensure proper convergence.

3.3.4 Rates of worker head-width evolution

To investigate the rates of phenotypic evolution across the phylogeny I used BAMM (Rabosky *et al.*, 2013; Rabosky, 2014). The output of this model is a posterior distribution of fitted models with a variable number of inferred shifts and shift locations, termed 'shift configurations'. Under conditions in which a trait has undergone many potential shifts in the past, or when the tree is large, there is unlikely to be a single best configuration. In this case, the probability of the best-fitting model may be low, and the posterior can be summarised into a maximum shift credibility (MSC) tree, which summarises the shift locations that are most frequently sampled from the posterior.

The phylogeny for the worker head-width data had a large polytomy of 22 genera in the Myrmicinae. Polytomies are a problem for the analysis of evolutionary rates, since a polytomy implies instantaneous speciation, and would therefore be interpreted as a significant and rapid increase in the rate of phenotypic evolution. For this reason I removed all but one of these genera from the tree prior to analysis in order to have a more accurate analysis of fewer genera. I elected to retain the genus with the greatest sample size for the head-width data (*Acanthomyrmex*, n=261).

I used the function setBAMMpriors from the R package BAMMtools to establish priors appropriate for the scale of the tree and trait values (Rabosky *et al.*, 2014). For each model I ran 3 MCMC chains of 10^9 generations, sampling every 10^6 generations, which resulted in 5000 samples per chain. I then discarded the first 20% of the samples from each chain as burn-in, combined the chains and used the R package coda (Plummer *et al.*, 2006) to check the chains for convergence. I ensured the effective sample size of each parameter was over 200, and visually inspected the traces of each parameter for proper convergence, mixing and lack of autocorrelation between samples. In all cases this chain length and sampling regime were adequate to ensure convergence and mixing. Finally, for the reasons mentioned previously, I fitted two different models to the worker head-width data, a model including the genus *Martialis* and a model excluding it.

3.4 Results

3.4.1 Ancestral state reconstructions

a) Head width

The most likely mean worker head-width (mean of the post-burnin samples) at the root of the tree was 0.91 mm, with a 95% credible interval of 0.30-1.32 mm and a 50% credible interval of 0.63-0.98 mm. The probability of the ancestral worker head-width being equal to or greater than the mean head-width for *Sphecomyrma* was 0.246 (figure 3.2) and the probability of the ancestral head-width being equal to or smaller than the mean head-width for *Leptanilla* + *Martialis* was 0.006 (figure 3.2). The 95% highest posterior density region included the mean head-width of *Sphecomyrma* but not the mean head-width of *Leptanilla* + *Martialis* (figure 3.2). Excluding *Martialis* from the analysis made very little difference to the estimate of ancestral head-width (Appendix 2, figure A2.1). The most likely mean worker head-width (mean of the post-burnin samples) at the root of the tree became 1.01 mm. The main effect of excluding *Martialis* was increase the uncertainty of the reconstruction, widening the 95% credible interval to 0.001-4.4 mm and the 50% credible interval to 0.25-1.29 mm. The probability of a *Sphecomyrma*-like ancestor increased to 0.376 and was still higher than the probability of a *Leptanilla*-like ancestor, which increased to 0.149 (Appendix 2, figure A2.1).

b) Social traits

The inferred mean colony size at the root of the tree (mean of post-burnin samples) was 39 (rounded down from 39.39), with a large 95% credible interval of 1-10967, and a 50% credible interval of 11-181. The most likely order of magnitude for the colony size of the ancestral ant was 10^2 (probability 0.361, figure 3.3), followed by 10^3 (probability 0.302, figure 3.3). There was very little evidence for an ancestral colony size with an order of magnitude of 10^4 or 10^5 (probabilities of 0.097 and 0.013, respectively; figure 3.3).

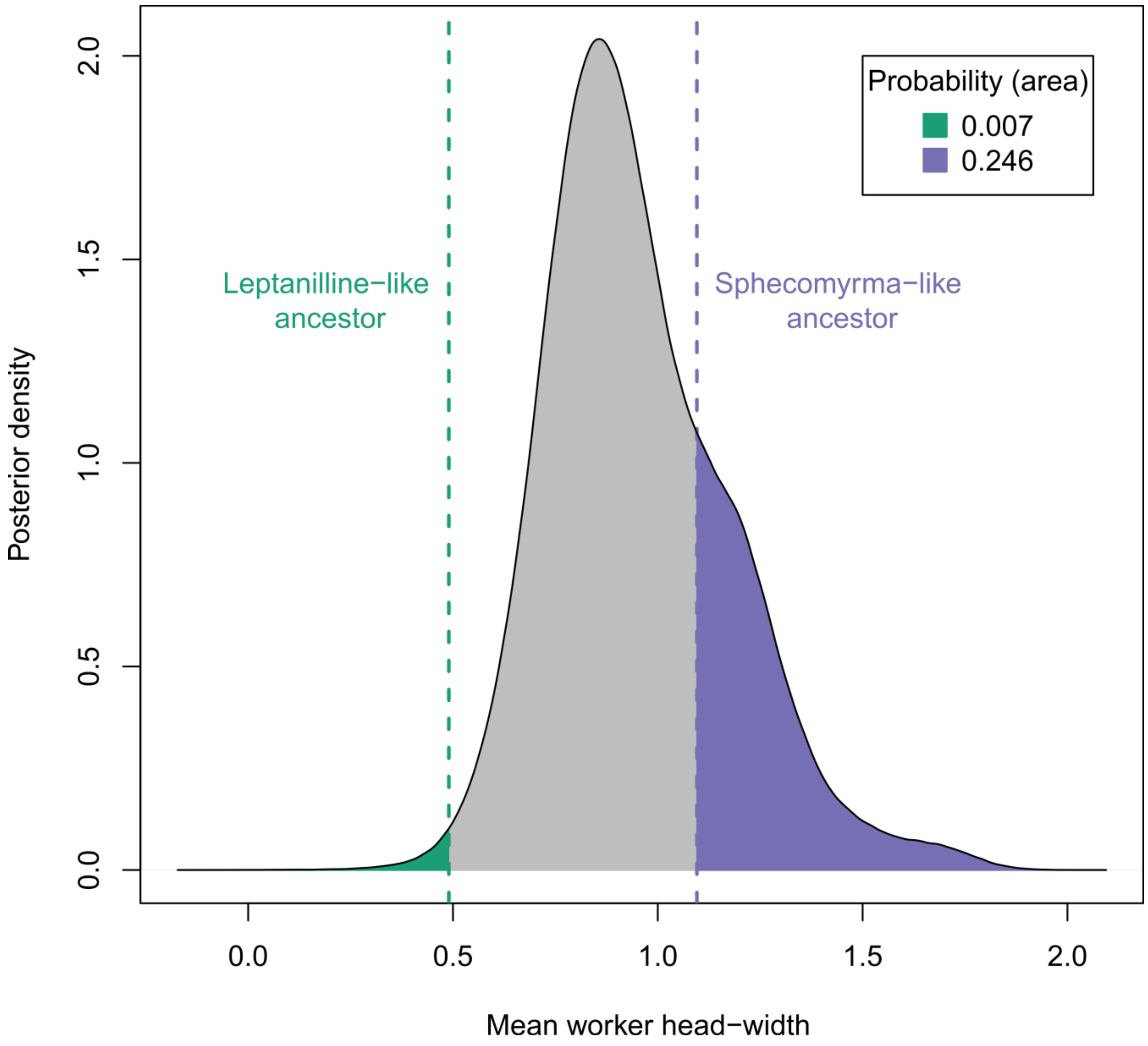


Figure 3.2 The posterior distribution of mean worker head-width at the root of a genus-level phylogeny of the ants including the genus *Martialis* (165 tips). Dotted lines indicate the expected head-widths under the *Leptanilla*-like ancestor hypothesis (green) and above the *Sphecomyrma*-like ancestor hypothesis (purple). Coloured areas show the areas of unambiguous support for the two respective hypotheses (green, ancestral worker head width less than or equal to worker head width of *Leptanilla*; blue, ancestral worker head width equal to or greater than worker head width of *Sphecomyrma*).

The most likely state at the root of the phylogeny was found to be the absence of worker castes, with a probability of 0.69. The most likely gyny status at the root of the phylogeny was found to be monogyny, with a probability of 0.89. The most likely mode of mating frequency at the root of the phylogeny was found to be monandry, with a probability of 0.62.

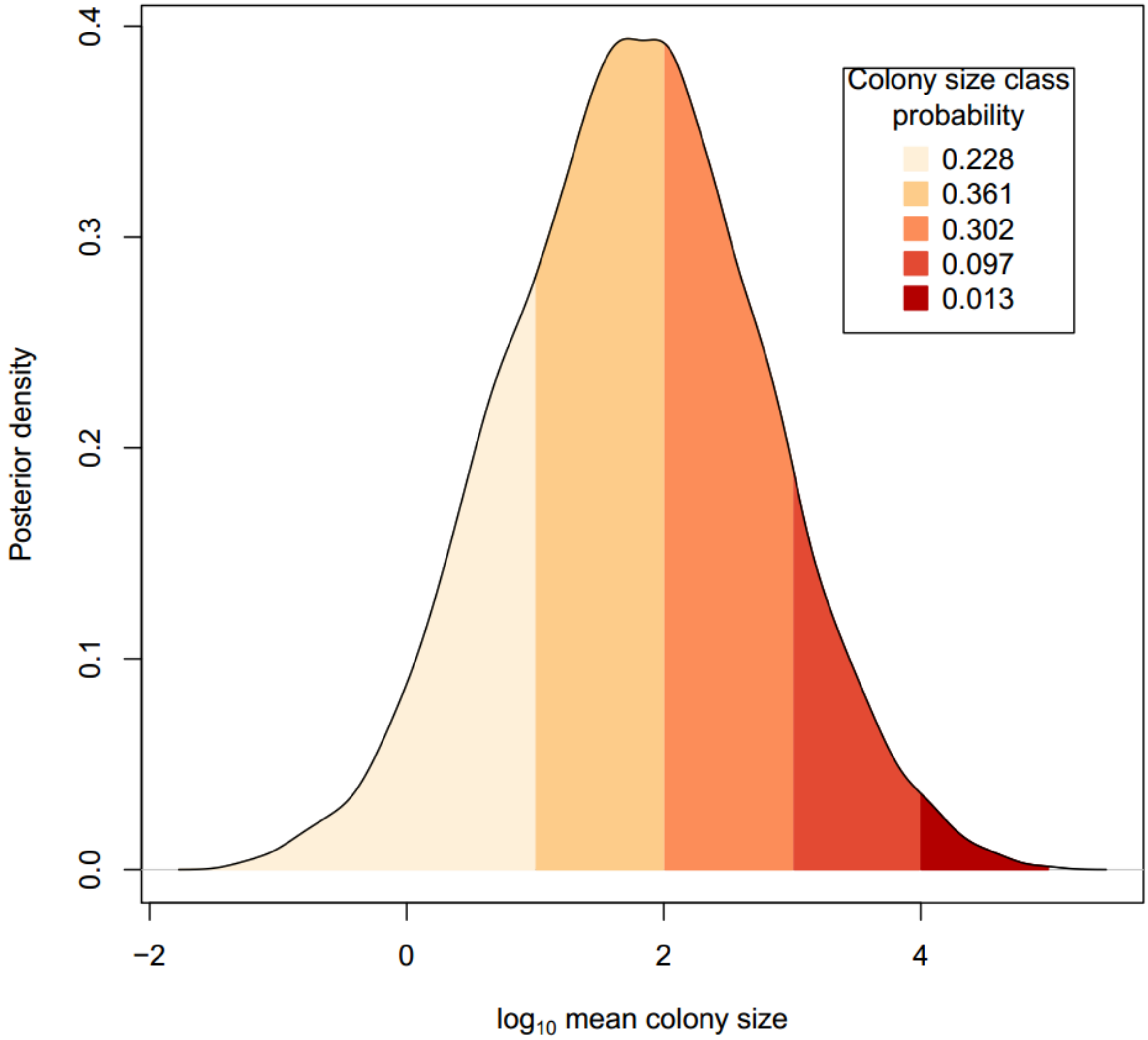


Figure 3.3 The posterior distribution of mean colony size at the root of a genus-level phylogeny of the ants (147 tips). Shaded regions indicate support for an ancestral colony size of the order of magnitude, from left to right, 10^1, 10^2, 10^3, 10^4 and 10^5+.

3.4.2 Rate shifts in worker head-width evolution

BAMM found strong evidence that a shift in the rate of worker head-width evolution had occurred in the phylogeny, sampling models with 5 shifts (6 rate regimes) the most frequently (Figure 3.4). Of all the unique shift configurations sampled, 458 accounted for the 95% credible set of models (the set of models that account for 95% of the posterior probability of the data). Of this credible set, the best model had a probability of 0.11, implying that there was not one shift regime that best accounted for the data.

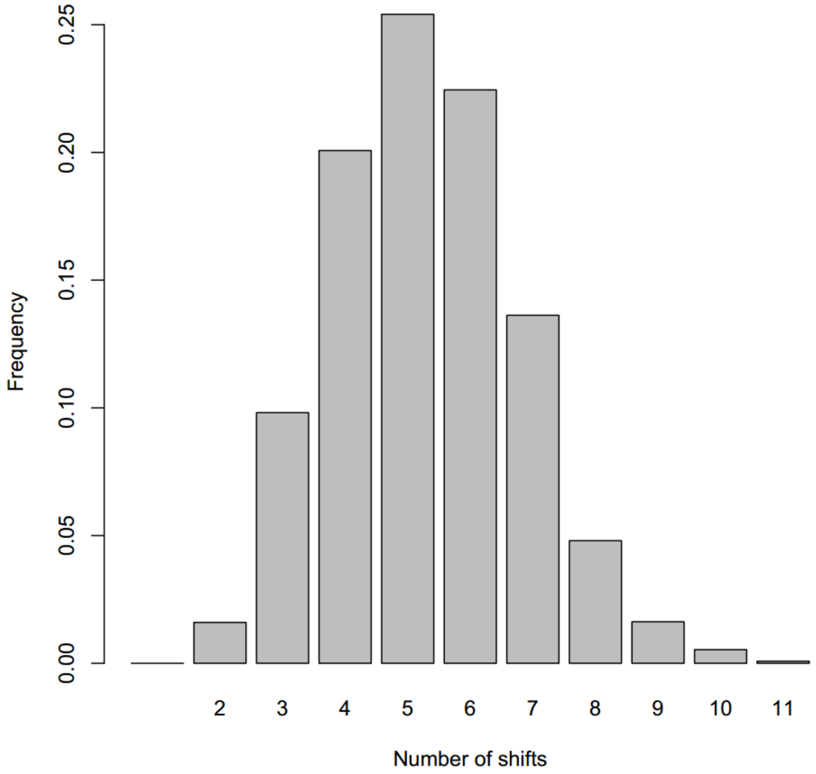


Figure 3.4 The posterior distribution of distinct shifts in the rate of worker head-width evolution present in a phylogeny of 165 genera of ants. The posterior probability of a model is proportional to the frequency with which the model was sampled using reversible jump Markov Chain Monte Carlo (i.e. a model that has a higher sampling frequency has a higher probability of being the correct model).

The summary of the 95% credible shift set suggests there are six distinct rate regimes across the phylogeny, with 5 shifts between these regimes. None of the inferred shifts between these regimes occurred on the branch leading to *Leptanilla* and *Martialis* (Figure 3.5). The most credible shifts show a slowdown in the rate of head width evolution where the rest of the ants diverge from the Ponerinae (shift 2, figure 3.5). Increases in the rate of worker head-width evolution occur within the Ponerinae on the branches leading to *Dinoponera* and a fragment of the paraphyletic genus *Pachycondyla* (shift 1, figure 3.5), the army ant genera *Eciton* and *Nomamyrmex* (shift 3, figure 3.5), *Myrmecia* (shift 4, figure 3.5) and *Daceton* (shift 5, figure 3.5).

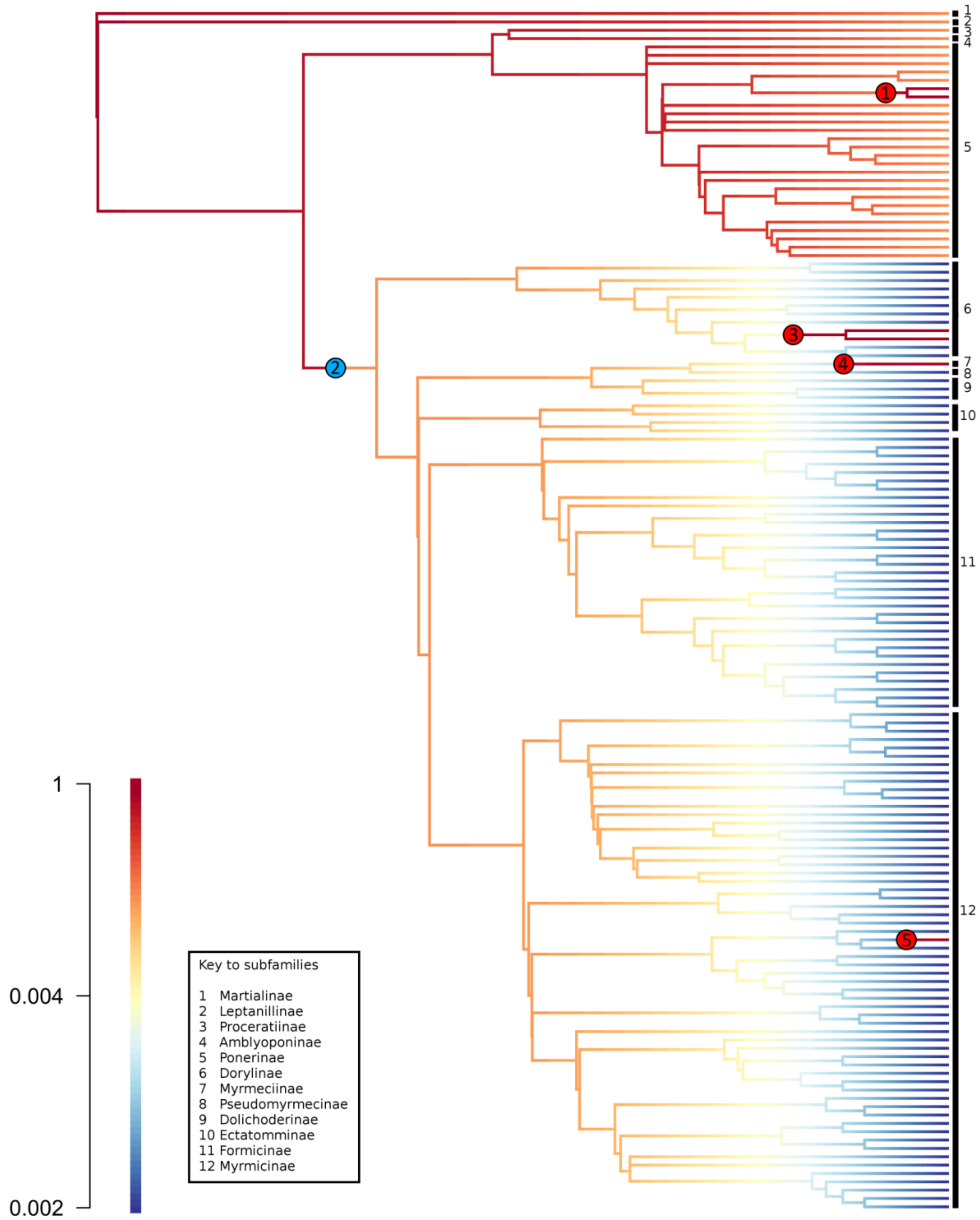


Figure 3.5 A phylogeny of 165 genera of ant showing shifts in the rate of worker head-width evolution. Branch colours show rate of phenotypic change with redder colours representing faster rates and bluer colours indicating slow rates. Red circles mark significant increases in evolutionary rate compared to the background rate and blue circles mark significant decreases. Shifts are summarised from 458 unique shift configurations that account for 95% of the posterior probability of the data. Black bars denote subfamily divisions.

3.5 Discussion

I conducted ancestral state reconstruction of worker head widths and colony size using a new genus-level phylogeny of ants to test hypotheses concerning the worker body size, colony size, gyny status and mating frequency of the ancestral ant. I also estimated rates of phenotypic evolution of worker head-width to investigate the hypothesis that the genera *Leptanilla* and *Martialis* are relict taxa that retained plesiomorphic characteristics and have remained unchanged for a long time.

The results showed that the most likely value for the worker head-width of the ancestral ant was 0.91 mm and the most likely ancestral colony size was approximately 40 workers. The value for the ancestral worker head-width falls between the hypothetical values that typify both the *Sphecomyrma*-like ancestor and the *Leptanilla*-like ancestor. However, the Bayesian posterior probability distribution function for worker head width demonstrated much stronger support for the *Sphecomyrma*-like ancestor hypothesis than for the *Leptanilla*-like ancestor hypothesis (area of the posterior = 0.246 versus 0.007 respectively). In addition, adding further weight to the *Sphecomyrma*-like ancestor hypothesis, the mean head-width of *Sphecomyrma* fossils (1.2 mm, the hypothetical head-width used to represent this hypothesis) falls within the 95% credible interval of the posterior distribution of head-widths at the root node of the tree, whereas the mean value of extant *Leptanilla* and *Martialis* species (0.5 mm, representing the small-bodied subterranean ancestor) falls outside of this interval. This is strong evidence that the ancestral head-width was larger than the mean of extant small-bodied subterranean ants, which have been hypothesised to be representative of the ancestral ants (Rabeling *et al.*, 2008; Lucky *et al.*, 2013), but smaller than the larger-bodied *Sphecomyrma* specimens that have been hypothesised to be ancestral to the ants. Moreover, analysis of the rates of phenotypic evolution in worker head-width show that the lineages leading to the basal genera *Leptanilla* and *Martialis* are unlikely to have experienced a significantly different regime of evolutionary rates to the rest of the ant phylogeny. This suggests that these lineages have not experienced evolutionary stasis, and are unlikely to represent relict taxa with plesiomorphic characteristics, at least in terms of their body size. In turn, this implies that the small head-widths observed in this clade are not indicative of the ancestor of the ants, but represent a more derived feature.

The traditional view of the earliest ants, based on the fossil record and morphology, is that they were active, terrestrial, visual predators (Wilson *et al.*, 1967; Wilson, 1985; Wilson & Hölldobler, 2005), whereas molecular analyses suggest that the ancestral ant had a closer affinity with the Leptanillines or the genus *Martialis*, groups characterised by their specialised subterranean or, in the case of *Martialis*, potentially subterranean habits (Brady *et al.*, 2006; Moreau *et al.*, 2006; Kück *et al.*, 2011; Lucky *et al.*, 2013; Moreau & Bell, 2013). By supporting the *Sphecomyrma*-like ancestor hypothesis, this study supports the traditional view. It has been hypothesised that adopting an exclusively subterranean habitat protected the basal ant groups found today from extinction, making them relict taxa retaining plesiomorphic traits (Rabeling *et al.*, 2008). In view of the present results, I suggest the alternative hypothesis that the protected nature of a subterranean habit explains the apparent basal position of these lineages, but that they also represent early specialisations in the evolutionary history of ants, rather than plesiomorphic forms. Recent phylogenomic studies suggest that the Scoliid wasps (wasps of the families Scoliidae and Bradynobaenidae) represent the sister group to the ants + Apoidea (Johnson *et al.*, 2013). These wasps form a group of relatively large solitary aculeate wasps that parasitise ground-dwelling scarab beetle larvae (O'Neill, 2001; Johnson *et al.*, 2013). While this lends credence to the hypothesis that the ancestral ant had subterranean nesting habits (Lucky *et al.*, 2013), Scoliid wasps feed on nectar as adults (O'Neill, 2001), which suggests that it is unlikely that the earliest ants to have diverged from this group of wasps were entirely subterranean and specialised. A more plausible scenario, taking into account the fossil record, previous morphological studies, molecular data and the evidence presented in this study, is that the earliest ants were intermediate in body size, relative to *Sphecomyrma*-like lineages and the Leptanillines. Then, as early lineages diverged and specialised, clades resembling the extant Leptanillines evolved derived subterranean characteristics. Protected from changing environments and extinction, these lineages persisted, resulting in their apparently basal nature that we see today. This interpretation is supported by the faster rate of change in head-width inferred along the branches leading to these clades (and the subsequent increases in rate observed on the branch leading to *Leptanilla*). If these ants have retained basal characteristics the expected rate of change from the root of the tree would be slow. Ants are rare in the fossil record up to the Eocene (LaPolla *et al.*, 2013), where the family appears to have undergone an explosion in diversity. This may explain why we do not see fossils of other early divergences from the ancestral ant phenotype, and why the Leptanillines appear to be basal.

In addition to providing evidence against the recent hypothesis that small subterranean ants may be representative of the ancestral ant (Rabeling *et al.*, 2008; Lucky *et al.*, 2013), this study also provides the first estimate of the ancestral colony size of the ancestral ant, as well as confirming the findings of an earlier study showing that the ancestral ant was monandrous and monogynous (Hughes *et al.*, 2008b). The size-complexity hypothesis (Bourke, 1999; Bourke, 2011) posits that it is increasing colony size that drives the increasing complexity of social systems in eusocial insects, including the evolution of physical worker castes. This hypothesis, then, implicitly suggests that the ancestral ant lived in small colonies and did not have physical worker castes. I find evidence that this was the case: ancestral state reconstruction suggests that the ancestral ant lived in colonies of approximately 40 individuals and suggest with a high probability (0.69) that these colonies did not have physical worker castes.

The current model for the evolution of eusociality predicts that the origin of eusociality requires positive relatedness and is facilitated by high relatedness, and hence predicts that at each origin of eusociality there is likely to have been a single queen (monogyny) who is mated once (monandry), maintaining high relatedness (Hamilton, 1964) (Charnov, 1978; Boomsma, 2007; Hughes *et al.*, 2008b; Boomsma, 2009; Boomsma, 2013). The results of the ancestral state reconstructions presented here strongly support this hypothesis, showing that the ancestral ant was monogynous and monandrous supporting the work of Hughes *et al.* (2008b). The present study includes more taxa than that of Hughes *et al.* (2008b), and thus both supports and strengthens this finding.

These results help to clarify our understanding of the phenotype of the ancestral ant and help resolve the apparent inconsistency between the evidence from the fossil record and that from molecular phylogenetic studies. Furthermore, they represent the first time the predictions that the ancestral ant had small colonies with monomorphic workers have been quantitatively tested. In total, the results of the analyses presented here suggest the ancestral ant had a worker head-width of approximately 0.91 mm and lived in colonies of around 40 monomorphic individuals with one, singly-mated queen. As a corollary, the present study provides evidence that the ancestral ant was not a small-bodied ant resembling *Leptanilla* or *Martialis*. In turn, this suggests that these cryptic and specialised extant lineages do not display plesiomorphic characters (Rabeling *et al.*, 2008) but instead represent an early divergence from the ancestral phenotype of the Formicidae. As more data accumulate, similar methods may be used to test hypotheses regarding other ancestral traits, building a better picture of the morphology, social biology and ecology of the ancestral ant.

4 Social trait evolution and coevolution in the ants.

4.1 Abstract

Colony size, worker polymorphism, polygyny and polyandry are predicted to shape the social evolution of the ants. As well as the predicted effects of these traits on social evolution traits such as the presence of discrete worker castes and polyandry are associated with colony-level ecological benefits such as increased resistance to parasites and enhanced division of labour. These traits are clearly important in both evolutionary and ecological terms, yet little is known of how many times they have arisen independently in the ants. Furthermore, some of the evolutionary associations between these traits that are predicted to exist have not before been tested under a rigorous phylogenetic framework. In this chapter I use a genus-level phylogeny and a comprehensive dataset to explore the patterns of evolution of colony size, discrete worker castes, polygyny and polyandry. I then test for predicted evolutionary correlations between colony size, discrete worker castes, polygyny and polyandry. I find evidence that polyandry was the first of these traits to evolve in the ants, followed by polygyny and finally discrete worker castes. Each of these traits has evolved independently and repeatedly. I also find strong evidence supporting many of the predicted trait associations, strengthening the ideas that colony size is an important driver of social evolution, and that selection for high genetic diversity through multiple queens or multiple mates is frequent in the ants.

4.2 Introduction

I previously showed (Chapter 3) that the ancestor of the ants is most likely to have lived in small colonies of monomorphic workers headed by a single, singly-mated queen. This finding sheds light on the evolution and development of traits that are thought to be key to the social evolution and ecological success, of the ants (Bourke & Franks, 1995; Lach *et al.*, 2010). However, little is known of how many times significant traits such as large colonies, discrete worker castes, polygyny and polyandry have evolved, and where in the ant phylogeny these traits may originate. Such exploratory analyses are of interest since the configuration of independent origins of these traits tells us much about the evolution of social complexity. For example, a single origin of discrete worker castes near the root of the phylogeny followed by repeated losses paints a different picture of social evolution to multiple independent origins near the tips of the tree. Here I explore the pattern of evolution of colony size and the pattern of independent origins of discrete worker castes, polygyny and polyandry, and investigate hypotheses of coevolution between these traits.

4.2.1 The evolution of social traits

a) Colony size

Colony size is thought to be a crucial factor in social evolution in the ants (Bourke, 2011). As colonies evolve to become larger, the evolutionary interests of workers (the non-reproductive or less reproductive population of the colony) and queens (the reproductive part of a colony) coincide, increasing the strength of selection for an altruistic worker phenotype leading to more efficient organisation and division of labour (Bourke, 1999; Bourke, 2011). The mechanism behind this hypothesis is the changing probability of direct fitness for any single worker in a colony as that colony becomes larger. There are two main routes to direct fitness for a worker ant – inheriting a nest either after the death of the current queen or through usurpation, and selfish reproduction. As colonies become larger, the probability of direct reproduction for a worker falls, and the role of indirect fitness (i.e. helping the queen to maximise her own reproductive output) becomes increasingly important (Wilson, 1971; Ratnieks, 1988; Alexander *et al.*, 1991; Bourke, 1999). Thus, understanding the patterns of the evolutionary changes in colony size is important. Evidence for the size-complexity hypothesis comes from both theory (Bourke, 1999; Gautrais *et al.*, 2002), and comparative studies (Fjerdingstad & Crozier, 2006; Rodriguez-Serrano *et al.*, 2012; Kramer & Schaible, 2013; Ferguson-Gow *et al.*, 2014).

The evolution of large colonies may also have contributed to the ecological success of the ants, by allowing them to produce more numerous winged reproductives (Cole & Wiernasz, 2000) and, through enhancing division of labour, forage more effectively (Beshers & Traniello, 1994; Beshers & Traniello, 1996; Arnan *et al.*, 2011). Colony sizes have evolved to be particularly large ($>10^5$ workers) in the subfamilies Dorylinae (*Aenictus, Eciton, Dorylus, Labidus*), Dolichoderinae (*Linepithema, Technomyrmex*), Formicinae (*Formica, Lasius, Myrmelachista*) and Myrmicinae (*Atta, Solenopsis, Daceton, Pheidologeton*). These subfamilies are all within the Formicoid clade, and so I predict that there will be at least 4 independent origins of colonies of $>10^5$ workers, with subsequent reductions in colony size, or at most a separate origin of large colonies for each genus in which they have evolved.

b) Discrete worker castes

Discrete worker castes are often thought to be a crucial factor in explaining the ecological success of the insects (Oster & Wilson, 1978; Hölldobler & Wilson, 1990; Bourke & Franks, 1995). The presence of physical worker castes allows better matching of worker size to a specific task, and has been associated with increased foraging efficiency (Powell & Franks, 2005; Arnan *et al.*, 2011) and improved nest defence (Passera *et al.*, 1996). Physical castes may also allow for the workers to specialise in novel tasks (for example, using specialised workers to close nest entrances

(Hasegawa, 1993a; Powell, 2008), or as living food caches (Wilson, 1974; Hasegawa, 1993b)). There is also some evidence that physical worker castes confer a level of phenotypic plasticity onto a species, which may enhance their ability to adapt to novel environmental challenges (Yang *et al.*, 2004; Rajakumar *et al.*, 2012). Finally, there is evidence that species have the developmental capacity to produce physical castes that they do not naturally express (Rajakumar *et al.*, 2012). This suggests that the capacity to produce physical worker castes could potentially have evolved relatively early in ant evolution, and that castes are expressed plastically based on short-term species-specific environmental or ecological conditions. There is considerable variation in the number of times physical worker castes have thought to have evolved independently: estimates include three times (Bourke, 2011), seven times (Wilson, 1974) and eighteen times (Smith *et al.*, 2008). None of these estimates are based on quantitative analyses. Employing quantitative methodology to estimate the number of independent origins of physical worker castes will provide a more accurate number of origins than previous estimates, and may also result in new hypotheses regarding the evolution and expression of this trait.

c) Mating systems

Mating systems are predicted to relate to the ecological success of any species; multiple queens (polygyny) and multiple mating (polyandry) increase genetic diversity within a colony, and this is associated with a range ecological benefits in the social insects such as more efficient division of labour (Schwander *et al.*, 2005; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007), faster colony growth and reproductive output (Cole & Wiernasz, 1999; Wiernasz *et al.*, 2004) and increased resistance to parasites and pathogen (Baer & Schmid-Hempel, 2001; Hughes & Boomsma, 2004; Seeley & Tarpy, 2007; Reber *et al.*, 2008). Another important aspect of the evolution of increased genetic diversity within colonies is the effect it has on social structure. Although multiple queens and multiple mating are associated with ecological benefits, increased genetic diversity weakens the selective forces that initially favoured worker altruism (Hamilton, 1964).

4.2.2 Correlated evolution in social traits

Theory predicts a number of correlations between combinations of colony size, discrete worker castes, polygyny and polyandry. Firstly, the size-complexity hypothesis predicts that colony size is the driving force behind increasing social complexity, and thus discrete worker castes are predicted to be correlated with larger colonies (Bourke, 1999; Bourke, 2011). There is some support for this hypothesis (Fjerdingstad & Crozier, 2006; Ferguson-Gow *et al.*, 2014), yet it remains untested over the whole of the Formicidae.

Secondly, it has been hypothesised that polygyny correlates negatively with both discrete worker castes and polyandry. Since under polygynous conditions selfish worker reproduction is expected to increase (Wenseleers *et al.*, 2004), there is an expectation that selection for discrete worker castes becomes weaker (Oster & Wilson, 1978). This relationship appears to exist (Frumhoff & Ward, 1992), although it has not been tested within a phylogenetic framework before. Given that it is also predicted that colony size might increase the likelihood of the evolution of discrete worker castes it is important to control for this factor when testing this prediction. The number of times a queen mates has been suggested to be dependent on number of queens in a colony such that queens in polygynous colonies mate less frequently (Keller & Reeve, 1994; Hughes *et al.*, 2008a). This leads to the prediction that polyandry should be negatively associated with polygyny (Keller & Reeve, 1994; Hughes *et al.*, 2008a). Evidence from small clades or single species is conflicting. In army ants mating frequency appears to be inversely correlated with queen number (Kronauer & Boomsma, 2007), however in the ant *Myrmica rubra* the opposite appears to be true (Pedersen & Boomsma, 1999). In testing this relationship it is also important to control for colony size, due to the predicted relationship between colony size and polyandry (Cole, 1983; Crozier & Page, 1985; Boomsma & Ratnieks, 1996).

Finally, there may be correlations between polyandry and other social traits. It has been hypothesised that the increased genetic diversity brought on by multiple mating can allow for the production of more diverse worker genotypes, and hence enhance the production of discrete worker castes (Crozier & Page, 1985). Furthermore, it has been thought that polyandry has evolved in the social insects as a mechanism to maintain large colonies by increasing the amount of sperm available to queens (Cole, 1983). There is some evidence that this correlation exists (Cole, 1983; Boomsma & Ratnieks, 1996), however these predictions have not before been analysed in a phylogenetic framework. Together, these ideas predict various univariate associations between social traits in the ants (Table 4.2.1). In addition to these univariate relationships, I will be fitting multivariate models to control for the effects of other social traits that may affect the predicted relationships (Table 4.2.1).

Table 4.2.1 a) Univariate and b) multivariate models describing predicted correlations between social traits in the ants.

	Response variable	Predictor variable(s)	Predicted direction of relationship
a)	Discrete castes	Colony size	+
	Discrete castes	Polygyny	-
	Discrete castes	Polyandry	+
	Polyandry	Colony size	+
	Polyandry	Polygyny	-
b)	Discrete castes	Colony size	+
		Polygyny	-
		Polyandry	+
	Polyandry	Colony size	+
		Polygyny	-

In this chapter I exploit the trait data and genus-level supertree (Chapter 2), and methods of ancestral state reconstruction in order to firstly understand the evolutionary history of colony size, discrete worker castes, polygyny and polyandry throughout the ant phylogeny. First, I reconstruct colony size, discrete worker castes, polygyny and polyandry across the genus-level ant supertree in order to explore the patterns of origination of these traits. Second, I test for the predicted evolutionary correlations in these traits (Table 4.1). I do this in two ways. Firstly, I use an adaptation of the threshold model for quantitative genetics (Felsenstein, 2005; 2012) to estimate the correlated change in the ancestral values of combinations of traits (Table 4.1) as they evolve throughout the tree. Secondly, I investigate correlations between the same combinations of traits (Table 4.1) in extant genera at the tips of the tree using phylogenetically controlled logistic models (Ives & Garland, 2010).

4.3 Method

4.3.1 Trait data

The trait data used in this chapter were the genus-level estimates of colony size (as a continuous variable, 148 genera), discrete worker castes (as a categorical variable, 96 genera), polygyny (as a categorical variable, 135 genera) and polyandry (as a categorical variable, 60 genera) described in chapter 2 of this thesis. Prior to all analysis colony size was natural log-transformed in order to conform to the assumption that trait values at the tips of a tree are normally distributed, an assumption that is common to all models employed in this analysis.

4.3.2 Supertree construction

To provide a framework for ancestral state reconstructions and to control for the effects of phylogeny in regression models I used the genus-level supertree as described in chapter 2 of this thesis.

4.3.3 Ancestral state reconstructions

In order to reconstruct continuous traits (in this case, colony size), I used a model-based approach implemented in a Bayesian framework, using Markov-chain Monte Carlo (MCMC) sampling to draw parameter estimates. The evolution of a trait is described by a Brownian motion model and by the branching pattern and branch lengths of the phylogeny. Estimates of the ancestral trait value parameters in this model were drawn from the posterior distribution by an MCMC sampling algorithm, as described in chapter 3 (section 3.3.3). Discrete traits were reconstructed according to the threshold model (Felsenstein, 2005) as applied to ancestral state reconstruction (Felsenstein, 2012; Revell, 2014). In brief, this model assumes that the changes in a discrete character are underpinned by an unobserved continuous variable termed "liability". This can be conceptualised as being analogous to the numerous environmental and genetic changes that accumulate, ultimately causing a shift in a discrete trait (Revell, 2014). The model can be applied by sampling estimates of the liability of a trait and the thresholds between character states from the posterior distribution (Revell, 2014). This was implemented as described in chapter 3 (section 3.3.3). For a detailed comparison of other ancestral state reconstruction techniques see the method section of chapter 3 of this thesis (section 3.3.3). For analysis, I defined the independent origin of a trait as any node where a trait is inferred as present when at the proceeding node the trait was inferred as absent.

4.3.4 Correlated evolution

I tested for correlated evolution using two methods. The first method was to test for correlated change in the ancestral values of the combinations of traits outlined in table 4.2.1. By simultaneously reconstructing the ancestral values of two traits under the threshold model (described above) the correlation coefficient of the relationship between the two traits can also be sampled from the posterior distribution, and in this way a correlated change between two traits as they evolve can be detected (Revell, 2014). In the case of a continuous trait and a discrete trait the correlation coefficient measures the relationship between the change in the continuous trait and the change in liability of the discrete trait, and in the case of two discrete traits it measures the correlation between the two liabilities.

The second method was to test for correlations between the trait values of extant genera, using the genus-level supertree to control for the effects of phylogeny using phylogenetic logistic regression models (Ives & Garland, 2010). This measures the correlation between trait values of extant species, controlling for the expected covariation caused shared ancestry (Felsenstein, 1985). The phylogenetically controlled logistic regressions were implemented using the R package 'phylolm' (Ané, 2014).

4.4 Results

4.4.1 Ancestral state reconstructions

There appear to be 4 independent origins of species with colonies with over 100,000 workers (figure 4.1, table 4.4.1; appendix 3, table A3.3, figure A3.3). Discrete worker castes were inferred to have evolved 6 times independently (figure 4.1, table 4.4.1; appendix 3, table A3.2, figure A3.2), polygyny 11 times independently and polyandry 8 times independently (figure 4.1, table 4.4.1, appendix 3, table A3.4, figure A3.4). Discrete worker castes occur at nodes both with and without polygyny and polyandry, polygyny occurs at nodes both with and without discrete castes and polyandry occurs at nodes both with and without discrete castes and polygyny. Colony size does not exceeded 100,000 at the root of any subfamilies, and the largest inferred colony size at the root of any subfamily is 6,471 at the root of the Dorylinae. All origins of colony sizes over 10,000 workers occur within the Dorylinae (figure 4.1, table 4.4.1; appendix 3 table A3.1, figure A3.1. All other subsequent increases in colony size occur beyond the level of subfamily division (figure 4.1, table 4.4.1). Of the three discrete traits reconstructed polyandry appears first at around 125 million years ago (figure 4.1), then polygyny at around 110 million years ago (figure 4.1) and finally discrete worker castes, at around 81 million years ago (figure 4.1).

4.4.2 Correlated evolution

a) Correlated evolutionary change

Threshold models revealed that all trait combinations tested showed significant (as indicated by confidence intervals that exclude zero) correlated change throughout the tree except for discrete worker castes and polygyny. The strength of these correlations ranged from 0.44 (polygyny and polyandry) to 0.61 (colony size and discrete castes). Specifically, threshold models estimated the correlation coefficients between colony size and discrete worker castes as 0.61 (CI_{95} = 0.37-0.83) and colony size and polyandry as 0.59 (CI_{95} = 0.25-0.86). The correlation coefficient between polygyny and discrete worker castes was estimated as 0.23 (CI_{95} = -0.17 - 0.59) and between polygyny and polyandry as 0.44 (CI_{95} = 0.09-0.80). The correlation coefficient between polyandry and discrete worker castes was estimated as 0.56 (CI_{95} = 0.20-0.86).

Table 4.4.1 Reconstructed ancestral states at the origins of the ant subfamilies. Colony size was reconstructed as a continuous trait using a Brownian motion model. discrete worker castes, polygyny and polyandry were reconstructed as discrete traits using a threshold model. The number of within clade origins is the number of times a trait evolved in a descendent of a node that did not have that trait. – denotes missing data.

		Discrete worker castes		**Polygyny**		**Polyandry**	
	Colony size at root	**Root**	**Within clade origins**	**Root**	**Within clade origins**	**Root**	**Within clade origins**
Myrmicinae	1.00E+03	Present	2	Present	2	Absent	3
Formicinae	1.00E+03	Present	1	Present	1	Absent	1
Ectatomminae	1.00E+02	Absent	0	Present	1	Absent	0
Heteroponerinae	1.00E+02	-	-	Absent	1	-	-
Dolichoderinae	1.00E+03	Absent	0	Present	1	-	0
Aneuretinae	1.00E+04	-	-	-	-	-	-
Pseudomyrmecinae	1.00E+03	Absent	0	Present	1	-	-
Myrmeciinae	1.00E+02	Absent	0	Absent	0	Present	1
Dorylinae	1.00E+04	Present	1	Absent	0	Present	1
Ponerinae	1.00E+03	Absent	1	Absent	3	-	1
Paraponerinae	-	Absent	0	Absent	0	-	-
Agroecomyrmecinae	-	-	-	-	-	-	-
Amblyoponinae	1.00E+02	Absent	0	Absent	1	-	-
Proceratiinae	1.00E+02	Absent	0	Absent	0	-	-
Leptanillinae	1.00E+02	Absent	0	Absent	0	-	-
Martialinae	-	-	-	-	-	-	-
Whole tree	1.00E+02	Absent	6	Absent	11	Absent	8

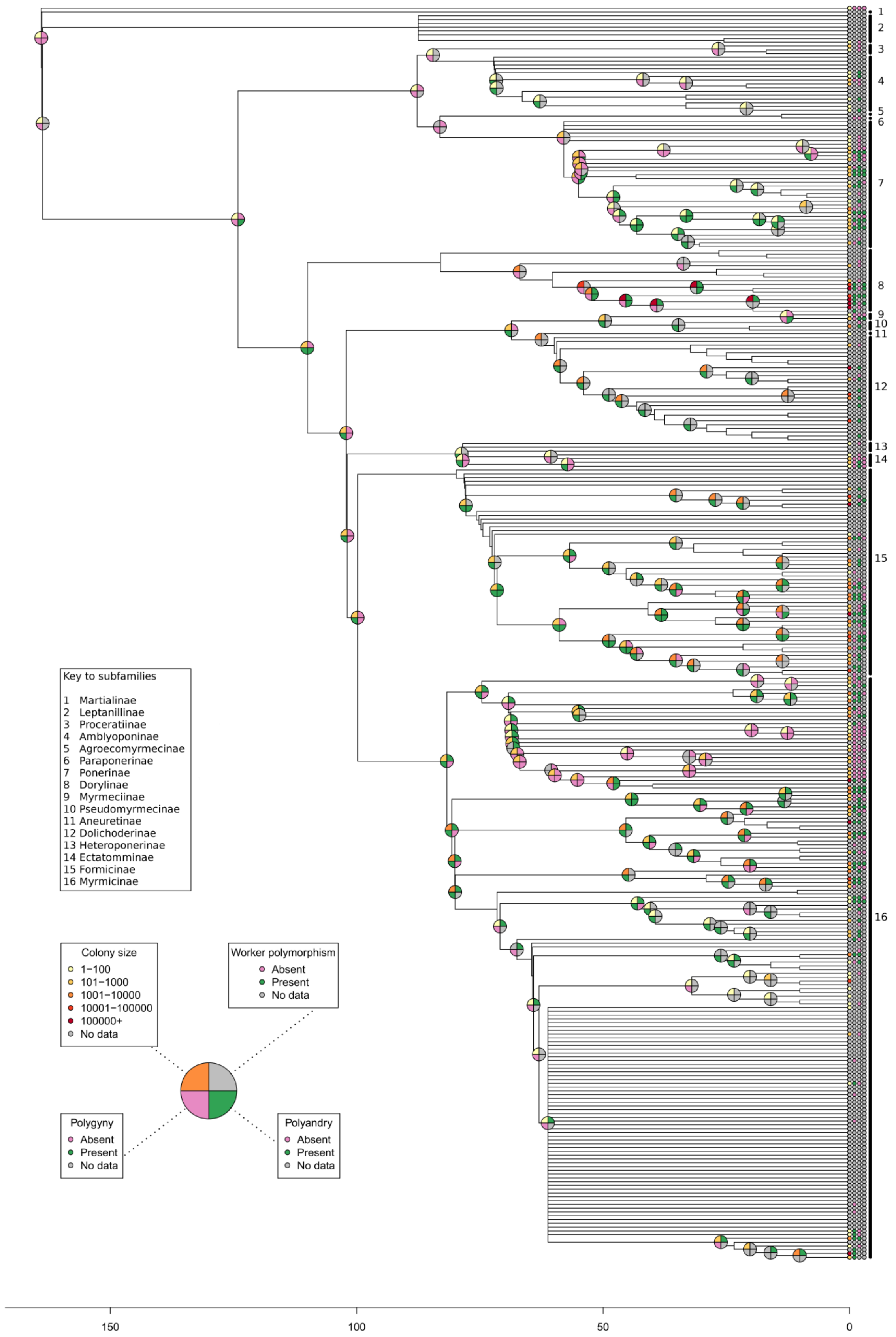


Figure 4.1 Ancestral state reconstruction of colony size, worker polymorphism (discrete worker castes), polygyny and polyandry on a genus-level supertree of the ants. Divided circles at nodes indicate ancestral inferred ancestral states.

Nodes without symbols did not have ancestral states inferred due to the absence of data for extant species subtending those nodes. Colony size was reconstructed as a continuous variable using maximum likelihood Brownian motion based models, and been simplified into categories of order of magnitude for ease of plotting. Worker polymorphism, gyny status (polygyny) and queen mating frequency (polyandry) were reconstructed as binary variables under a threshold model. Circles at tips correspond to data for extant genera and represent, from left to right, colony size, worker polymorphism, gyny status and queen mating frequency. Colour coding for tip labels follows colour coding for node labels. The black bars at the tips denote subfamily divisions. The scale bar shows millions of years before present.

b) Correlated extant traits

In univariate models all predicted relationships were positive and significant except for the relationship between discrete worker castes and polygyny, which was not significant (Table 4.4.2a).

Table 4.4.2 The results of a) univariate and b) multivariate logistic regression models testing the predicted correlations between discrete worker castes and colony size, polygyny and polyandry; and between polyandry, colony size and polygyny. Δlogodds is the expected change in log odds of exhibiting a trait per unit increase in ln colony size.

	Response variable	**Predictor variable**	**Δ logodds**	**S.E.**	**z.value**	**p value**
a)	Discrete worker castes	Colony size	0.436	0.130	3.355	**0.0008**
	Discrete worker castes	Polygyny	0.693	0.479	1.450	0.148
	Discrete worker castes	Polyandry	2.050	0.690	2.974	**0.003**
	Polyandry	Colony size	0.422	0.160	2.630	**0.0086**
	Polyandry	Polygyny	1.536	0.565	2.717	**0.006**
b)	Discrete worker castes	Colony size	0.502	0.244	2.054	**0.040**
		Polygyny	0.305	0.948	0.322	0.748
		Polyandry	1.617	0.828	1.952	0.051
	Polyandry	Polygyny	1.295	0.623	2.019	**0.038**
		Colony size	0.367	0.149	2.469	**0.014**

In a multivariate model only colony size had a significant effect on the probability of worker polymorphism, showing that higher colony sizes are associated with a higher probability of a species having discrete worker castes (Table 4.4.2b). Both larger colony sizes and the presence of polygyny were associated with an increased probability of a species being polyandrous (Table 4.4.2b).

4.5 Discussion

I set out to explore the patterns of change in colony size, discrete worker castes, polygyny and polyandry throughout the ant phylogeny (including the number of independent origins of each trait), and also to test predictions concerning the correlations between colony size and discrete worker castes, polygyny and polyandry, in terms of both correlated change throughout the tree, and correlation between the traits of extant genera at the tips. I found that the data and tree suggest 6 independent origins of discrete worker castes, 11 independent origins of polygyny and 8 independent origins of polyandry. In addition, I found significant correlations between discrete worker castes and colony size; discrete worker castes and polyandry; polyandry and colony size; and polyandry and polygyny.

The first trait to evolve is polyandry, which appears deep in the tree at the split between the Poneroids and Formicoids, followed by polygyny at the split between the Dorylinae and the rest of the Formicoids. Finally, discrete worker castes are the last trait to evolve at the origin of the Myrmicinae, with subsequent later evolutions within the Ponerinae, Formicinae and Dorylinae. That polygyny and polyandry appear to pre-date discrete worker castes suggests support for the hypothesis that a committed worker caste must have evolved before selection for discrete worker castes begins, since it is expected that divergence from a monogynous, monandrous mating system can only occur once a dedicated worker caste has evolved (Hughes *et al.*, 2008a; Boomsma, 2009; Boomsma *et al.*, 2014), although this is not strong quantitative support. This makes sense, since if workers are still faced with the decision of helping or selfishly pursuing direct fitness, selection for a specialised worker phenotype will be considerably weaker. However, within lineages there are instances of polymorphism that are preceded by nodes where monandry is inferred (Figure 4.1). The early origin of polyandry may, however, be due to the coarse scale of the polyandry data in the literature. The only Ponerinae genus for which polyandry appears to be present is *Pachycondyla* (Kellner *et al.*, 2007), which is also highly paraphyletic (Schmidt, 2013). Since the taxonomy of this genus is yet to be resolved (this was true at the time of writing, but see Schmidt and Shattuck (2014)), it is methodologically very difficult to know which of the sections of the genus have evolved polyandry and which have not, and as a result in the present analysis polyandry appears to have evolved in the Ponerines six times. If, in reality, this figure is closer to one then the origin of polyandry is likely to have been inferred further up the tree, perhaps at the node where the Dorylinae diverge from the rest of the Formicoids. This node is also where colonies first evolve into the thousands of workers range, and where polygyny is inferred to have evolved. This reflects the importance of basic taxonomy in the study of macroevolutionary processes.

The pattern of colony size evolution inferred by the ancestral state reconstructions suggests that colony sizes have not evolved to exceed 100,000 workers at any internal nodes outside of the Dorylinae. This leads to the hypothesis that extremely large colonies outside of the Dorylinae have evolved relatively recently. It is thought that external factors such as competition (Adams & Tschinkel, 2001; Boswell *et al.*, 2001) or environmental pressures (Kaspari & Vargo, 1995; Adams & Tschinkel, 2001; Kaspari, 2005) can select for increasingly large colony sizes. One hypothesis to explain the deep evolution of large colonies in the Dorylinae, and the apparently recent development of large colony sizes in other lineages (for example *Formica* and *Atta*) is that the selective forces that have favoured large colonies are variable between lineages. The Dorylinae reproduce through colony fission, (Kronauer *et al.*, 2004; Kronauer *et al.*, 2007), which reduces dispersal ability and brings daughter colonies immediately into competition with their parent colony. Since it appears that inter-colony competition is strongly mediated by group size (Palmer, 2004; Hardy *et al.*, 2013) large colonies may be advantageous in species that reproduce through fission. Other lineages with very large colonies tend to reproduce by producing winged queens that act as propagules, increasing dispersal ability and potentially eliminating the high potential for competition. This suggests the hypothesis that in lineages that experience high levels of competition colony sizes may evolve to gradually become large, whereas in lineages where colony size is shaped by environmental pressures large colonies may evolve more rapidly.

It was predicted that discrete worker castes would positively associated with colony size (Bourke, 1999; Bourke, 2011) and polyandry (Cole, 1983; Boomsma & Ratnieks, 1996), and the correlation associated with this pattern was found in the data. That discrete worker castes tend to occur in species with larger colonies supports the idea that the evolution of larger colonies drives the development of social complexity (Bourke, 1999; Bourke, 2011). The correlation of discrete worker castes with polyandry supports the idea that the higher genetic diversity associated with multiple mating allows for a more diverse worker caste (Cole, 1983). However, when using multivariate models to test the predictors of discrete worker castes only colony size emerged as a significant predictor. This suggests that colony size is likely to be the dominant driver of the evolution of worker polymorphism in the ants, rather than polyandry. That polyandry is correlated with larger colony sizes in both univariate and multivariate models suggests that perhaps the benefits of increased genetic diversity brought on by multiple mating are stronger in larger colonies. For example, a large, long-lived colony may benefit from increased disease and parasite resistance more than a small and ephemeral one. The prediction that discrete worker castes should be negatively associated with polygyny (Oster & Wilson, 1978; Frumhoff & Ward, 1992) was not confirmed in this analysis, and no significant relationship was detected.

There was no relationship between discrete worker castes and polygyny and a significant positive relationship was found between polygyny and polyandry, converse to previous studies (Keller &

Reeve, 1994; Hughes *et al.*, 2008a). This relationship could be due to the fact the analysis was conducted at genus level; genera contain both polygynous and polyandrous species, but within the genus these two are negatively correlated. The nature of the relationship between these traits seems to be unclear – the predicted association has been documented in army ants (Rettenmeyer & Watkins, 1978; Kronauer *et al.*, 2007), and the reverse has been reported in the Myrmicine species *Myrmica sulcinodis* (Pedersen & Boomsma, 1999). It has been suggested that the occurrence of facultative polyandry obscures the predicted relationship between polygyny and polyandry (Kronauer & Boomsma, 2007). The data used in this analysis is at the genus level in order to maximise the coverage of extant ant diversity. This precludes the assignment of facultative or obligate polygyny to the taxa in this analysis, and hence the relationship between polygyny and polyandry at the species level (Keller & Reeve, 1994; Hughes *et al.*, 2008a) cannot be ruled out, even if absent at genus-level.

The inference of ancestral states depends strongly on the topology of the phylogeny. For this reason, I elected to use data at the genus level in order to preserve as much of the topology of the phylogeny in the analysis as possible. However, a potential cost of this decision is the fairly coarse scale of the data. This may limit the power of these analyses if, for example, predicted relationships occur beyond the genus level. Furthermore, there may be effects of environment that confound the analyses presented here. For example, colony size appears to have a hump-shaped relationship with net primary productivity (Kaspari, 2005). This suggests that by finding correlations with colony size, I could be in fact finding a correlation with an underlying environmental variable. Defining the environmental niche a genus occupies is problematic, since many genera have a global distribution. Although on one hand this might help to buffer models against the effects of environment, on the other hand it makes including environment as a cofactor extremely problematic.

The ancestral state reconstructions presented in this chapter reveal previously unknown patterns of social trait evolution in the ants. A quantitative estimate of the number of times discrete worker castes have evolved within the tree has been established, and the revealed patterns of the locations and number of origins of polygyny and polyandry suggest a role for selection for high genetic diversity relatively early in the history of the ants. The reconstructed patterns of colony size evolution lead to interesting hypotheses regarding the selective forces that favour large colonies between different groups. In addition, the evolutionary associations between social traits presented in this chapter confirm hypotheses concerning the process of social group transformation in the ants (Bourke, 2011), and strengthen the position of inclusive fitness as a tool for the study of cooperation in nature.

5 Colony size predicts division of labour in Attine ants

5.1 Abstract

Division of labour is central to the ecological success of eusocial insects, yet the evolutionary factors driving increases in complexity in division of labour are little known. The size-complexity hypothesis proposes that, as larger colonies evolve, both non-reproductive and reproductive division of labour become more complex as workers and queens act to maximise inclusive fitness. Using a statistically robust phylogenetic comparative analysis of social and environmental traits of species within the ant tribe Attini, we show that colony size is positively related to both non-reproductive (worker size variation) and reproductive (queen-worker dimorphism) division of labour. The results also suggested that colony size acts on non-reproductive and reproductive division of labour in different ways. Environmental factors, including measures of variation in temperature and precipitation, had no significant effects on any division of labour measure or colony size. Overall, these results support the size-complexity hypothesis for the evolution of social complexity and division of labour in eusocial insects. Determining the evolutionary drivers of colony size may help contribute to our understanding of the evolution of social complexity.

5.2 Introduction

Insect eusociality represents one of the major transitions in evolution (Maynard-Smith & Szathmary, 1995; Queller & Strassmann, 2009; Boomsma, 2013). In these events, groups of formerly free-living individuals become sufficiently integrated to be considered individuals in their own right. A key component of this process is the evolution of division of labour (Maynard-Smith & Szathmary, 1995; Bourke, 2011; Simpson, 2012). In eusocial societies, the presence of a sterile caste (workers) and a dedicated reproductive caste (queens) creates a reproductive division of labour, while behavioural or morphological specialization within the worker caste on tasks such as brood care, nest maintenance, foraging and defence creates a non-reproductive division of labour. In 'simple' eusocial societies, queens are morphologically similar to workers, and workers are monomorphic. In 'complex' eusocial societies, queen-worker dimorphism is extreme and there is wide variation in worker size, often accompanied by discrete physical worker castes (Hölldobler & Wilson, 1990; Bourke, 1999; Bourke, 2011). Previous studies have suggested positive effects of division of labour on the foraging efficiency and colony productivity of social insects, and hence on their ecological success (Beshers & Traniello, 1994; Passera *et al.*, 1996; Yang *et al.*, 2004; Arnan *et al.*, 2011). However, the evolutionary determinants of division of labour have been less well researched.

The 'size-complexity hypothesis' proposes that, as colony size increases, workers and queens maximize their inclusive fitness by specializing in non-reproductive and reproductive roles, respectively (Alexander *et al.*, 1991; Bourke, 1999; Bonner, 2004; Bourke, 2011). Since such specialization permits further increases in colony size, the degree of non-reproductive and reproductive division of labour both increase via positive feedback between social complexity and colony size. The hypothesis therefore leads to the prediction that colony size is positively associated with two key aspects of social complexity - non-reproductive and reproductive division of labour.

Although theoretical models (Gautrais *et al.*, 2002; Jeon & Choe, 2003) and single taxon experimental studies (Jeanne, 1986; Karsai & Wenzel, 1998; Thomas & Elgar, 2003) offer some support for the size-complexity hypothesis, whether the predicted across-species relationships occur remains unclear, as early comparative studies (Bourke, 1999; Anderson & McShea, 2001) were informal and lacked an explicit evolutionary framework (Dornhaus *et al.*, 2012). More recent phylogenetic comparative studies across formicoid ant species (Fjerdingstad & Crozier, 2006) and corbiculate bees (Rodriguez-Serrano *et al.*, 2012) found positive correlations between colony size and measures of social complexity. While informative, these studies either omitted species with very large colony sizes (10^6 workers or more) (Fjerdingstad & Crozier, 2006), potentially missing the predicted relationships (Bourke, 2011), or measured social complexity as a single variable (Rodriguez-Serrano *et al.*, 2012), potentially missing the independent effects of colony size on individual components of social complexity, namely the extent of reproductive and non-reproductive division of labour (Fjerdingstad & Crozier, 2006).

Moreover, no previous study has considered possible effects of environmental factors, yet these also potentially influence the relationship between colony size and division of labour. For example, in ants, a non-linear relationship exists between colony size and primary productivity such that higher primary productivities are associated with decreasing colony size (Kaspari, 2005). This suggests that it is important to control for environmental factors when analysing correlates of colony size across species. Environmental factors may also influence division of labour directly. Experiments show that in the desert ant *Cataglyphis velox*, smaller workers forage at lower temperatures than larger ones, suggesting that worker size variation has evolved as a mechanism for colonies to cope with diurnal fluctuations in temperature (Cerdá & Retana, 1997). Overall, therefore, the potential role of environmental factors needs to be considered to gain a full understanding of the evolution of division of labour.

To test for evolutionary relationships between division of labour, colony size and environmental factors, we gathered species-specific data on social traits and evolutionary relationships and conducted a phylogenetically-controlled comparative analysis within the neotropical ant tribe Attini. We used worker size variation and queen-worker dimorphism as measures of non-reproductive and reproductive division of labour, respectively. We selected ants as the focal taxon because ants are the most socially diverse and ecologically successful social insect group (Hölldobler & Wilson, 1990; Moreau & Bell, 2013). We focused on the tribe Attini because this taxon (252 species) exhibits wide variation in worker size, queen-worker dimorphism and colony size, and occurs in a relatively broad range of habitats and latitudes (Mueller *et al.*, 1998; Murakami *et al.*, 2000; Mueller *et al.*, 2001; Hughes *et al.*, 2003; Rabeling *et al.*, 2007; Mehdiabadi & Schultz, 2010; Henrik *et al.*, 2013). In addition, the Attini are predominantly monogynous (Mehdiabadi & Schultz, 2010), i.e., having a single queen heading a colony, such that the size-complexity hypothesis can be tested in the absence of confounding effects of variation in colony genetic and social structure brought about by polygyny (multiple queens heading colonies) (Frumhoff & Ward, 1992; Bourke, 2011). Controlling for environmental variation, we show that evolutionary increases in colony size across the Attini are associated with increases in both worker size variation and queen-worker dimorphism.

5.3 Method

5.3.1 Data collection

We used all Attini genus names, including synonyms, as search terms in Web of Knowledge, Scopus and Google Scholar literature databases up to 2013. Literature sources resulting from this search were scanned manually and relevant data were extracted. Data from secondary sources were excluded. Additional data were collected from AntWeb (http://www.antweb.org). Data from 58 sources covering 632 observations of populations for 57 out of a total of 252 species in the Attini were collected (see electronic supplementary material, table S1). These data represented all Attine genera (except for the socially parasitic *Pseudoatta,* a derived form of *Acromyrmex* (Cristiano *et al.*, 2013), and the recently erected genus *Paramycetophylax*). Taxonomic names followed the Bolton World Catalogue (http://www.antweb.org).

Data were collected and stored in a database following recommendations in Kattge et al. (Kattge *et al.*, 2011b). The following traits were recorded: worker and queen size measured as head width in mm (92 observations of populations for 36 and 39 species for worker and queen head widths, respectively), colony size (number of workers at colony maturity) (178 observations, 43 species) and geographical location (362 observations, 48 species). Where specific coordinates were not supplied in the source reference, they were inferred from the description of the locality except where the specified area exceeded 20 km^2. In these cases the locality was deemed to be uninformative and excluded from analysis. Head-width measurements taken from AntWeb (http://www.antweb.org) (17 and 13 species for worker and queen head widths, respectively) were measured using the image analysis software ImageJ (Schneider *et al.*, 2012). To ensure the measurements obtained from the specimens on AntWeb were representative, we compared the measurements obtained from images of seven species well represented both in the literature and on AntWeb. In all cases the AntWeb measurements were not significantly different from those obtained from the literature (paired *t*-test, *t* =1.044, *p* = 0.34, n = 7).

We calculated per-species means for colony size and worker and queen head width (see electronic supplementary material, table S1) by averaging the mean value from each observation weighted by its sample size as:

$$\bar{x}\ mean\ trait\ value = \frac{\sum(x_s n_s)}{\sum n_s}$$

where x_s is the mean of the observation, n_s is the observation sample size, and Σn_s is the sum of all sample sizes of the observations contributing to the per-species mean for each trait. Observation sample sizes ranged from 1-1016; however, in many cases, observation sample sizes were not given in the original source and here we assumed it to equal 1. We report Σn_s as the sample size for each per-species mean trait value as this is more appropriate to the nature of our data than the number of sources.

To measure non-reproductive division of labour for each species, we quantified worker size variation using the coefficient of variation in worker head width (36 species) following previous authors (Fjerdingstad & Crozier, 2006). We selected the coefficient of variation as it was an objective measure of trait variation that avoided subjective assessment of the number of discrete worker castes. In addition, using number of worker castes to measure worker size variation would not quantify non-reproductive division of labour correctly in species with size-based polyethism and a continuous distribution of worker sizes (Beshers & Traniello, 1994; Arnan *et al.*, 2011). Worker size variation was calculated as:

$$Worker\ size\ variation = 100\left(\frac{\sigma\ worker\ head\ width}{\bar{x}\ worker\ head\ width}\right)$$

where $\bar{x}$ = mean, σ = standard deviation. Standard deviation of worker head width was calculated as the standard deviation of all mean worker head width observations contributing to each per-species value, and $\bar{x}$ worker head width was calculated by averaging the mean value from each observation weighted by its sample size. Our measure of worker size variation was not influenced by sample sizes: a linear regression model (for data where observation sample sizes were known, controlling for study effort) of square root worker size variation and log Σn_s was not significant (log Σn_s, beta = 0.002, df = 2, 30, *p* = 0.857).

To measure reproductive division of labour for each species, we quantified queen-worker dimorphism as the percentage difference between mean queen head width and mean worker head width (30 species), i.e. as:

$$Queen - worker\ dimorphism = 100\left(\frac{2(\bar{x}\ queen\ head\ width - \ \bar{x}\ worker\ head\ width)}{\bar{x}\ queen\ head\ width + \ \bar{x}\ worker\ head\ width}\right)$$

For both measures we selected head width as a measure of body size because it is the most commonly reported measure of queen and worker size in the literature and, although showing allometric variation in some cases (e.g. *Atta* (Oster & Wilson, 1978)), it correlates well with body size (Hölldobler & Wilson, 1990; Kaspari, 1993; Vainio *et al.*, 2004; Weiser & Kaspari, 2006).

To quantify environmental variation we downloaded the following data layers from the online database BioClim (http://www.worldclim.org/bioclim): diurnal temperature range, isothermality, temperature seasonality, and precipitation seasonality. We resampled BioClim data from its original resolution into a grid size of 10 arc-minutes per pixel (approximately 20km^2 at the equator) to reflect the threshold at which we discarded locality information. The R package "raster" (Hijmans & van Etten, 2012) was used to extract these environmental values for sets of coordinates derived from the source references for each ant species and mean values for each species were calculated for use in subsequent analyses (48 species). Species locations ranged from latitudes between 41.0^o (DEC) and -29.7^o (DEC), showing a broad range of environmental variation (see appendix 4, table A4.1, figure A4.1).

5.3.2 Phylogenetic reconstruction

Analyses of traits across species are often confounded by non-independence because closely related taxa have similar traits due to shared evolutionary history (Felsenstein, 1985). This non-independence can be statistically controlled for in analyses by incorporating an estimate of evolutionary relatedness. However, constructing rigorous and unbiased estimates of evolutionary relationships for all the taxa of interest is challenging when existing phylogenetic studies are incomplete and conflicting and use non-overlapping datasets (Bininda-Emonds, 2004). Previous phylogenetic analyses of social traits in ants have not used formal methods to link separate phylogenies or cover missing taxa (Fjerdingstad & Crozier, 2006; Armitage *et al.*, 2012; Kramer & Schaible, 2013), resulting in phylogenetic estimates that may be biased and that contain no estimates of uncertainty.

Here, we go beyond previous studies and construct an Attini consensus phylogeny that analyses the available phylogenetic hypotheses to generate a new, unbiased estimate, accompanied by calculations of uncertainty. We constructed a phylogeny using supertree protocols (Jones *et al.*, 2002; Bininda-Emonds, 2004; Nyakatura & Bininda-Emonds, 2012), since these methods allowed us to produce a tree that maximised the number of species in the resulting phylogeny and therefore the phylogenetic overlap with the species in our trait dataset. Available phylogenetic information for Attini is mainly based on morphological characters and is not well represented by genetic sequences in GenBank. As other consensus phylogenetic methods rely on constructing an estimate from genetic sequences (e.g. the supermatrix approach (de Queiroz & Gatesy, 2007)), we chose the supertree method as the most appropriate for these data as it can combine both morphological and genetic evidence. We used matrix representation with parsimony (MRP) (Bininda-Emonds, 2004; Nyakatura & Bininda-Emonds, 2012). This method involves coding the topologies of published phylogenies into a weighted character matrix that is analysed using maximum parsimony to produce a composite tree (Bininda-Emonds *et al.*, 2005). MRP was selected for consistency with previous studies employing supertree methods (Buerki *et al.*, 2011; Nyakatura & Bininda-Emonds, 2012) and has been shown to return trees as well supported as those derived using other methods (Gaubert *et al.*, 2009; Davis *et al.*, 2010b; Nguyen *et al.*, 2012). Prior to analysis we implemented safe taxonomic reduction (Wilkinson, 1994) to remove species that had little or no phylogenetic signal, which if retained would reduce the resolution of the final tree. The final matrix had 71 out of 252 species drawn from 12 source phylogenies (see the electronic supplementary material, table S2), representing all genera of Attini (except for *Paramycetophylax*). We implemented a parsimony ratchet (Nixon, 1999) in PAUP* v.4.0b10 (Swofford, 2002) to analyse the matrix, and took the resulting consensus. Support values for each node of the tree were generated using rQS (Price *et al.*, 2005), which prunes the supertree and each source tree to confer identical taxon sets on them and then compares the topologies, assigning each node a score between +1 (full support) and -1 (total conflict). Positive rQS values indicate support for a node. We obtained, aligned and concatenated 4321 bp of sequence data for five genes (*wingless*, *long-wavelength Rhodposin*, *elongation factor 1 alpha 1*, *elongation factor 1 alpha 2* and *cytochrome oxidase subunit 1*) from species of the Attini represented in GenBank (Benson *et al.*, 2010). We used the software packages BEAST (Drummond *et al.*, 2012) in conjunction with the alignment to calculate relative branching time estimates for the species shared between the alignment and the supertree following previous studies (Nyakatura & Bininda-Emonds, 2012) under a strict molecular clock (Purvis, 1995). Three Attini fossils were used as calibration points at nodes 11 (Baroni Urbani, 1980), 50 (de Andrade, 2003) and 54 (Schultz, 2007) and a non-Attini fossil (*Pheidole*) (Dubovikoff, 2011) was used to date node 1 (see electronic supplementary material, figure S2), allowing dates to be calculated from relative branch lengths. The Perl script chronographer.pl (Bininda-Emonds, 2012b) was used to infer missing node ages based on a pure-birth model resulting in a supertree topology with branching time estimates following (Nyakatura & Bininda-Emonds, 2012). The final supertree was deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S14540).

5.3.3 Data analysis

We tested all social traits for phylogenetic signal using the phylogenetic generalised least squares (PGLS) function of the R package "caper" (Orme *et al.*, 2012). All traits contained phylogenetic signal (worker size variation lambda = 0.97, queen-worker dimorphism lambda = 0.94 and colony size lambda = 0.91), and so we used phylogenetically-controlled regression models in subsequent analyses.

Data were checked for normality and outliers. We used a square-root transformation for worker size variation and a natural log. transformation for queen-worker dimorphism and colony size to normalize the data. We checked for colinearity in all models separately by calculating variance inflation factors (VIF) for each covariate. Covariates were sequentially eliminated starting with the largest VIF until all VIFs were less than three (Zuur *et al.*, 2010).

Before fitting any models we removed species from the analysis with any missing data, resulting in a dataset of 19 species. We adopted an information-theoretic approach to analyse the effects of social and environmental factors on non-reproductive and reproductive division of labour. PGLS models describing each possible iteration of specific hypotheses were fitted to the data. We used the corrected Akaike information criterion (AICc) to assess model fit, and calculated small-sample AICc weight and ΔAICc (the difference in AICc between the model in question and the best fitting model) for each model. Models with ΔAICc <7 were considered uninformative and were discarded (Burnham *et al.*, 2011). Since no model had an AICc weight >0.44 and the informative models for each hypothesis included between them all covariates, we do not report a single best model. We instead report relative importance and averaged parameter estimates from the set of informative models (Burnham *et al.*, 2011).

The averaged models were based on a single consensus phylogenetic tree (a strict consensus of 10,000 equally parsimonious trees). Parameter estimates of the models are influenced by the phylogenetic estimate used and therefore are sensitive to other reconstructions (Pearse & Hipp, 2012). To investigate the effects of phylogenetic uncertainty on our analysis, we fitted PGLS models on a dated sample of 1,000 of the 10,000 most parsimonious trees from the PAUP* analysis of the MRP matrix. We selected only variables that had a cumulative AICc weight of >0.4 for these models. This allowed more accurate measurements of parameter estimates, which were generated as means from the sample of models, and of 95% phylogenetic uncertainty intervals (Pearse & Hipp, 2012).

5.4 Results

5.4.1 Trait data

Mean worker size variation ranged from 0.23 to 64.37 (36 species), queen-worker dimorphism from 1.54% to 84.25% (30 species) and colony size from 16 to 6×10^6 workers (43 species). The largest values for all these traits were found in the genera *Atta* and *Acromyrmex* (the leafcutter ants) (Figure 5.1).

5.4.2 Phylogenetic reconstruction

The topology of our supertree (Appendix 4, figure A4.2) was broadly in agreement with the most recent molecular phylogeny for the Attini (Schultz & Brady, 2008). Clades that emerged as paraphyletic were *Cyphomyrmex* (with respect to *Mycetophylax conformis*) (node 7) and *Trachymyrmex* (with respect to *Sericomyrmex*) (node 12). None of these relationships are novel (Schultz & Meier, 1995; Villesen *et al.*, 2002; Schultz & Brady, 2008) and no novel clades were generated (Bininda-Emonds, 2003). Furthermore, the supertree recovered the three clades of Attini defined by the nature of their fungal-agricultural system, i.e. the lower Attines (which cultivate environmentally derived fungi), the higher Attines excluding leafcutters (which engage in obligate fungal symbiosis but do not harvest fresh leaves) and the leafcutters (which engage in obligate fungal symbiosis and harvest fresh leaves) (Schultz & Brady, 2008; Henrik *et al.*, 2013). The mean rQS score over 10000 bootstrap replicates of the tree was 0.282 and only three (nodes 52, 59 and 60) of the 60 nodes had a negative rQS score (reflecting more mismatches than matches in the source trees) (see electronic supplementary material, table S3). We dated the root node (node 1) to 37.7 million years (MY) ago, the node representing the origin of the higher Attini to 17.3 MY ago and the origin of the leafcutters to 12 MY ago. While this root estimate is 8.3-17.3 MY younger than equivalent nodes on other molecular trees (Schultz & Brady, 2008), the other values of the other nodes are within the confidence intervals of previous estimates (Schultz & Brady, 2008).

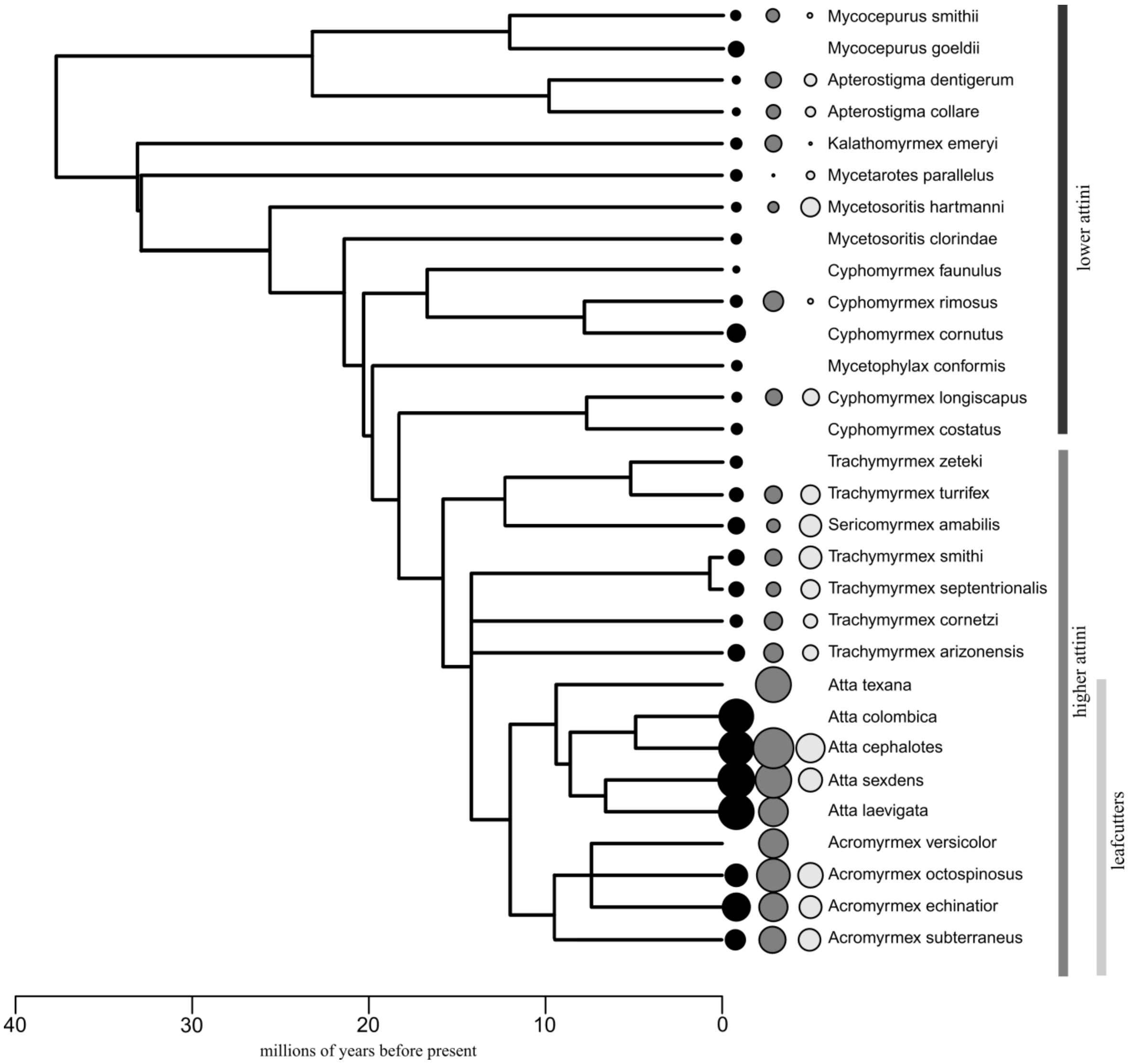


Figure 5.1 Distribution of colony size, worker size variation and queen – worker dimorphism on a phylogenetic supertree for the Attini (30 species). The full tree (Appendix 4, figure A4.1) was pruned to include only the species for which there were data on at least one trait and appeared in the phylogeny. Black circles are proportional to ln mean colony size, grey circles to the square root of worker size variation and white circles to ln queen – worker dimorphism. Branch lengths are proportional to time (Myr).

5.4.3 Determinants of non-reproductive division of labour

Colony size was significantly positively correlated with worker size variation (Table 5.1; figure 5.2). All models featured colony size as a covariate and had a range of high R^2 values (0.770-0.818), and colony size had a cumulative AICc weight of 1, showing its importance in all supported models. Furthermore, colony size was the only covariate in the averaged model to have confidence intervals that did not include zero (Table 5.1). The presence of queen-worker dimorphism, mean diurnal temperature range and precipitation seasonality in the averaged model suggest they have an effect on worker size variation; however, all three of these covariates had confidence intervals that included zero (Table 5.1). Models omitting colony size had no support (w_i=0 in both cases, appendix 4, table A4.4a). These models were robust to phylogenetic uncertainty (table 1).

Differences in mating systems among the Attini could have potentially confounded our analyses as species that were found to exhibit the largest colony sizes and worker size variation (leafcutter ants) are polyandrous (Villesen *et al.*, 2002). To investigate this, we reanalysed our data including mating system as a dichotomous variable (0, monandrous and 1, polyandrous) in the models. We used all data on the presence and absence of polyandry from the literature and, for non-leafcutter ant species where data were not available, we assumed monandry (electronic supplementary material, table S1). We found the significance of the correlation between colony size and worker size variation to be unchanged whilst controlling for queen-worker dimorphism and mating system (for colony size, $\beta = 0.271$ (CI = 0.133, 0.509), W = 0.93, results from an averaged model).

5.4.4 Determinants of reproductive division of labour

To complement the analysis of Fjerdingstad & Crozier (Fjerdingstad & Crozier, 2006), which found that colony size and worker size variation across 35 ant species were not significantly associated after controlling for queen-worker dimorphism, we first ran a model that included worker size variation as a covariate. This found no effect of colony size on queen-worker dimorphism. The resulting averaged model had only parameter estimates with confidence intervals that included zero (Table 5.1). The best fitting model set also captured less of the variation in queen-worker dimorphism than the models for worker size variation ($r^2 = 0.031\text{-}0.342$). These analyses were robust to phylogenetic uncertainty (Table 5.1). However, according to our VIF threshold (VIF for worker size variation = 4.80), colony size and worker size variation could not be in the model together. We therefore ran models omitting worker size variation, which showed colony size to be a positive predictor of queen-worker dimorphism (Table 5.1). The effect was not as powerful as the effect of colony size on worker size variation, and the covariate was not universally shared in the most informative models (cumulative AICc weight = 0.85). Overall, therefore, we found a significant positive correlation between colony size and queen-worker dimorphism, but this result was weaker than the correlation of colony size with worker size variation. Moreover, it disappeared when worker size variation was included as a covariate, either because of shared variance or because worker size variation predicts queen-worker dimorphism better than colony size.

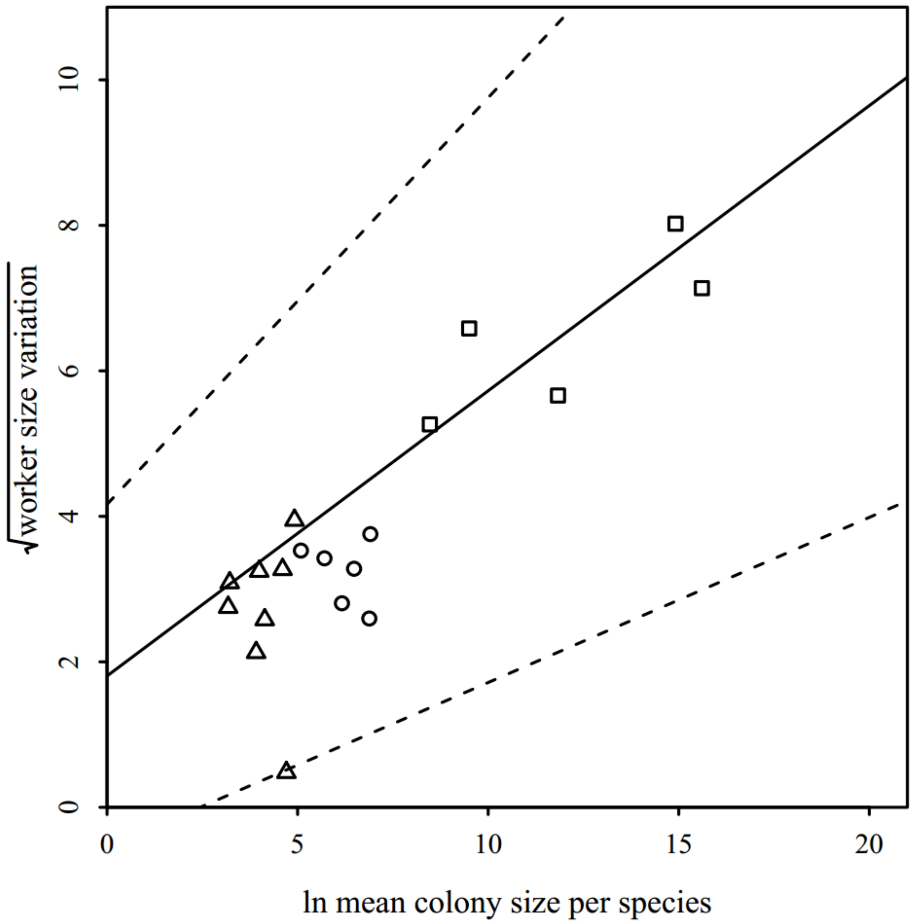


Figure 5.2 The relationship between ln mean colony size and square-root worker size variation in the 19 species of Attini for which colony size and worker size variation data were available; triangles represent the lower Attini, circles the higher Attini (excluding the leafcutter ants) and squares the leafcutter ants. Slope and intercept are taken from the phylogenetically controlled averaged model (Table 5.1), and dotted lines are +95% CIs from the same model.

5.4.5 Environmental determinants of colony size

We found no significant correlations between colony size and any of the environmental variables tested (Table 5.1). The r^2 value of all models was low (range 0.001-0.211) and in all resulting average models the confidence intervals of the covariates overlapped with zero.

Table 5.4.1 Averaged models describing effects of covariates on worker size variation, queen-worker dimorphism (where (a) and (b) represent models excluding and including worker size variation, respectively) and colony size in the Attini. Regression coefficients and confidence intervals are reported from best (ΔAICc < 7) phylogenetic generalised least squares (PGLS) models from full candidate sets (Appendix 4, tables A4.4a, b and c). Bold type indicates significant covariates.

Covariates	**Worker size variation**	**Queen-worker dimorphism (a)**	**Queen-worker dimorphism (b)**	**Colony size**
(intercept)	*β*=1.806 (-0.554, 4.165), *pCI*±0.000	*β*=1.659 (1.644, 1.675), *pCI*±0.031	β=0.923 (-0.957, 2.802), pCI±0.010	*β*=4.230 (-3.954-12.414), *pCI*±0.146
Colony size	***β*=0.392 (0.227, 0.559), *pCI*±0.000, W=1.00**	***β*=0.159 (0.042, 0.276), *pCI*±0.001, *W*=0.85**	*β*=0.135 (-0.030, 0.301), *pCI*±0.005, *W*=0.60	-
Worker size variation	-	-	*β*=0.235 (-0.127, 0.598), *pCI*±0.011, *W*=0.52	-
Queen-worker dimorphism	*β*=0.108 (-0.497, 0.713), *pCI*=±0.000, *W*=0.48	-	-	-
Mean diurnal temperature range	*β*=-0.015 (-0.035, 0.0058), *pCI*±0.000, *W*=0.69	-	-	*β*=-0.021 (-0.071, 0.029), *pCI*±0.001, *W*=0.40
Isothermality	-	*β*=-0.004 (-0.044, 0.036), *W*=0.28	*β*=-0.003 (-0.046, 0.038), *W*=0.33	*β*=0.022 (-0.126, 0.170), *pCI*±0.001, *W*=0.50
Temperature seasonality	-	-	-	-
Precipitation seasonality	*β*=0.013 (-0.017, 0.043), *pCI*±0.000, *W*=0.041	*β*=0.0009 (-0.014, 0.016), *W*=0.28	*β*=0.004 (-0.009, 0.016), *W*=0.36	*β*=-0.015 (-0.210, 0.179), *pCI*±0.001, *W*=0.62
Isothermality*precipitation seasonality	-	-	-	*β*=0.003 (-0.0002, 0.006), *W*=0.13
Latitude	-	-	-	*β*=0.009 (-0.077, 0.096), *W*=0.19

5.5 Discussion

In agreement with the size-complexity hypothesis (Alexander *et al.*, 1991; Bourke, 1999; Bonner, 2004; Bourke, 2011), our study shows that colony size is significantly positively correlated with measures of non-reproductive and reproductive division of labour in a tribe of ants. These findings provide novel support for the size-complexity hypothesis; we detected a strong relationship between colony size and worker size variation independent of the effects of queen-worker dimorphism, we controlled for environmental factors and we separated social complexity into component traits. Our results are also consistent with a recent study linking colony size with another predicted correlate of social complexity (Alexander *et al.*, 1991; Bourke, 1999; Bourke, 2011), namely divergence in queen and worker lifespans in the eusocial Hymenoptera (Kramer & Schaible, 2013). In addition, our results strengthen the idea that group size and complexity are positively related in the evolution of other levels of complexity within the hierarchy of major transitions, such as the evolution of multicellularity (Bonner, 2004; Bourke, 2011; Simpson, 2012; Fisher *et al.*, 2013).

We found no evidence for any effects of environmental factors on worker size variation, queen-worker dimorphism or colony size. Although colony size and primary productivity appear to be associated in ants, the relationship is non-linear (Kaspari, 2005) and, in general, relationships between colony size, latitude and climatic variables vary considerably across ant taxa (Purcell, 2011). Therefore, the lack of effects of environmental factors in our study could have arisen because Attini are exceptions to the colony size-primary productivity relationship or because the study sampled species across the range of primary productivities where the relationship is approximately flat (Kaspari, 2005).

Our results suggest that colony size acts upon the two forms of division of labour in different ways. Specifically, we found that the positive association between colony size and queen-worker dimorphism became non-significant when worker size variation was included, whereas the positive association between colony size and worker size variation remained significant in both the presence and absence of queen-worker dimorphism. If the two forms of division of labour responded to increasing colony size in the same way, we would have expected to see any combination of the two measures result in the absence of a positive association (due to very high colinearity). One plausible scenario that could account for our findings is non-simultaneous evolution of the two traits. A potential mechanism for this arises from an assumption of the size-complexity hypothesis, namely that the chance of any given worker attaining direct fitness falls as colonies evolve to become larger (Alexander *et al.*, 1991; Bourke, 1999; Bourke, 2011). If so, this would lead workers' inclusive fitness interests to coincide more closely with those of queens at larger colonies sizes (Bourke, 2011), since workers would be more strongly selected to maximise their fitness indirectly by aiding the direct reproduction of queens. Selection for worker size variation, which helps improve colony productivity (Beshers & Traniello, 1994; Fournier *et al.*, 2008), might then lead to even stronger selection for increased fecundity in queens and hence to greater queen-worker dimorphism. This hypothesis could be tested by investigating the order of trait divergence among worker size variation, queen-worker dimorphism and colony size, or by investigating the rates of evolutionary change of these traits.

An unexpected association from our results was a link between fungal-agricultural system and colony size. This was shown by the clustering of the three agricultural groups within the Attini, i.e., lower Attines, higher Attines (excluding leafcutter ants) and leafcutter ants, within the continuum of association between worker size variation and colony size (figure 2). To investigate this more formally, we examine the relationship between colony size and fungal-agricultural system. We find that colony size has a highly significant effect on agricultural system when treated as either a continuous variable (PGLS, β=0.12, $p < 0.001$), or a categorical variable (univariate multinomial logistic regression, Appendix 4, multinomial model analysis). Although it is not possible from current data to determine the evolutionary sequence of events, a possible scenario is that shifts in the fungal-agricultural system in the Attini act as ecological drivers permitting increases in colony size, and that these then lead to increases in the complexity of division of labour proposed by the size-complexity hypothesis and detected by our analysis.

As phylogenetic reconstructions and large datasets of social and environmental trait data become increasingly available, studies like the present one that combine the power of phylogenetically-controlled analyses with the rich social and ecological diversity of eusocial insects will help test the size-complexity hypothesis in additional taxa and, more generally, investigate further how social and environmental factors influence the evolution of social complexity and division of labour within societies.

6 Colony size, worker polymorphism and polygyny are associated with increased diversification rates in ants.

6.1 Abstract

Explaining the imbalance in species richness of phylogenies is a central goal of the study of biodiversity and macroecology. The ants are the most diverse of the eusocial Hymenoptera, numbering nearly 13,000 species. These species are not evenly distributed throughout the ant phylogeny, and evidence suggests that there have been several significant increases in diversification rates in the ant tree of life. Theory suggests that the evolution of complex eusociality within the ants might be a driver of these increases in diversification rate. Large colonies may enable species to exploit new environments more efficiently, and the presence of discrete worker castes may confer phenotypic plasticity at the colony level, enabling species exhibiting this trait to adapt and diversify into new environments more rapidly than competitors. The evolution of polygyny and polyandry increases the genetic diversity within colonies, which is associated with several colony-level benefits, including enhanced division of labour, but are also associated with the weakening of the selective forces that favour cooperation. The evolution of mating systems may therefore have positive or negative effects on the diversification patterns in ants. In this chapter I begin by using a complete-genus level phylogeny to test for significant shifts in the diversification rates of ants. I then adopt a model-based approach to test the hypotheses that colony size, discrete worker castes, polygyny and polyandry are associated with increased rates of diversification. I find evidence of 15 diversification shifts in the history of the ants, and evidence that intermediate colony sizes, discrete worker castes and polygyny are associated with increased diversification rates.

6.2 Introduction

The ants are the most diverse clade of all eusocial insects (the family Formicidae contains 12,981 species) and have achieved ecological dominance in every habitat in which they occur, filling ecological roles as predators, scavengers, herbivores, detritivores and possibly even biotic weathering agents (Hölldobler & Wilson, 1990; Wilson & Hölldobler, 2005; Dorn, 2014). The ant phylogeny is characterised by an extreme imbalance in the distribution of diversity within it (for example, the subfamily Myrmicinae contains 6,497 species, and the subfamilies Martialinae and Paraponerinae contain only 1 species each), as is typical of phylogenies of large clades, suggesting that diversification rates are not uniform between ant clades (Wilson & Hölldobler, 2005). Three previous studies have investigated diversification patterns in ants. The first suggested that the ants had diversified in conjunction with the angiosperms (Moreau *et al.*, 2006). However, a second study reanalysed the same data and suggested that the exceptional increase in diversification rates during the radiation of the angiosperms (Moreau *et al.*, 2006) was an artefact of incomplete taxon sampling, and demonstrated that the net rate of lineage accumulation has been constant throughout the history of the ants (Pie & Tschá, 2009). Furthermore, Pie and Tschá (2009) found evidence for heterogeneous diversification rates between ant lineages. This variation in diversification rate between lineages was not related to lineage age, and instead was hypothesized to be driven by a highly heritable trait (Pie & Tschá, 2009). Finally, a third study used a large phylogeny to examine whether the high tropical diversity of ants is a result of long occupation time or an inherently higher diversification rate in the tropics (Moreau & Bell, 2013). This work identified 10 diversification shifts in the ant phylogeny and found evidence for both hypotheses (Moreau & Bell, 2013). None of these studies used a complete phylogeny, but, combined, they provide evidence that shifts in diversification rate have occurred in the history of ant evolution. As phylogenies become larger, the number and position of these shifts will be estimated with more accuracy.

Patterns of diversification across phylogenies have long been of interest to evolutionary biologists (Coyne & Orr, 2004). Such patterns arise from the balance between the rate of lineage accumulation (e.g. speciation) and the rate of lineage extinction. Explaining the balance of speciation and extinction can help researchers understand the processes that generate biodiversity on Earth, and identifying traits that are important to diversification deepens the understanding of the biology of a clade of interest. When compared to null models, phylogenies exhibit imbalance, i.e. some clades have more species in than others, implying non-uniform patterns of diversification (Mooers & Heard, 1997; Purvis *et al.*, 2011). For example, the Myrmicinae ant genera *Pheidole* and *Pilotrochus* contain 1006 and 1 species, respectively (Bolton, 2012). Explaining this lack of uniformity remains a central goal in macroecology (Gaston & Blackburn, 2000). It has been suggested that diversification is driven by increases in speciation rate when new geographical ranges and niche spaces are colonised and/or by decreases in speciation rate when they become saturated (Purvis *et al.*, 2011). Shifts in diversification rates have been empirically associated with both extrinsic factors (e.g. ecology (Kelley & Farrell, 1998; Nylin *et al.*, 2014), range shifts (Moore & Donoghue, 2007), latitude (Wiens, 2007), climate (Schweizer *et al.*, 2011) and the diversification of other clades (Roelants *et al.*, 2007)), and intrinsic factors (e.g. shifts in morphology (Blackledge *et al.*, 2009; Dumont *et al.*, 2011), niche shifts (Marvaldi *et al.*, 2002), dispersal ability (Gianoli, 2004) and dietary shifts (Fordyce, 2010; Schweizer *et al.*, 2011)). These studies show an interplay between intrinsic and extrinsic factors, suggesting that the relationships between organismal biology, environmental factors and diversification patterns is complex and not straight-forward.

Early methods for characterising the rate of diversification within phylogenies relied on relatively simplistic models. For example, the earliest models of diversification patterns assumed constant speciation and extinction rates, both within and between clades, and through time (Nee *et al.*, 1994). These same assumptions applied to the γ-statistic approach of Pybus and Harvey (2000), which measured whether the nodes (points of lineage diversification) in a phylogeny were concentrated more towards the root ($\gamma < 0$) or the tips ($\gamma > 0$) of the phylogeny when compared to a pure-birth model (a model of lineage accumulation with no extinction parameters (Yule, 1925)). As methods were developed that relaxed this assumption, it became clear that the equal-rates assumption was not biologically realistic (e.g. Rabosky *et al.* (2007); Alfaro *et al.* (2009); Freckleton and Jetz (2009)), such that the equal-rates models then served as null models against which more complex models could be compared. The more complex models now incorporate speciation and extinction rates that vary through time (Rabosky & Lovette, 2008b) and across clades (Rabosky *et al.*, 2007; Alfaro *et al.*, 2009), the effect of environmental variation, the effects of clade diversity (diversity dependence, e.g. as clades grow diversification slows, reflecting saturation (Rabosky & Lovette, 2008a; Etienne & Haegeman, 2012)), and the effects of traits on diversification (trait dependence (FitzJohn, 2012)). Of these methods, the most widely used in recent years is MEDUSA (Modelling Evolutionary Diversification Using Stepwise AIC, (Alfaro *et al.*, 2009)). This method has been applied to investigate patterns of diversification in many clades, including jawed vertebrates (Alfaro *et al.*, 2009), flies (Wiegmann *et al.*, 2011), birds (Jetz *et al.*, 2012), ray-finned fish (Near *et al.*, 2012), and ants (Moreau & Bell, 2013). The strengths of the MEDUSA method are that it identifies shifts in diversification rates between clades without an *a priori* hypothesis, so allowing for between-clade variation in diversification rate, and explicitly accounts for incompletely sampled phylogenies.

A potential drawback of this method is that it makes the assumption that speciation and extinction rates are fixed within each rate regime in the model. Another drawback is that, by taking a stepwise approach, the model could miss configurations of rate shifts that might fit the data better if the best fitting model exists beyond the first optimum model the algorithm reaches.

Models of trait-dependent diversification enable investigators to examine the effect of a binary discrete character, multistate discrete character or continuous character on the diversification within a phylogeny of species. Early models of this nature compared the diversity of clades possessing a trait of interest to the diversity of their sister clades (Slowinski & Guyer, 1993). More sophisticated models, however, allow the speciation and extinction rate parameters of a model of diversification to covary with the value of a binary discrete character, a multistate discrete character or a continuous character (FitzJohn, 2012).

Eusociality is almost certainly responsible for the ecological success of the ants as a whole (Hölldobler & Wilson, 1990; Lach *et al.*, 2010). Within the ants, variation in social traits may be responsible for potential variation in diversification rates. For example, it has been hypothesized that the evolution of large colony size is responsible for the large diversity of species in subfamilies such as the Dolichoderinae and the Formicinae (Grimaldi & Engel, 2005), and such considerations may generalise to explain the variation in diversification observed across the entire family.

Phenotypic plasticity has been suggested as a general driver of diversification, by allowing a species to rapidly produce new phenotypes to exploit new niches and/or environments (West-Eberhard, 1986; Pfennig *et al.*, 2010). In ants, it is possible that phenotypic plasticity in the extent of non-reproductive division of labour, i.e. discrete worker castes, enables lineages to diversify into new ecological niches more rapidly (Passera *et al.*, 1996; Yang *et al.*, 2004; Rajakumar *et al.*, 2012). For this reason I hypothesise that lineages in which physical worker castes have evolved have experienced increased rates of speciation compared to lineages with monomorphic worker castes. This process may also be related to colony size, since colony size is thought to be the causal factor in the evolution of complex sociality (Bourke, 1999; Bourke, 2011; Ferguson-Gow *et al.*, 2014).

Finally, there is reason to think that diversification rates may have been affected by evolutionary changes in the social and mating system. As colonies evolve to acquire more queens (polygyny) and queens evolve to mate more frequently (polyandry), genetic variation within the colony increases. This may confer benefits at the colony level such as enhanced disease resistance (ants (Hughes & Boomsma, 2004; Reber *et al.*, 2008); bees (Baer & Schmid-Hempel, 2001; Seeley & Tarpy, 2007)) or more efficient division of labour (Schwander *et al.*, 2005; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007). On the one hand, these benefits may contribute to niche exploitation and range expansion, and hence diversification. On the other hand, extremely low relatedness brought about by high levels of polygyny combined with a unicolonial population structure (in which conspecific colonies are mutually non-hostile) has been hypothesised to be an evolutionary "dead end" (Helanterä *et al.*, 2009). This makes it difficult to predict the exact relationship between the social and mating system and diversification pattern.

In this study I utilise the genus-level phylogeny of the Formicidae developed in Chapter 2 to investigate diversification patterns across the family, employing the MEDUSA method. This work adds to previous studies because it employs a more complete tree, thereby potentially allowing an expanded understanding of past diversification shifts within the ants. In addition, I use the same phylogeny, along with data gathered from the literature, to test the hypotheses that larger colony size (as a categorical variable in orders of magnitude), and discrete worker castes, are associated with higher diversification rates. Likewise, I investigate the nature of the relationship between mating systems and diversification rates.

6.3 Method

6.3.1 Supertree construction

Diversification analyses were based on the genus-level supertree described in Chapter 2. I used the genus-level tree since every known ant genus is represented on it. This means that it samples the phylogeny of the Formicidae far more representatively than the species level supertree. The method of diversification analysis employed below can be used to analyse a genus-level tree by accounting for the missing taxa at species-level.

6.3.2 Trait data

Trait data on colony size, discrete worker castes, polygyny and polyandry were used, as they are relevant to the proposed hypotheses explaining diversification patterns. These data were collected and processed as described in Chapter 2.

6.3.3 Analysis of diversification pattern

In order to investigate overall patterns of diversification within the Formicidae, I employed the MEDUSA method (see Introduction). MEDUSA, is a stepwise AIC-based method, that returns a single set of rate shifts. In short, a model with two parameters - speciation rate and extinction rate - is fitted to the data, and an AIC score calculated. Next, a model with a single "break point" parameter (a hypothetical location within the tree where a shift in speciation and extinction rate has occurred), a speciation rate and an extinction rate for the clade descended from the break point and a speciation and extinction rate for the rest of the tree is fitted, and an AIC score obtained for this model. Then the algorithm searches for the break point location that minimises the AIC score for the model. If this AIC score exceeds a certain threshold of improvement compared to the 2 parameter model, this model is retained. The algorithm then moves on to fit a model with 8 parameters (2 break points, and 3 sets of speciation and extinction parameters), optimising the locations of the two break points and calculating an AIC score which is then compared to the 5 parameter model. This process continues until a model fails to exceed a pre-determined AIC threshold. Once a final model is reached, the algorithm performs a backward elimination process, removing break points individually and using the same AIC-based model selection criteria to arrive upon the simplest model required to explain the data in terms of speciation, extinction and break points.

In order to use MEDUSA, a phylogeny and a diversity tree are required. A diversity tree describes the extant diversity of the clade under analysis; for example, in the present case (a genus-level tree), a diversity tree describes how many species are present in each genus. I used the taxonomic information provided by AntWeb (Bolton, 2012) to construct a genus-level diversity tree in conjunction with the genus-level supertree constructed in Chapter 2. Subsequently, I fitted the

MEDUSA model to the genus-level supertree, using the diversity tree to describe the diversity beyond species-level, using the R package "Geiger" (Harmon *et al.*, 2008).

The genus-level supertree has a large polytomy in the Myrmicinae (figure 6.1). Polytomies such as this imply extremely rapid diversification, but are often present in the tree due to the lack of data. Since this polytomy almost certainly arose from lack of data and hence incorrectly implies rapid diversification, I repeated the MEDUSA analysis with the polytomy replaced by a single genus. In so doing, I retained the most diverse of the genera in the polytomy, in order to preserve as much diversity in the remaining tree structure as possible. The remaining genus was *Octostruma*, which contains 34 species. The genera removed were: *Acanthomyrmex*, *Adelomyrmex*, *Adlerzia*, *Ancyridris*, *Anilomyrma*, *Anisopheidole*, *Ankylomyrma*, *Austromorium*, *Baracirdris*, *Bariamyrma*, *Bondroita*, *Carebarella*, *Chimaedris*, *Cryptomyrmex*, *Dacatria*, *Dacetinops*, *Decamorium*, *Diaphoromyrma*, *Dicroaspis*, *Diplomorium*, *Dolopomyrmex*, *Epopostruma*, *Formosimyrma*, *Gauromyrmex*, *Goaligongidris*, *Indomyrma*, *Ishakidris*, *Kartidris*, *Lasiomyrma*, *Lenomyrmex*, *Liomyrmex*, *Machomyrma*, *Mesostruma*, *Oxyepoecus*, *Paramycetophylax*, *Paratopula*, *Perissomyrmex*, *Peronomyrmex*, *Phalacromyrmex*, *Poecilomyrma*, *Propodilobus*, *Protalaridris*, *Recurvidris*, *Rhopalothrix*, *Rhoptromyrmex*,*Romblonella*, *Rotatstruma*, *Secostruma*, *Stegomyrmex*, *Stereomyrmex*, *Talaridris*, *Tetheamyrma*, *Tricytarus*, *Tropidomyrmex*, *Tyrannomyrmex*, and *Vombisidris*.

6.3.4 Trait-dependent diversification

The R package 'diversitree' provides a range of models to test the association between binary or multistate discrete traits, continuous traits and diversification rates(FitzJohn, 2012). These methods work by comparing models in which speciation, extinction, or both, are constant across the tree, to models where one or both parameters is free to have a different value with each trait state (in the case of a discrete trait) or to vary proportionally to the value of a continuous trait (FitzJohn, 2012).

I used the functions BiSSE (for 2-state discrete traits, i.e. the presence/absence of discrete worker castes, polygyny and polyandry), MuSSE (for multistate discrete traits, i.e. colony size expressed in orders of magnitude) and QuaSSE (for continuous traits, i.e. colony size expressed in whole numbers) from the R package Diversitree (FitzJohn, 2012). In all cases, I first fitted a model to the tree with a single speciation rate, and then compared the fit of this model to a model where speciation rate has a unique optimum for each trait class (in the case of BiSSE and MuSSE), or is allowed to covary with trait value (in the case of QuaSSE). In the case of QuaSSE models, I also investigated the shape of the relationship between the continuous trait and diversification. I did this by modelling the relationship as linear, sigmoidal or hump-shaped and comparing the fit of each model to the observed data. For none of the traits did I have data for every genus in the tree, and so I accounted for incomplete taxon sampling in each model by including a term that describes the proportion of tips of the tree sampled in the model. I did not allow for extinction rate variation since estimating extinction rates from incompletely sampled phylogenies may produce misleading results (Rabosky, 2010).

6.4 Results

6.4.1 Diversification patterns

The analysis of diversification patterns using MEDUSA identified 16 unique rate patterns across the tree, with 11 increases in diversification rate, and 4 decreases in diversification rate (table 6.4.1, figure 6.1).

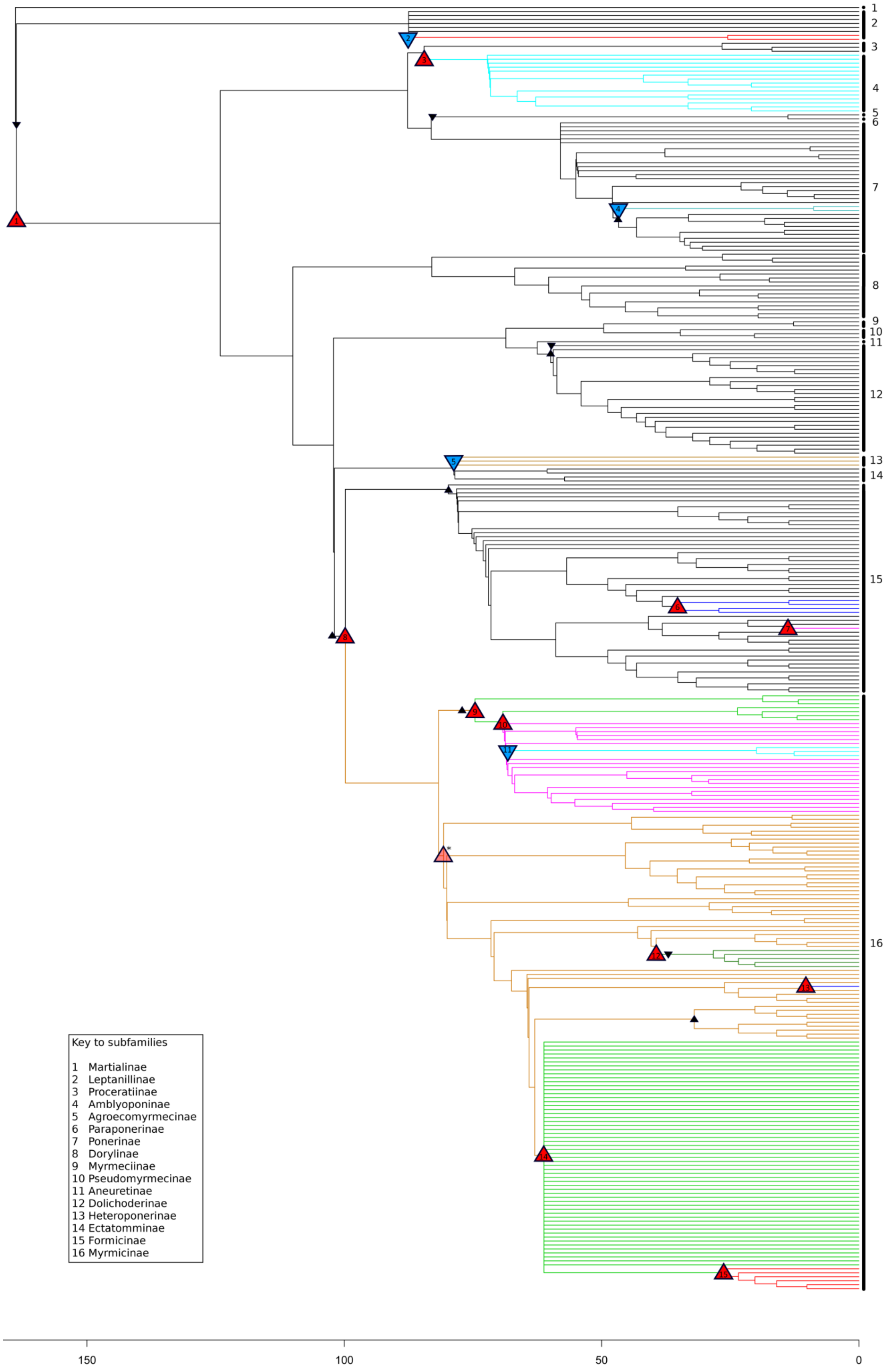
The first increase in diversification rate occurs at the base of all the ants excluding the Martialinae and Leptanillinae. Nested within this clade positive shifts occur at the Amblyoponinae; the Heteroponerinae; *Polyrhachis* + *Camponotus* + *Calomyrmex*; *Formica*; and at the origin of the Myrmicinae. Further positive shifts nested within the Myrmicinae occur at the origin of the clade *Strumigenys* + *Eurhopalothrix* + *Basiceros* + *Tranopelta* + *Pheidole* + *Procryptocerus* + *Cephalotes*, which has another positive shift nested within it consisting of the clade *Ochetomyrmex* + *Pristomyrmex* + *Blepharidatta* + *Wasmannia* + *Allomerus* + *Orectognathus* and the Attini. Finally there are positive shifts located at the origin of the clade *Leptothorax* + *Harpagoxenus* + *Formicoxenus*; at the origin of the genus *Tetramorium*; and at the root of the large polytomy.

Negative shifts occur at the origin of the clades: *Leptanilla* + *Protanilla*; *Myopias* + *Leptogenys*; and *Apterostigma* + *Myrmicocrypta* + *Mycocepurus*. Finally, there is a negative shift nested within the Myrmicine polytomy consisting of the genera *Crematogaster* + *Meranoplus* + *Nesomyrmex* + *Atopomyrmex* + *Pheidologeton* + *Carebara*.

The exclusion of the large Myrmicine polytomy had little effect on the inferred diversification shifts outside of the Myrmicinae (Table 6.4.1; figure 6.1). Shifts 9, 14 and 15 were not inferred, and a new positive shift within the Myrmicinae was inferred (Figure 6.4.1). All other shifts remained the same (Table 6.4.1).

Table 6.4.1 Results from modelling diversification patterns within the ants using 'MEDUSA'. Shift number corresponds to figure 6.1. + indicates an increase diversification rate, and – indicates a decrease shift. r = net diversification rate (λ-μ, where λ = speciation rate and μ = extinction rate) and ε = relative extinction rate (μ/λ). Background rate was determined from a fixed-rate model for the entire tree. Number of species refers to the number of extant species in the clade specified.

Shift	**Clade**	**Shift direction**	**r**	**ε**	**Crown group age (millions of years)**	**# of species**	**Without polytomy?**
-	Background	n/a	0.0116	0.0000	163.7	12986	-
1	All ants except Martilinae	+	0.0288	0.9722	163.7	12985	Yes
2	*Protanilla + Leptanilla*	-	0.0000	1.0000	87.5	52	Yes
3	Amblyoponinae	+	0.0386	0.4729	84.5	124	Yes
4	*Myopias + Leptogenys*	-	0.0000	1.0000	46.7	304	Yes
5	Heteroponerinae	+	0.0288	0.9722	78.5	24	Yes
6	*Polyrhacis + Camponotus + Calomyrmex*	+	0.0288	0.9722	35.2	1825	Yes
7	*Formica*	+	0.1820	0.9554	13.6	175	Yes
8	Myrmicinae	+	0.0451	0.9731	99.8	6497	Yes
9	*Strumigenys + Eurhopalothrix + Basiceros + Tranopelta + Pheidole + Procryptocerus + Cephalotes*	+	0.0451	0.9731	74.6	2465	No
10	*Ochetomyrmex + Pristomyrmex + Blepharidatta + Wasmannia + Allomerus + Orectognathus +* Attini	+	0.0616	0.0000	69.2	367	Yes
11	*Apterostigma + Mycocepurus + Myrmicocrypta*	-	0.0000	1.0000	68.5	80	Yes
12	*Leptothorax + Harpagoxenus + Formicoxenus*	+	0.0853	0.0000	39.4	29	Yes
13	*Tetramorium*	+	0.4401	0.8373	10.1	560	Yes
14	See figure 6.1	+	0.0451	0.9731	61.2	1133	No
15	*Crematogaster + Meranoplus + Nesomyrmex + Atopomyrmex + Pheidologeton + Carebara*	-	0.9996	0.0451	26.1	837	No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Key to subfamilies
1 Martialinae
2 Leptanillinae
3 Proceratiinae
4 Amblyoponinae
5 Agroecomyrmecinae
6 Paraponerinae
7 Ponerinae
8 Dorylinae
9 Myrmeciinae
10 Pseudomyrmecinae
11 Aneuretinae
12 Dolichoderinae
13 Heteroponerinae
14 Ectatomminae
15 Formicinae
16 Myrmicinae
150
100
50
0

Figure 6.1 (previous page) A complete genus-level tree of the ants showing the results of an analysis of diversification analysis using MEDUSA. Red triangles indicate increases in diversification rate and blue triangles indicate decreases in diversification rate. The pale red triangle marked with an asterisk marks the location of an increase in diversification rate inferred when the large polytomy in the Myrmicinae was removed (see text). Upward and downward pointing black triangles indicate increases and decreases in diversification rate, respectively, as inferred by (Moreau & Bell, 2013). The black bars at the tips of the tree denote subfamily divisions, and the scale bar represents millions of years before present. Branch colours denote lineages within a shift regime, but are otherwise arbitrary.

6.4.2 Trait-dependent diversification

Colony size had a significant effect on diversification rates, when considered as a categorical variable. The model that allowed speciation rate to vary according to the order of magnitude of colony size was most strongly supported (Table 6.4.2). The highest speciation rate was found in genera with a mean colony size of 10^4, with lower rates in the 10^2 and 10^3 colony size-categories, and intermediate rates in the remaining 2 categories, 10^1 and 10^5+ (Table 6.4.2). Analysing colony size as a continuous variable using QuaSSE models, however, did not show the same relationship between colony size and diversification. There was little evidence that a linear, sigmoidal or hump-shaped relationship exists between colony size and diversification rate when compared to a minimal model in which rates are constant, as evidenced by the negligible improvement in AICc score between these models (Table 6.4.3).

Table 6.4.2 Results from analysis of diversification rate and the order of magnitude of colony size using the 'MuSSE' model. λ is speciation rate and μ is extinction rate. Full constraint refers to a model with a fixed value for speciation rate, and free lambda is a model where lambda is allowed to vary between colony size class. p-value is from a log-likelihood ratio test between the two models.

	AIC	**λ_1**	**λ_2**	**λ_3**	**λ_4**	**λ_5**	**μ**	**p-value**
Colony size		**10^1**	**10^2**	**10^3**	**10^4**	**10^5+**		
Full constraint	1706.21	0.0309	n/a	n/a	n/a	n/a	4.14E-09	n/a
Free lambda	1683.87	0.0429	1.47E-08	3.92E-07	0.1690	0.0336	2.32E-08	<0.001

Table 6.4.3 Results from models testing the association between colony size and diversification rate using 'QuaSSE'. Constant rate refers to a model with a tree-wide constant speciation and extinction rate. Linear refers to a model where speciation rate is allowed to vary as a linear function of colony size, sigmoidal as a sigmoidal function and hump as a hump shaped function.

Model	**Df**	**lnLik**	**AIC**	**ΔAIC**
Constant rates	3	-1038.9	2083.8	52.6
Speciation rate vairable				
Linear	4	-1038.9	2085.7	54.5
Sigmoidal	6	-1038.4	2088.8	57.6
Hump	6	-1038.2	2088.4	57.2

Table 6.4.4 Results from the analysis of diversification rate and discrete worker castes, polygyny and polyandry using 'BiSSE' models. Lambda is speciation rate and mu is extinction rate. Full constraint refers to a model where speciation rate and extinction rate were constant across the tree. Free lambda refers to a model where speciation rate was allowed to vary between the two states of the trait and mu is fixed, free mu refers to the same but with a variable mu and fixed lambda and full model refers to a model where speciation rate and extinction rate were both allowed to vary with the state of the trait. λ_0 is the speciation rate estimate when the trait is absent and μ_0 is the extinction rate when the trait is absent. λ_1 is the speciation rate estimate when the trait is present and μ_1 is the extinction rate when the trait is present. p-values are from log-likelihood ratio tests comparing each model to the fully constrained model. AICc is sample-size adjusted Akaike Information Criterion.

Worker polymorphism		**AICc**	λ_0	λ_1	μ_0	μ_1	**p-value**
	Full constraint	1025.4136	0.0361	n/a	2.75E-07		n/a
	Free lambda	1006.5746	2.18E-06	0.0820	6.58E-07		<0.001
	Free mu	1027.4140	0.0361	n/a	6.59E-08	1.54E-06	1
	Full model	1008.5650	4.18E-08	0.0832	3.55E-06	9.59E-09	<0.001
Polygyny		**AICc**	λ_0	λ_1	μ_0	μ_1	**p-value**
	Full constraint	1536.2911	0.0323	n/a	2.67E-07		n/a
	Free lambda	1522.1799	1.52E-06	0.0534	5.77E-06		<0.001
	Free mu	1538.3275	0.0322	n/a	6.71E-05	1.39E-05	1
	Full model	1521.1409	0.0080	0.0417	3.21E-06	3.79E-07	<0.001
Polyandry		**AICc**	λ_0	λ_1	μ_0	μ_1	**p-value**
	Full constraint	603.4777	0.0417	0.0417	2.38E-06		n/a
	Free lambda	602.0265	0.0880	1.58E-07	1.02E-05		1
	Free mu	605.4787	0.0417	0.0417	9.81E-06	9.90E-06	0.97
	Full model	604.0254	0.0879	6.10E-06	3.43E-07	3.24E-08	1

Worker polymorphism appeared to have had a positive effect on diversification, as shown by the stronger support for a BiSSE model that allowed different speciation rates in the absence and presence of discrete worker castes (Table 6.4.4). The BiSSE model suggested that genera that have evolved discrete worker castes have a higher speciation rate, and lower extinction rate, than those without (Table 6.4.4). The same pattern was observed with respect to levels of polygyny, with genera that have exhibit polygyny having higher speciation and lower extinction rates than those that are monogynous (Table 6.4.4). Polyandry appeared to have had no effect on diversification rates, since the BiSSE model that allowed speciation to vary between monandrous and polyandrous genera was statistically indistinguishable from a constant rates model (Table 6.4.4).

6.5 Discussion

Analysis of diversification rates using a genus-level supertree of the ants and MEDUSA revealed 15 shifts in the diversification patterns of the ants throughout their 140 million year history. Previous analysis of diversification patterns in the ants showed 10 such shifts (Moreau & Bell, 2013). However, the tree used in Moreau & Bell 2013 represented a smaller portion of ant diversity than the tree used here, since, although it was resolved to species level, it omitted 155 of the genera included in the present study. The tree used in the final analysis in the present study contained all extant genera. This difference does not necessarily mean that the results presented here supersede those of Moreau and Bell (2013), but the different approach yields an alternative possible configuration of rate shifts.

In common with Moreau and Bell (2013), I found an increase in diversification rate at the base of the Myrmicinae, and an increase in diversification rate nested within the Myrmicinae leading to the clade including *Strumigenys* (shifts 8 and 9, figure 1). Several of the shifts identified by Moreau and Bell (2013) were not specifically identified in the present analysis, for example, Moreau and Bell (2013) found a positive shift at the origin of the Formicinae. The present study did not find a positive shift in this location, but did find two positive shifts (shifts 6 and 7, figure 1) nested within the Formicinae.

It is possible that the shift identified at the root of the Formicinae by Moreau and Bell (2013) is explained by the two shifts nested within the clade, which are apparent with the inclusion of more genera. Moreau and Bell (2013) also found a positive shift nested within the Myrmicinae, and a negative shift associated with Leptanillinae and Martialinae, both of which were not matched here. The present study, however, found a shift at the root of the Myrmicinae (shift 9, figure 6.1) with subsequent shifts nested within (shifts 9, 10, 12, 13 and 14, figure 6.1), and a negative shift nested within the Leptanillinae. These may represent the same shifts identified by Moreau and Bell (2013), only in slightly different locations of the tree caused by an increase in taxonomic coverage. Moreau and Bell (2013) found four shifts that were not identified at all in this study: a downshift leading to the monotypic subfamilies Agroecomyrmecinae and

Paraponerinae; an upshift leading to a subclade of ponerine ants including *Odontoponera* and *Anocehtus*; a downshift leading to *Aneuretus* and an upshift at the root of the Dolichoderinae. Finally, Moreau and Bell (2013) identified a negative shift in diversification rate on the branch leading to the clade containing *Leptothorax*, *Formicoxenus* and *Harpegoxenus*, where this study finds a positive shift (shift 12, figure 6.1).

A possible reason for such mismatching arises from the way in which paraphyletic genera were treated in the two studies. In Moreau and Bell (2013), *Leptothorax* was not identified as paraphyletic, whereas in the tree used in the present study the extant diversity of *Leptothorax* was distributed among 3 distinct groups (reflecting the paraphyly of the genus (Baur *et al.*, 1996)). This may have caused a change in the estimation of diversification rates as, under the latter scenario, more diversification events are required to generate the 3 paraphyletic components of *Leptothorax*. The difference in results between these two studies highlights the importance of an accurate taxonomy and the effects of missing taxa on diversification analyses. Ant taxonomy is still very much in flux, even at higher levels. For example, as recently as 2014 major subfamily revisions have been published (Brady *et al.*, 2014)

In addition to broad patterns of diversification, I also found evidence that increases in colony size and the evolution discrete worker castes and polygyny have each had positive effects on the diversification of the ants. The relationship between colony size and diversification patterns appears not to be linear. I find that the genera with the smallest (10^1) and largest (10^6) colony sizes have comparable speciation rates, and that genera with intermediate colony sizes (10^2-10^3) have a decreased rate of diversification, and genera with colony sizes of the order of 10^4 have the highest rates of speciation. Large colonies have been hypothesised to be a driver of diversification (Grimaldi & Engel, 2005), but previously formal analytical support for this hypothesis has been lacking. A possible ecological explanation for this link is that as colonies evolve to become more socially complex they are better able to exploit their environment, and adapt to new niches and food sources that may be available. In addition, more efficient division of labour could lead to the increased output of sexual forms, and therefore to an increased capacity for dispersal and colonisation of new environments. Social complexity and more efficient division of labour have been linked to increasing colony sizes (Bourke, 1999; Bourke, 2011), and evidence for these links is growing (Fjerdingstad & Crozier, 2006; Rodriguez-Serrano *et al.*, 2012)(Chapters 4 and 5). As a corollary, this supports the view that colony size affects diversification. The evolution of eusociality has been linked to diversification shifts in the dictyopteran (termites, cockroaches and mantids) phylogeny (Davis *et al.*, 2009), further suggesting a role for the benefits of social organisation and complex sociality in diversification.

The same study also showed, although did not statistically test, that large colonies are likely to have evolved at the same node where an increase in diversification rate was detected.

The finding that discrete worker castes are associated with increased speciation rates further suggests that social complexity and division of labour promote diversification. This supports the analogous idea that phenotypic plasticity in unitary organism promotes diversification (Pfennig *et al.*, 2010). There is some evidence that the expression of physical worker castes in ants is plastic itself, depending on environmental pressures and requirements. For example, it seems likely that all species of the hyperdiverse genus *Pheidole* are able to produce a supersoldier caste with laboratory stimulation, yet the only species that are observed doing so in a natural environment are those that co-occur with army ants that prey mainly upon other ants (Passera *et al.*, 1996; Rajakumar *et al.*, 2012). Furthermore it has been suggested that the range of physical castes expressed in *Eciton* army ants varies depending on variation in the size of their prey (Powell & Franks, 2005), and geographical variation in within-species caste ratios consistent with microevolutionary specialisation divergence has been observed (Yang *et al.*, 2004). I suggest that once a species has evolved the ability to produce workers of a range of sizes suited to a range of tasks, that species is able to more rapidly adapt to exploit new resources, and to react to the novel challenges that a new environment may present. In this manner, phenotypic plasticity at the colony level could promote diversification in the same way that phenotypic plasticity at the organismal level is hypothesized to promote diversification in unitary organisms (Pfennig *et al.*, 2010).

The links between polygyny, polyandry and diversification seem less straightforward to interpret. It has been suggested that increasing within-colony genetic diversity increases the efficiency of division of labour within a colony, and there is experimental evidence that this is true (Schwander *et al.*, 2005; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007). This would suggest that, if division of labour can positively affect diversification, one might expect to see both polygyny and polyandry having positive effects on diversification rates, but the present study found support for the effect of polygyny but not polyandry. There may be, however, other reasons that ants might fall under selection to increase genetic diversity within a colony, for example improved resistance to disease and parasites (Baer & Schmid-Hempel, 2001; Hughes & Boomsma, 2004; Seeley & Tarpy, 2007; Reber *et al.*, 2008), which may not have strong effects on the ability of a species to exploit new niches or colonise new geographical areas. There is another possible reason that polygyny may affect diversification rates, while polyandry does not. Polygyny is associated with being unicolonial, a condition where ants form supercolonies with almost zero within-colony relatedness (Helanterä *et al.*, 2009). Whilst not all polygynous ants are unicolonial, it has been hypothesised that unicoloniality evolves due to extremely valuable short-term rewards, but that in the long term unicolonial species are unlikely to persist since low intracolonial relatedness leads to selection for altruism and worker traits to fail (Crozier, 1977; 1979; Helanterä *et al.*, 2009). Interestingly, I find evidence that polygyny is associated with lower extinction rates as well as elevated speciation rates. The increase in diversification rate associated with polygyny could result from several ecological advantages of polygyny, such as the ability to survive in colder regions (Bourke & Heinze, 1994), whereas the reduced extinction rate could result from short-term competitive advantages of polygyny. This hypothesis requires extensive testing, however, and the results of this study only suggest it as a possibility.

A possible confounding factor on the results presented here is the effects of environment and geography. For example, colony size appears to have a hump shaped relationship with net primary productivity (which varies across space (Kicklighter *et al.*, 1999)), and worker mass polymorphism has a negative relationship with mean monthly temperature (Kaspari, 2005). In addition, the timing and frequency of nuptial flights, the main mode of dispersal for many ant species, appears to have a spatial element to it (Dunn *et al.*, 2007). If traits are non-independent of geography, and geography drives diversification in the ants, then the effect of traits on diversification may in fact be indicative of the underlying effects of geography. However, Moreau and Bell (2013) tested for biogeographic effects on diversification patterns, and found no evidence to support the idea that diversification rate increases in the ants are associated with geographical range shifts, and chapter 4 of this thesis finds no effect of latitude on colony size in the Attini.

In conclusion, this study finds evidence for diversification rate shifts within the Formicidae which are both expected and contrasting with previous analyses: the dynamics of lineage accumulation in this group are clearly more complex than previously thought require further work. Differences between some of the current results and those of previous studies suggest that problems with tree completeness, topology and cryptic paraphyly need to be resolved before a consensus can be reached. The present study has also shown, for the first time, links between colony size, discrete worker castes and polygyny and diversification rates in ants. If larger colonies and discrete worker castes confer higher colony-level phenotypic plasticity on species, these traits may allow them to better adapt to the ecological niches of new environments. In addition, if enhanced division of labour through larger colony size increases reproductive output, species may stand a better chance to colonise new habitats and geographic regions, enhancing their potential for diversification. As more comparative data accumulate and phylogenies improve, these hypotheses will become more rigorously testable, and our understanding of the drivers of diversification in the ants will become more refined.

7 Discussion

7.1 Summary of results

The overall aim of this thesis was to explain patterns of social trait evolution in the ants and to quantify the effects of social traits on the patterns of diversification in the ants. I accomplished this by using supertree methods to construct a complete genus-level phylogeny of the ants and by creating a large database of social trait data. These tools enabled me to use rigorous statistical comparative methods to identify the phenotype of the ancestral ant; to explore the patterns of evolution on key social traits and test predictions of evolutionary associations between these traits across the whole ant phylogeny; to test the predicted association between colony size and division of labour (both non-reproductive and reproductive) on a finer scale within the Attini; and to test hypotheses concerning the effects of social traits on diversification patterns in the ants.

First, I constructed a robust genus-level supertree, and developed and populated a database of social traits (Chapter 2). I found that the quantity and quality of source data (both literature-derived phylogenies and database-derived molecular data) were too low to reconstruct a complete species-level phylogeny. The species-level supertree featured 1656 species (12.7% of extant ant species). However, when summarised to genus-level, the quantity and quality of the source data were sufficient to recover a genus-level phylogeny covering every extant genus with positive support. This phylogeny was 82.5% resolved. The final trait database contained data from 949 sources, with at least one data point for 1957 species and 208 genera. It contained data for worker head-width, queen head-width, colony size, the presence/absence discrete worker castes, gyny level (colony queen number) and queen mating frequency. Summarising the data to genus-level not only allowed the overlap between the tree and the database to be improved, but also increased the number of observations contributing to the generic means for each genus. It also allowed the topology of the tree to be more comprehensive (many comparative analyses being sensitive to missing topology of the tree) and retained information about processes occurring higher than the genus level.

Second, I used the genus-level phylogeny and data at the genus level on mean worker-head width, mean colony size, discrete worker castes, gyny level and queen mating frequency to investigate the size and social phenotype of the ancestral ant. There is conflicting evidence from the fossil record and from molecular phylogenetics concerning the inferred phenotype of the ancestral ant. The fossil record suggests a large-bodied, wasp-like ancestor (Wilson *et al.*, 1967; Agosti *et al.*, 1998; Wilson & Hölldobler, 2005), whereas molecular phylogenetics suggest a small, subterranean ancestor (Brady *et al.*, 2006; Lucky *et al.*, 2013). I found evidence that supports the hypothesis that the ancestor of the ants was large-bodied and very little evidence that the ancestral ant was small (Chapter 3). I also found support for the hypotheses that the earliest ants lived in small colonies with monomorphic workers (Bourke, 1999; Bourke, 2011) and were both monogynous and monandrous (Charnov, 1978; Boomsma, 2007; Hughes *et al.*, 2008b; Boomsma, 2009; Boomsma, 2013). That monogamy is the ancestral state of the ants, and of other lineages of eusocial Hymenoptera, has been shown previously (Hughes *et al.*, 2008b), but predictions concerning colony size and discrete worker castes have not been tested before. Moreover, none of these predictions have been tested across such a large phylogeny for the ants.

Next, I explored the patterns of evolution in colony size, discrete worker castes, gyny level and queen mating frequency throughout the ant phylogeny, and tested hypotheses regarding evolutionary correlations between these traits. I found that, in the traits tested, the first important change to evolve was a change from monandry to polyandry (at the split between the Poneroids and Formicoids), followed by a change from monogyny to polygyny (at the node where the Dorylinae diverge from the remainder of the Formicoids), and then by a change from worker monomorphism to worker polymorphism (at the root of the Myrmicinae). Each of these traits had other, later, origins throughout the tree. Colony size appeared to evolve gradually, and the only case of colonies that exceed 100,000 workers at ancestral nodes (i.e. non-terminal nodes) of the phylogeny occurred within the Dorylinae. The remainder of genera that exhibit colonies exceeding 100,000 workers in size appear to have evolved such large colonies relatively recently. The early origin of polyandry may be an artefact of the way in which paraphyletic genera were treated. Due to the only Ponerine genus that displays polyandry, *Pachycondyla* (Kellner *et al.*, 2007), being highly paraphyletic (Schmidt, 2013), in this analysis polyandry appeared to have evolved six times in the Ponerinae. If polyandry evolved in only one of the subdivisions within the genus, then the inferred early origin of polyandry may stem from a shortcoming of the mapping of traits onto the phylogeny caused by a lack of understanding of systematic relationships within the genus *Pachycondyla*. I also tested for the presence of predicted associations between: discrete worker castes and colony size (Bourke, 1999; Bourke, 2011); discrete worker castes and polygyny (Oster & Wilson, 1978; Frumhoff & Ward, 1992); discrete worker castes and polyandry (Crozier & Page, 1985); polyandry and colony size (Cole, 1983); and polyandry and polygyny (Keller & Reeve, 1994). I did this in two different ways: firstly I tested for correlations between the inferred liabilities of trait change between the ancestral nodes of the phylogeny, and secondly I tested for correlations in the trait values of extant genera using both univariate and multivariate logistic models and controlling for phylogeny. I found significant correlations of varying strength between the change in traits throughout the tree for: discrete worker castes and colony size; polyandry and colony size; polyandry and discrete worker castes; and polygyny and polyandry. In both univariate and multivariate analyses there were significant relationships between discrete worker castes and colony size; polyandry and colony size and polyandry and polygyny. A significant relationship between discrete worker castes and polyandry was only detected in a univariate model. This implies that colony size is, of the traits tested, the main driver of discrete worker castes as predicted by the size-complexity hypothesis (Bourke, 1999; Bourke, 2011). The prediction that large colony sizes are associated with polyandry (Cole, 1983) appears to hold as well, although it is not clear if this is due to sperm limitation, or due to benefits of polyandry being more important in larger colonies. Previous authors have suggested that increased genetic diversity is a stronger driver of the evolution of multiple mating than sperm limitation (Kronauer & Boomsma, 2007).

I then moved on to test the predicted associations between colony size and social complexity (Bourke, 1999; Bourke, 2011) using finer-scale data. Of all the groups in the database, the Attini had the most data on worker head-widths and queen head-widths, which facilitated the calculation of a coefficient of worker size variation, and a measure of queen-worker dimorphism. This allowed me to test the prediction that colony size correlates with non-reproductive and reproductive division of labour on a fine scale not possible using the whole genus-level phylogeny. I used supertree methods to produce a phylogeny for the Attini, and showed that, in accordance with the predictions, colony size was positively associated with non-reproductive and reproductive division of labour (Ferguson-Gow *et al.*, 2014). The results suggested that colony size has a stronger effect on worker size variation, and that worker size variation first evolves in response to increasing colony size, and then facilitates the evolution of queen-worker dimorphism through increased colony efficiency. However, this hypothesis requires more data for further testing.

Finally, I used the genus-level tree in conjunction with the MEDUSA model (Alfaro *et al.*, 2009) to identify 11 increases and 4 decreases in diversification rate throughout the history of ant evolution. This is the first time that models of diversification have been fitted to a complete genus-level phylogeny for the ants. I compared models with a fixed diversification rate to models where the diversification rate was allowed to covary with colony size, the presence or absence discrete worker castes, gyny level and queen mating frequency. When allowing speciation and extinction rates to vary with trait values, I found significant evidence that higher diversification rates are associated with colony sizes in the range of 1,000-10,000 workers, the presence of discrete worker castes and the presence of polygyny. I found no evidence that the presence of polyandry effects diversification rates. The best fitting model did not include extinction rate, but a model including extinction rate had significantly greater support than a model where diversification rate was independent of discrete worker castes. In this model the presence of discrete worker castes was associated with higher speciation rates, and lower extinction rates, and hence a higher net diversification rate. The best fitting model for polygyny suggested that polygyny was associated with both higher speciation rates and higher extinction rates. This is the first time that the variation in diversification rates in the ants has been associated with a social trait.

7.2 Tools for comparative ant biology

The complete genus-level phylogeny for the ants developed in this thesis should prove to be an invaluable tool for future comparative analysis in the ants. However, further data are required before a complete species-level tree for the ants becomes available to researchers. The construction of a complete species-level phylogeny was hampered by the lack of phylogenetic information for a large majority (87.4%) of the ants. Despite the taxonomic overlap of each contributing data source in the species-level analysis, problems were caused by the taxonomically incomplete nature of the source data. For example, if a source tree features a sister relationship between two genera that are, in reality, distantly related, and this hypothetical source tree is the only one in which one of these genera occurs, the final analysis will only be aware of this "sister" relationship. In order for supertree methods to recover an accurate species-level phylogeny for the ants, two things are required. Firstly, many more sources of phylogenetic data are required for the species for which no data are present. Secondly, phylogenies that are more taxonomically dense, i.e. that feature many or all representatives of a single genus or subfamily rather than one or two representatives of disparate groups from across the Formicidae, are needed. It seems that a "divide and conquer" approach is a tractable way to approach the construction of large phylogenies for extremely diverse clades. Recent developments in the ability to sequence degraded DNA from pinned insects in museum collections while minimally damaging the specimens are also likely to increase the amount of available data rapidly, particularly in rare species that are not often encountered in the field (Tin *et al.*, 2014).

The collation of trait data from the varied literature also represents a valuable tool. One problem with this, however, is that many non-morphological traits are measured in ways that make it difficult to produce continuous or fine scaled summaries of the data. This is because these data are often collected ad-hoc, in a way specific to the demands of the particular study. A recent call to standardise methodologies for the study of polyandry within the social insects reflects this problem (Jaffé, 2014), and such standardisation of data collection methods would be beneficial to the study of all traits across all taxa in which questions of a comparative nature are of interest.

The relative scarcity in the ants of suitable data, both phylogenetic data and trait data, is highlighted when the results of this study are compared to corresponding values in the mammals, a clade for which a supertree (Bininda-Emonds *et al.*, 2007) and a comprehensive trait database (Jones *et al.*, 2009) exist and that has been the focus of much macroevolutionary investigation (Table 7.1).

Table 7.2.1 Comparisons between the available data, both phylogenetic and trait data, for the ants, and for the mammals. Total species numbers for mammals are taken from Wilson and Reeder (2005), and the supertree for mammals refers to Bininda-Emonds *et al.* (2007). The trait database for mammals refers to Jones *et al.* (2009), and species numbers refer to species with data for at least one morphological, behavioural or life history trait in the database. Species numbers for ants are taken from AntWeb (Bolton, 2012), and the supertree and database refer to those in the present thesis.

	Total species number	Species in supertree	Species in trait database
Mammals	5416	4510	4998
		83.3%	92.3%
Ants	12986	1656	1944

7.3 Developing an improved understanding of social trait evolution

Together, the results of this thesis help further the understanding of the evolution of social traits and social complexity in the ants, along with the understanding of the evolution of cooperation in general. Several key predictions from social evolution theory have been tested in this thesis.

First, predictions regarding the colony size, the presence of discrete worker castes, gyny status and mating frequency of the ancestral ant have been confirmed across a phylogeny of all extant genera of ants. These findings represent an important contribution to the study of inclusive fitness, since confirming these predictions adds to an already large body of theoretical, experimental and comparative evidence that supports inclusive fitness theory (Abbot *et al.*, 2011). This is also of broader significance, since inclusive fitness theory underpins not just the evolution of eusociality, but the evolution of cooperation in general (Bourke, 2011).

Secondly, the reconstruction of ancestral states throughout the ant phylogeny reveals the pattern of evolution of key traits, and leads to some interesting patterns and hypotheses. A quantitative estimate of the number of independent evolutions of discrete worker castes, polygyny and polyandry is established. That polygyny and polyandry seem to appear on the tree before discrete worker castes suggests that selection for increased within-colony genetic diversity precedes selection for a diverse work force, however the occurrence of discrete worker castes at nodes descended from monandrous ancestors makes this prediction uncertain. This may be due to the relative importance of the factors that select for high genetic diversity within a colony (through either polygyny or polyandry) and the factors that select for a diverse work force. For example, it has been suggested that polygyny evolves due to environmental constraints or pressures (Bourke & Franks, 1995; Keller, 1995), whereas, as shown in this thesis, the evolution of discrete worker castes may be driven primarily by the evolution of large colonies. Quantitatively testing the order of trait evolution of these traits requires a larger and more complete dataset, but these results suggest that this would be an interesting endeavour. Furthermore, the pattern of evolution of colony size suggests that very large colonies evolved much earlier in the Dorylinae (the army ants) than in other clades where very large colonies occur. This suggests that large colonies in non-Doryline species are a recent development. This is also suggested by the fact that within the army ants large colonies appear to be the rule, not the exception, whereas in other groups containing species with colonies of over 100,000 workers, such as the Attini, large colonies are less common. Investigating the causes of this apparent pattern would yield further insight into the selective forces that favour very large colonies, and how they vary between army ants and other lineages.

I also present evidence of the importance of colony size in the evolution of social traits and of social complexity in the ants. This is the first time these correlations have been investigated across all the ants, and the findings add considerable support to the size-complexity hypothesis. This is important not just for the understanding of the evolution of eusociality, but, by analogy, the evolution of any system where related individuals cooperate. Inclusive fitness theory helps to explain the major transitions in evolution (Bourke, 2011), which are major events that have shaped the history of life on earth (Maynard-Smith & Szathmary, 1995). Aside from eusociality, all of these transitions occurred deep in the history of life on earth (Maynard-Smith & Szathmary, 1995). Eusociality, however, is a relatively recent phenomenon, and as such eusocial systems are positioned as excellent models in which to test hypotheses concerning the processes of social group formation, social group maintenance, social group transformation and the evolution of individuality (Bourke, 1999; Herron & Michod, 2008; Bourke, 2011). This means that tests of hypotheses such as those presented in this thesis are valuable contributions to the understanding of major transitions, including those that occurred too long ago to be studied comprehensively.

Finally, I offer evidence of a link between social traits and increased rates of diversification in ants. This has interesting implications for other clades in which social behaviour has evolved. First, although there appear to be links between diversification, colony size, discrete worker castes and polygyny in the ants, it is not clear that it is these traits that have made the ants in total such a diverse clade. This hypothesis would need to be tested using a phylogeny incorporating both eusocial and solitary lineages of Hymenoptera. A study of diversification on a supertree of Hymenopteran families identified several increases in diversification rates. However, apart from an ambiguous shift at the origin of the clade containing the Apidae (a major family of bees containing eusocial species), the shifts do not appear to be associated with eusociality (Davis *et al.*, 2010c). Conversely, there is evidence that the evolution of eusociality in termites has promoted their diversification (Davis *et al.*, 2009). Hence these studies, and the results presented in this thesis, suggest that the origin of eusociality and the development of social complexity within a eusocial clade have different effects on patterns of diversification.

7.4 Further research

The tests of the hypotheses considered in this thesis could be improved by a more comprehensive dataset. First, data for more genera would increase the amount of the topology of the phylogeny included in any analysis. Ideally, macroevolutionary analyses should be conducted with complete datasets for each clade in question. Even more desirable would be the ability to conduct these analyses to species level. However, there are outstanding questions that could be addressed under the current framework with the aid of reliable data for other social traits. For example, worker policing is expected to increase under conditions of polygyny with related queens or under polyandrous conditions (Bourke & Franks, 1995; Crozier & Pamilo, 1996). Furthermore the relationship between colony size and social complexity encompasses traits other than just discrete worker castes and measures of division of labour (Bourke, 2011). As colonies evolve to become larger, several other changes are expected to occur, such as the reduction of worker reproductive potential, the segregation within a nest of sexual brood, and the early fixation of caste fate during larval development (Bourke, 2011). Although data exist that describe these phenomena in some species, the state of these traits in much of the extant diversity of the ants is unknown, which severely limits the power of such comparative analyses of them. Furthermore, greater standardisation of the reporting of key social traits such as gyny status, queen mating frequency (Jaffé, 2014) and worker polymorphism will facilitate the study of the evolution of these traits using a more finely-grained data (i.e. as continuous traits), which may reveal new and interesting patterns and allow the testing of key hypotheses in greater detail.

This thesis also highlights the importance of accurate taxonomy in comparative analyses. For example, as described above, the inference that polyandry evolved early in the history of the ants may be an artefact of the extreme paraphyly in the Ponerine genus *Pachycondyla*. The fundamental units of comparative analysis are taxonomic, be they species, genus, subfamily of higher levels of classification, hence the accurate description of these units is of extreme importance. Taxonomy in some groups appears to relatively stable, but in the ants this is not the case. For example, in 2014 a major revision of the Dorlyinae was published in which five subfamilies (Aenicitinae, Aenictogitoninae, Cerapachyinae, Ecitoninae and Leptanilloidinae) were subsumed into the Dorylinae, and the paraphyly of the genus *Pachycondyla* was resolved by breaking it into 19 new genera (Schmidt & Shattuck, 2014) (these publications occurred after the writing of this thesis, and the construction of the supertrees presented here). This, combined with the apparent uncertainty surrounding some of the higher-level relationships in the ants (Chapter 2.2), shows that the topology of the ant phylogeny is in flux. The resolution of this taxonomic and systematic problem will improve the clarity of macroevolutionary inferences made in the ants, and the accumulation of comprehensive trait data for a variety of traits will expand the range of questions that can be accurately addressed.

7.5 Conclusion

This thesis provides a valuable tool for comparative investigations in the ants in the form of a genus-level phylogeny that features all extant ant genera, and exploits that tool to test important hypotheses concerning social evolution in the ants. In addition, ancestral state reconstructions have generated new hypotheses for future research. The importance of colony size as a driver of the evolution of worker polymorphism and worker size variation, polyandry and queen-worker dimorphism is also confirmed in the largest test of the size-complexity hypothesis to date. The results presented here add to the strength of inclusive fitness theory as a powerful tool to address questions concerning the evolution of cooperation in nature, and enhance the understanding of the specifics of social evolution and the evolution of biodiversity in the ants. A link between social traits and diversification patterns within the ants is established for the first time, representing a contribution to the understanding of the evolution of biodiversity in the ants.

This thesis also highlights some major obstacles to the further study of macroevolutionary processes in the ants, namely the lack of phylogenetic data for much of the extant diversity of the group, the corresponding lack of trait data, and the incompatible nature of trait data between studies for many key social traits. As taxonomic issues in the ants are resolved, and the structure of the true ant phylogeny becomes clearer, some of the patterns and processes identified in this thesis are likely to change. However, this thesis represents an important step in laying the ground work for future supertrees in the ants, and the study of macroevolutionary processes in the Formicidae.

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9 Appendices

9.1 Appendix 1

Table A1.1 Fossils used to date the supertree. Node numbers refer to figure A1.1 (appendix).

Node	Age	Clade	Reference
1	143.5		[1, 2]
27	44.1	Proceratium	[3]
37	15	Prionopelta	[4]
43	39.5	Sitmgatomma	[5]
45	15.5	Myopopone	[6]
55	39.5	Pachycondyla	[5]
70	39.5	Platythyrea	[5]
71	51.5	Ponera	[5]
117	15.5	Leptogenys	[6]
153	15	Odontomachus	[7, 8]
203	15	Cylindromyrmex	[9]
231	15	Neivamyrmex	[10]
251	78.5	Canapone	[11]
254	44.1	Rhytidoponera + Gnampotgenys	[12, 13]
260	39.5	Gnamptogenys	
267	54.5	Myrmeciinae	[5]
307	53.5	Tetraponera	[14]
324	15	Pseudomyrmex	[15]
365	100	Aneuretniae	[13]
367	48.5	Dolichoderus	[16]
395	39.5	Liometopum	[5]
400	52	Tapinoma	[5]
478	44.1	Iridomyrmex	[12]
483	92	Formicinae	[17]
488	53.5	Gesomyrmex	[15]
521	39.5	Lasius	[5]
565	44.1	Plagiolepis	[5]
581	39.5	Pseudolasius	[5]
584	15	Paratrechina	[18]
635	44.1	Formica	[12]
666	44.1	Camponotus	[12]
934	39.5	Temnothorax	[5]
940	44.1	Stenamma	[5]
1131	44.1	Tetramorium	[5]
1339	15	Strumigenys	[19]
1384	15	Apterostigma	[20]
1495	15	Cephalotes	[21]

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Table A1.2 Literature derived phylogenies used to construct the supertrees. Figure number refers to the figure presenting the phylogeny that was encoded into the data matrix for supertree construction.

Reference	Figure number	Data type	Citation
Ayala et al 1996	1	mtDNA	[1]
Bacci Jr. et al 2009	1	mtDNA	[2]
Baur et al 1996	2	mtDNA	[3]
Beibl et al 2005	1	mtDNA	[4]
Chenuil and Mackay 1996	4	mtDNA	[5]
Hasegawa and Crozier 2006	3	mtDNA	[6]
Hasegawa et al 2002	2b	mtDNA	[7]
Johnson et al 2003	3a	mtDNA	[8]
Knaden et al 2005	1	mtDNA	[9]
Sameshima et al 1999	2	mtDNA	[10]
Shoemaker et al 2006	2	mtDNA	[11]
Steiner et al 2004	1	mtDNA	[12]
Steiner et al 2006	1	mtDNA	[13]
Steiner et al 2010	5	mtDNA	[14]
Degnan et al 2004	1b	mtDNA	[15]
Astruc et al 2004	1	mtDNA	[16]
Baur et al 1995	4	mtDNA	[3]
Sumner et al 2004	1	mtDNA	[17]
Biebl et al 2007	2c	mtDNA	[18]
Dentiger 2009	1	mtDNA	[19]
Villesen et al 2007	6	mtDNA	[20]
Kronauer et al 2004	1	mtDNA	[21]
Bacci Jr. et al 2009	2	nDNA	[2]
Hung et al 2004	2	nDNA	[22]
Kim and Kim 2002	2	nDNA	[23]
Kim and Kim 2006	2	nDNA	[24]
Seal et al 2011	2	nDNA	[25]
Astruc et al 2004	1	nDNA	[16]
Blaimer et al 2012	2	nDNA	[26]
Blaimer er al 2012	3	nDNA	[27]
Lucky 2011	2	nDNA	[28]
Krieger and Ross 2005	1a	nDNA	[29]
Ouellette et al 2006	1	rDNA	[30]
Saux et al 2000	3	rDNA	[31]
Ward and Brady 2003	20	rDNA	[32]
Brady et al 2006	1	mixed DNA	[33]
Chiotis et al 2000	3c	mixed DNA	[34]
Jansen and Savolainen 2010	1	mixed DNA	[35]
Kautz et al 2009	4	mixed DNA	[36]
LaPolla et al 2010	3	mixed DNA	[37]
LaPolla et al 2012	2	mixed DNA	[38]
Maruyama et al 2008	2	mixed DNA	[39]
Mertl et al 2010	1	mixed DNA	[40]
Spagna et al 2008	1	mixed DNA	[41]

Ward 2007	4	mixed DNA	[42]
Ward et al 2010	2	mixed DNA	[43]
Schmidt 2013	7	mixed DNA	[44]
Bacci Jr et al 2009	3	mixed DNA	[2]
Heinze et al 2005	4	mixed DNA	[45]
Oettler et al 2010	S1	mixed DNA	[46]
Sarnat and Moreau 2011	2	mixed DNA	[47]
Schultz and Brady 2008	1	mixed DNA	[48]
Wild 2009	4	mixed DNA	[49]
Kronauer et al 2007	1	mixed DNA	[50]
Moreau 2008	1	mixed DNA	[51]
Moreau et al 2006		mixed DNA	[52]
Janda et al 2004	6	DNA + morphology	[53]
Ward and Brady 2003	19	DNA + morphology	[32]
Wetterer et al 1998	2	DNA + morphology	[54]
Dengan et al 2004	2	DNA + morphology	[15]
Astruc et al 2004	3	DNA + morphology	[16]
Agosti 194	2	Morphology	[55]
Agosti 1994	1	Morphology	[56]
Baroni Urbani et al 1992	4	Morphology	[57]
Brady and Ward 2005	1	Morphology	[58]
Brandao et al 1999	89	Morphology	[59]
Fontenla Rizo 2000	3	Morphology	[60]
Jonhson et al 2007	3	Morphology	[61]
Kim and Kim 2002	1	Morphology	[23]
Kim and Kim 2006	1	Morphology	[24]
Lopez et al 1994	10	Morphology	[62]
Mayhe-Nunes and Brandao 2007	2	Morphology	[63]
Pitts et al 2005	1c	Morphology	[64]
Schultz and Meier 1995	3	Morphology	[65]
Ward and Downie 2004	1	Morphology	[66]
Sanetra 2000	2	Morphology	[67]
Santera 2000	3	Morphology	[67]

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Table A1.3 rQS scores for the species-level supertree of the ants. Node refers to the numbered nodes in figure A2.1. The rQS algorithm prunes the supertree to match a source tree, and measures the degree of agreement between the two trees. This is repeated for each node and each source tree to generate a mean rQS score for each node. Positive rQS scores indicate support for a node, showing that more source trees agreed on the placement of that node than disagreed.

Node	rQS	Node	rQS	Node	rQS	Node	rQS	Node	rQS	Node	rQS
1	0	277	0.011	553	0.022	829	0	1105	0.022	1381	0.022
2	0	278	0.022	554	0	830	0	1106	0	1382	0.088
3	-0.105	279	0.033	555	0.022	831	0.033	1107	0	1383	-0.033
4	0.055	280	0.011	556	0.011	832	0.022	1108	0	1384	0.099
5	0.033	281	0.033	557	0.011	833	0.022	1109	0	1385	0.077
6	0.022	282	0.033	558	0.011	834	0.011	1110	0	1386	0.033
7	0.011	283	0.033	559	0.033	835	0	1111	0	1387	0.066
8	0.011	284	0.011	560	0.033	836	0	1112	0	1388	0.033
9	0.011	285	0.022	561	0.022	837	0	1113	0	1389	0.066
10	0.011	286	0.011	562	0.011	838	0.429	1114	-0.033	1390	0.022
11	0.011	287	0.022	563	0.011	839	-0.011	1115	-0.011	1391	-0.055
12	0.011	288	0.011	564	-0.099	840	-0.011	1116	-0.066	1392	0.11
13	-0.011	289	0.011	565	0.055	841	0.077	1117	0.022	1393	0
14	0.011	290	0.011	566	0.044	842	0.121	1118	0.022	1394	0.011
15	0.011	291	0.055	567	0	843	0.088	1119	0.022	1395	0.011
16	0.011	292	0.044	568	0	844	0.11	1120	0.011	1396	0.022
17	0.011	293	0.011	569	0.011	845	0.11	1121	-0.011	1397	0.011
18	0.011	294	0.011	570	0.011	846	0.088	1122	0	1398	0.011
19	0.011	295	0.011	571	0.033	847	0.088	1123	0.077	1399	0.055
20	0.011	296	0.044	572	0.11	848	0.066	1124	0.022	1400	0.033
21	0.011	297	0.033	573	0.022	849	0.055	1125	0.055	1401	0.044
22	0.011	298	0.022	574	-0.055	850	0.011	1126	0.055	1402	0.187
23	0.011	299	0.022	575	-0.055	851	0.055	1127	0.044	1403	0.165
24	0.011	300	0.011	576	0.022	852	0.077	1128	0	1404	0.165

25	0.055	301	0.011	577	0	853	0.044	1129	0	1405	0.143
26	0.033	302	0.011	578	0.055	854	0.011	1130	-0.055	1406	0.066
27	-0.044	303	0.011	579	0.022	855	-0.022	1131	-0.044	1407	0.044
28	0.022	304	0.011	580	-0.022	856	0.077	1132	-0.044	1408	0.187
29	0.011	305	0.011	581	-0.055	857	-0.022	1133	0	1409	0.165
30	0	306	0.011	582	-0.033	858	0.011	1134	0	1410	0.066
31	0	307	0.165	583	0.055	859	0.253	1135	0.022	1411	0.121
32	0.044	308	0.022	584	-0.055	860	0.253	1136	0.033	1412	-0.022
33	0.044	309	0.033	585	0	861	0.055	1137	0.022	1413	0.044
34	0.066	310	0.033	586	0.044	862	0.077	1138	0.011	1414	0.011
35	0	311	-0.011	587	0.088	863	0.077	1139	0.011	1415	0
36	-0.022	312	-0.011	588	0.088	864	0.033	1140	-0.033	1416	0.011
37	-0.033	313	0.033	589	0.022	865	0.055	1141	0.022	1417	0.055
38	-0.033	314	0.022	590	-0.033	866	0.022	1142	0.011	1418	0
39	0.033	315	0	591	0.077	867	0.066	1143	0.022	1419	0
40	0.033	316	0.033	592	0	868	0.055	1144	0.022	1420	0
41	0.055	317	0	593	0.011	869	0.033	1145	0.055	1421	0.022
42	0.033	318	0	594	0.033	870	0.011	1146	0	1422	0
43	0.011	319	-0.011	595	-0.011	871	0.011	1147	0.022	1423	0
44	0.011	320	0.022	596	-0.033	872	0.011	1148	0	1424	0
45	0	321	0.011	597	-0.011	873	-0.022	1149	0	1425	0.11
46	0.011	322	-0.011	598	0.011	874	-0.066	1150	0	1426	0.132
47	-0.011	323	0.011	599	0.022	875	0	1151	0.011	1427	0.121
48	0.022	324	0.055	600	0.011	876	-0.033	1152	-0.011	1428	-0.022
49	0	325	0.077	601	0	877	-0.022	1153	0.011	1429	0
50	0.077	326	0.011	602	0	878	-0.022	1154	0.011	1430	0.011
51	0.044	327	0.011	603	-0.033	879	0	1155	0.011	1431	0
52	0.044	328	0.033	604	-0.022	880	0	1156	0.011	1432	0

53	0.055	329	0.033	605	0.011	881	0	1157	0.011	1433	0.011
54	0	330	0.022	606	0	882	0.011	1158	0.011	1434	0.011
55	0.088	331	0	607	0	883	0	1159	0.011	1435	0.011
56	0.022	332	0.011	608	-0.022	884	0.022	1160	0.011	1436	0.011
57	0.011	333	0.044	609	-0.011	885	0	1161	0.077	1437	0.011
58	0.022	334	0.033	610	0.011	886	0.022	1162	0.022	1438	0.055
59	-0.022	335	0.022	611	0.011	887	0	1163	0.011	1439	0.055
60	0.022	336	-0.044	612	0.044	888	-0.011	1164	0.011	1440	0.011
61	0.022	337	-0.022	613	-0.044	889	0	1165	0.011	1441	0.011
62	0.022	338	0.011	614	0.176	890	0	1166	0.099	1442	0.011
63	0	339	0.033	615	0.044	891	0	1167	0.11	1443	0.011
64	0.033	340	0	616	0	892	-0.044	1168	0.11	1444	0
65	0.033	341	0.011	617	0.011	893	0	1169	0	1445	0.011
66	0.022	342	0	618	0.055	894	-0.022	1170	0.066	1446	0.011
67	0.022	343	0.022	619	0.011	895	0.022	1171	0	1447	0.011
68	0.077	344	0	620	0	896	0.022	1172	0.022	1448	0.011
69	0.055	345	-0.033	621	0.044	897	0	1173	0	1449	0.011
70	0.033	346	0.011	622	0.033	898	0.011	1174	0	1450	0.011
71	-0.011	347	-0.011	623	0.033	899	-0.055	1175	0.022	1451	0.011
72	-0.066	348	-0.011	624	0.044	900	0	1176	0	1452	0.099
73	-0.044	349	0.055	625	0.044	901	-0.022	1177	0.022	1453	0.099
74	-0.033	350	0	626	0.044	902	0	1178	0.044	1454	0.121
75	0.066	351	-0.022	627	0.044	903	0.011	1179	0.055	1455	0
76	0.055	352	-0.033	628	0.022	904	0.044	1180	0	1456	0.022
77	0.022	353	-0.022	629	0	905	0	1181	-0.022	1457	0.066
78	0.011	354	0.033	630	0.022	906	0	1182	0	1458	0.055
79	0.011	355	-0.011	631	0.011	907	0	1183	0	1459	0.011
80	0	356	0.011	632	0.154	908	0	1184	0.033	1460	0.099

81	0.055	357	0.033	633	0.022	909	0	1185	0.055	1461	0.044
82	0.022	358	0.011	634	0.033	910	0.033	1186	0.033	1462	0.011
83	0.022	359	-0.022	635	0.022	911	-0.011	1187	0.022	1463	0.033
84	0.044	360	0.011	636	0.077	912	0	1188	0.022	1464	0.11
85	0	361	0.044	637	0	913	0.011	1189	0.022	1465	0.066
86	0.044	362	0.033	638	0	914	0.011	1190	0.011	1466	0.132
87	0.011	363	0.044	639	0.022	915	0.011	1191	0.022	1467	0.044
88	0.011	364	0.033	640	0.055	916	0.011	1192	0.011	1468	0.044
89	0.011	365	0	641	0.044	917	-0.011	1193	0.011	1469	0.044
90	-0.011	366	0.198	642	0.044	918	-0.011	1194	-0.055	1470	0.044
91	-0.033	367	0.176	643	0.022	919	-0.022	1195	-0.077	1471	0.055
92	-0.033	368	0.066	644	0.011	920	-0.022	1196	-0.044	1472	0.044
93	0	369	0.011	645	0.033	921	0.022	1197	0.055	1473	0.022
94	0.044	370	-0.033	646	0.011	922	-0.033	1198	0.022	1474	-0.011
95	0.055	371	0.055	647	0.011	923	-0.055	1199	0.033	1475	0.011
96	0.044	372	0.011	648	0.011	924	0.022	1200	-0.066	1476	0.022
97	0.022	373	0.055	649	0.022	925	0.022	1201	-0.011	1477	0.022
98	0.011	374	0.044	650	0.011	926	-0.033	1202	-0.022	1478	-0.033
99	0.033	375	0.044	651	0.022	927	0	1203	0.066	1479	0.011
100	0.011	376	0.044	652	0.022	928	0	1204	0.011	1480	-0.011
101	0	377	-0.077	653	0.022	929	0	1205	0	1481	-0.011
102	0.033	378	0.022	654	0.022	930	0	1206	-0.066	1482	0.011
103	0.011	379	0.011	655	0.044	931	0	1207	0.011	1483	-0.011
104	0.022	380	0.077	656	0.033	932	0	1208	0	1484	0.022
105	0.044	381	0.077	657	0.022	933	-0.011	1209	0.022	1485	0.033
106	0.044	382	0.044	658	0.011	934	0.143	1210	0.011	1486	0.033
107	0.044	383	0.022	659	0.011	935	0.066	1211	-0.033	1487	0
108	0.044	384	-0.055	660	0.055	936	0.077	1212	-0.022	1488	0

109	0.044	385	0.088	661	0.055	937	0.044	1213	-0.011	1489	0.044
110	0.044	386	0.088	662	0.022	938	0.022	1214	0.011	1490	0.044
111	0.044	387	0.011	663	0.066	939	0.033	1215	0.011	1491	-0.044
112	-0.022	388	0.011	664	0.154	940	-0.011	1216	0	1492	0.033
113	0.044	389	0.066	665	0.165	941	-0.022	1217	0.033	1493	-0.066
114	-0.088	390	0.077	666	0.033	942	0	1218	0	1494	0.011
115	0.011	391	-0.055	667	0.099	943	-0.022	1219	0.033	1495	0.044
116	0.033	392	0.088	668	0.022	944	-0.022	1220	-0.011	1496	0.033
117	0.011	393	0.011	669	0.011	945	0.011	1221	0	1497	0.088
118	0.033	394	-0.011	670	0.022	946	0	1222	0.011	1498	0.088
119	0.055	395	0.088	671	0.011	947	0.011	1223	0.165	1499	0.066
120	0.011	396	0.099	672	0.022	948	0.011	1224	0.022	1500	0.055
121	0	397	0.077	673	0.088	949	0.033	1225	0.033	1501	0.055
122	0.011	398	-0.011	674	0.011	950	0.011	1226	0.055	1502	0.055
123	0.011	399	0.088	675	0.088	951	0.011	1227	0	1503	0.033
124	0.011	400	0.011	676	0.011	952	-0.011	1228	0	1504	0.011
125	0.011	401	0.055	677	0.088	953	0.011	1229	0.022	1505	0.033
126	0.011	402	-0.011	678	0	954	-0.011	1230	0.033	1506	0.033
127	0.011	403	0.077	679	0.033	955	-0.011	1231	0.033	1507	0.033
128	-0.066	404	0.066	680	0.011	956	0.022	1232	0.022	1508	-0.011
129	0	405	-0.033	681	0.011	957	0.011	1233	0	1509	0.033
130	0.011	406	0.033	682	0.011	958	0.011	1234	0.011	1510	0
131	0	407	0.033	683	0.033	959	-0.011	1235	0	1511	0.044
132	0.044	408	0.011	684	0	960	0.011	1236	-0.011	1512	0.011
133	0.022	409	0.055	685	0.033	961	-0.011	1237	0	1513	0.011
134	0.011	410	0.033	686	0.033	962	-0.011	1238	0.011	1514	0.011
135	0.011	411	0.044	687	0.022	963	0	1239	0.011	1515	0.011
136	0	412	0.055	688	0.011	964	-0.033	1240	0.011	1516	0.011

137	-0.066	413	0.055	689	0.011	965	0.033	1241	0	1517	0.044
138	-0.033	414	0.044	690	0.011	966	-0.011	1242	-0.011	1518	0.011
139	-0.033	415	0.033	691	0.011	967	-0.011	1243	-0.011	1519	0.011
140	-0.011	416	0.055	692	0.011	968	0	1244	0.011	1520	0
141	-0.022	417	0.011	693	0.066	969	0.033	1245	0.033	1521	0.022
142	-0.011	418	0.033	694	0.011	970	0.077	1246	0.055	1522	0
143	0	419	0.055	695	0.077	971	0.044	1247	0.055	1523	0.011
144	0	420	0.033	696	-0.022	972	0.066	1248	0.055	1524	0.022
145	0.011	421	0.055	697	0.022	973	0	1249	0.011	1525	0.022
146	0.055	422	0.055	698	0	974	0.011	1250	0.033	1526	0.022
147	0.055	423	0.033	699	0.011	975	0.022	1251	-0.011	1527	0.022
148	0.044	424	0.011	700	0.011	976	0.022	1252	-0.011	1528	0
149	0.022	425	0.033	701	0	977	0.022	1253	0.033	1529	0
150	0.022	426	0.011	702	-0.011	978	0.011	1254	0.011	1530	0.011
151	0.022	427	0.033	703	0.011	979	0.044	1255	0.011	1531	0.022
152	-0.011	428	0.055	704	0.011	980	-0.033	1256	0.055	1532	0.011
153	0.088	429	0.055	705	0.011	981	0.022	1257	0.011	1533	0.011
154	0	430	0.055	706	0.011	982	0.011	1258	0.11	1534	0.011
155	0.066	431	-0.066	707	0.011	983	0	1259	-0.011	1535	0
156	0.044	432	0.055	708	0.055	984	0.022	1260	0.011	1536	-0.022
157	0.033	433	0	709	0	985	0.022	1261	0.055	1537	0
158	0.011	434	0.011	710	0.011	986	0.011	1262	0.033	1538	0
159	0.011	435	0.055	711	0.011	987	0.011	1263	0.033	1539	0
160	0.011	436	0.022	712	0.022	988	0.011	1264	0.011	1540	0
161	0.011	437	0.033	713	0.011	989	0.011	1265	0.011	1541	0.011
162	0.011	438	0.088	714	0.033	990	0.022	1266	0.033	1542	0
163	0.066	439	0.077	715	-0.033	991	0.011	1267	0.011	1543	0
164	0.088	440	-0.066	716	-0.033	992	0.011	1268	-0.011	1544	0

165	-0.011	441	-0.055	717	-0.055	993	0.011	1269	0	1545	0
166	-0.011	442	0.088	718	0.011	994	0.011	1270	0.055	1546	0
167	0.033	443	0	719	0.044	995	0.011	1271	0.011	1547	0
168	0.044	444	0.022	720	0.044	996	0.011	1272	-0.011	1548	0.022
169	-0.055	445	0.022	721	0.033	997	0.011	1273	0.055	1549	0
170	-0.011	446	0.011	722	0.011	998	0.011	1274	0.11	1550	0.022
171	-0.011	447	0.022	723	-0.044	999	0.033	1275	0	1551	0.022
172	0	448	0.011	724	-0.022	1000	0.022	1276	0.044	1552	-0.022
173	-0.033	449	0.011	725	-0.022	1001	0.022	1277	0	1553	0.011
174	-0.033	450	0.011	726	0.044	1002	0.044	1278	0.022	1554	0
175	-0.011	451	0	727	0.077	1003	0.022	1279	0.066	1555	0
176	0.011	452	0.044	728	0.055	1004	0.022	1280	0.044	1556	0.011
177	0.011	453	0	729	0.033	1005	-0.044	1281	0.033	1557	0.011
178	0.692	454	0	730	0.033	1006	0.011	1282	0.011	1558	0.022
179	0.132	455	0.044	731	0.055	1007	0.077	1283	0.033	1559	0.022
180	0.132	456	0	732	0.077	1008	0.055	1284	0.033	1560	0.022
181	0.11	457	0	733	0.011	1009	-0.011	1285	0.011	1561	0.022
182	0.022	458	0	734	0.011	1010	-0.011	1286	0.033	1562	0.022
183	0.011	459	0.022	735	0.044	1011	-0.033	1287	0.033	1563	0
184	0.099	460	0.044	736	-0.011	1012	0.033	1288	0.033	1564	-0.033
185	0.033	461	0	737	0.055	1013	0.022	1289	0.033	1565	-0.033
186	0.011	462	0.022	738	0.022	1014	0.022	1290	0.011	1566	0
187	0.011	463	0.044	739	0.022	1015	-0.022	1291	0.033	1567	-0.011
188	0.055	464	0	740	0.011	1016	-0.033	1292	0	1568	-0.011
189	-0.044	465	-0.022	741	0.033	1017	-0.011	1293	0.022	1569	0.011
190	0	466	0.011	742	0.033	1018	0.044	1294	0.033	1570	0.011
191	0.011	467	0.033	743	0.022	1019	0	1295	-0.011	1571	0
192	0.011	468	0.022	744	-0.033	1020	0.011	1296	-0.033	1572	0.011

193	0.011	469	-0.022	745	-0.077	1021	0	1297	0.022	1573	0.033
194	0.022	470	-0.055	746	0	1022	0.011	1298	0.033	1574	0.033
195	-0.033	471	-0.022	747	0	1023	0.022	1299	0.033	1575	0.011
196	0.011	472	0.055	748	0.011	1024	0.022	1300	0.011	1576	0.011
197	0	473	0	749	-0.044	1025	0.011	1301	0.033	1577	0.011
198	0.011	474	0.066	750	-0.044	1026	0.011	1302	0.066	1578	0
199	0.033	475	0.077	751	-0.011	1027	0.011	1303	0	1579	-0.022
200	0.011	476	0.077	752	0	1028	0.022	1304	0.044	1580	0
201	0	477	0.066	753	0.011	1029	0.011	1305	0.011	1581	0
202	-0.066	478	0.033	754	0.033	1030	0.011	1306	0	1582	0
203	0.044	479	0.066	755	0.011	1031	0.011	1307	-0.011	1583	0
204	0	480	0.055	756	0.011	1032	0.011	1308	-0.011	1584	0
205	0	481	0.022	757	0.022	1033	0.011	1309	-0.011	1585	0
206	-0.011	482	0.033	758	0.022	1034	0.011	1310	0.055	1586	0
207	-0.022	483	0.396	759	0.011	1035	0.011	1311	0.033	1587	0
208	0.088	484	0.33	760	0.011	1036	0.011	1312	0	1588	0
209	0.11	485	0.099	761	0.011	1037	0.044	1313	0.022	1589	0.022
210	0.11	486	0.011	762	0.011	1038	0.011	1314	-0.011	1590	0
211	0.044	487	0.022	763	0.011	1039	0.044	1315	0.033	1591	0
212	0.011	488	0.011	764	0.011	1040	0.011	1316	0.033	1592	0
213	0	489	0.011	765	0	1041	0.011	1317	-0.011	1593	0.022
214	0.022	490	0.011	766	0	1042	0.011	1318	0.033	1594	0.022
215	0.022	491	0.099	767	0.033	1043	-0.022	1319	0.011	1595	0.022
216	0.022	492	0.011	768	0.011	1044	0	1320	0.011	1596	0
217	0.022	493	0.011	769	0	1045	0.022	1321	-0.022	1597	0.022
218	0.044	494	0.011	770	0.011	1046	0.033	1322	-0.011	1598	0.022
219	0	495	0	771	0.011	1047	0	1323	0.011	1599	0
220	0.022	496	0.099	772	0.011	1048	0.077	1324	0.011	1600	0.011

221	0	497	0.044	773	0.011	1049	0.011	1325	0.011	1601	0
222	-0.022	498	0	774	0.011	1050	0.055	1326	0.011	1602	0
223	0.044	499	0.088	775	0.011	1051	0.033	1327	0.033	1603	0
224	0.044	500	-0.011	776	0.044	1052	0.011	1328	0.033	1604	0
225	0.011	501	0	777	0.044	1053	0.011	1329	0.011	1605	0
226	0.066	502	0	778	0.022	1054	0.011	1330	-0.011	1606	0
227	-0.011	503	0.022	779	0.022	1055	-0.011	1331	0.011	1607	0.022
228	-0.011	504	0.011	780	0.011	1056	-0.011	1332	0.011	1608	-0.022
229	0.011	505	0.011	781	0.011	1057	0.011	1333	0.011	1609	-0.011
230	0.143	506	0.011	782	0.011	1058	0.011	1334	0.022	1610	-0.011
231	0.044	507	-0.022	783	0.011	1059	-0.011	1335	0.055	1611	0
232	-0.011	508	0.011	784	0.011	1060	-0.011	1336	-0.011	1612	0
233	0.011	509	0.044	785	0.011	1061	0.011	1337	0.033	1613	0
234	0	510	0.011	786	0.011	1062	-0.033	1338	0.099	1614	0.011
235	0.011	511	0	787	0.011	1063	-0.033	1339	0.11	1615	0.022
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237	0.011	513	-0.033	789	-0.011	1065	0.011	1341	0	1617	0.011
238	0.011	514	0.022	790	-0.033	1066	0.011	1342	0.011	1618	-0.011
239	0.055	515	-0.011	791	-0.044	1067	-0.011	1343	0	1619	0.011
240	0.011	516	-0.044	792	-0.044	1068	-0.033	1344	0.022	1620	-0.011
241	0.022	517	-0.022	793	0	1069	0	1345	0.011	1621	0.011
242	0.044	518	0	794	0.022	1070	0.033	1346	0.011	1622	0.022
243	0.022	519	-0.022	795	-0.011	1071	-0.011	1347	0.011	1623	0.011
244	0.044	520	-0.022	796	-0.055	1072	0.077	1348	0.011	1624	0.033
245	0.033	521	-0.022	797	0	1073	0.088	1349	0.011	1625	0.033
246	0.011	522	0.099	798	-0.011	1074	0	1350	0.022	1626	0.011
247	0.011	523	0.077	799	-0.022	1075	-0.022	1351	0	1627	0
248	0	524	0.055	800	0	1076	0.044	1352	0.011	1628	0

249	0.011	525	0.011	801	0.022	1077	-0.011	1353	0	1629	0
250	0.626	526	0.011	802	0.022	1078	-0.022	1354	0.011	1630	0.011
251	0.066	527	0.044	803	0.022	1079	0.055	1355	-0.011	1631	0
252	0.077	528	0.044	804	-0.055	1080	0	1356	0.011	1632	0
253	0.044	529	0.022	805	-0.033	1081	0.066	1357	0.011	1633	0
254	0.088	530	0.066	806	-0.022	1082	0	1358	-0.011	1634	0
255	0.044	531	0.044	807	-0.022	1083	0	1359	-0.011	1635	0
256	0.022	532	0.011	808	0.022	1084	-0.022	1360	0.011	1636	0
257	0.033	533	-0.011	809	0	1085	-0.022	1361	0.011	1637	0
258	0.022	534	-0.011	810	0	1086	0.066	1362	-0.011	1638	0
259	0.022	535	0.022	811	0	1087	0.022	1363	-0.011	1639	0.022
260	0.055	536	0.011	812	0.022	1088	0.066	1364	0.022	1640	0.022
261	0.011	537	0.011	813	-0.033	1089	0.033	1365	-0.022	1641	0
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263	0.011	539	0.011	815	0.011	1091	0	1367	0	1643	0
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265	0.473	541	-0.011	817	-0.022	1093	-0.044	1369	0.022	1645	0
266	-0.088	542	-0.033	818	0	1094	0.011	1370	0.033	1646	0
267	0.011	543	0.033	819	-0.022	1095	0.022	1371	0.033	1647	0
268	0.132	544	0.022	820	-0.022	1096	0.033	1372	0	1648	0
269	0.121	545	0.022	821	0.022	1097	0.022	1373	0.022	1649	0
270	0.011	546	0.022	822	-0.022	1098	0.011	1374	0.011	1650	0
271	0.099	547	0.022	823	0.022	1099	0.033	1375	0	1651	0
272	0.055	548	-0.033	824	0	1100	0	1376	0.044	1652	0.022
273	0.055	549	0.022	825	0.011	1101	0.022	1377	0.066	1653	0
274	0.011	550	0.022	826	-0.011	1102	0	1378	-0.066	1654	0
275	0.011	551	0.033	827	-0.011	1103	0.022	1379	0		
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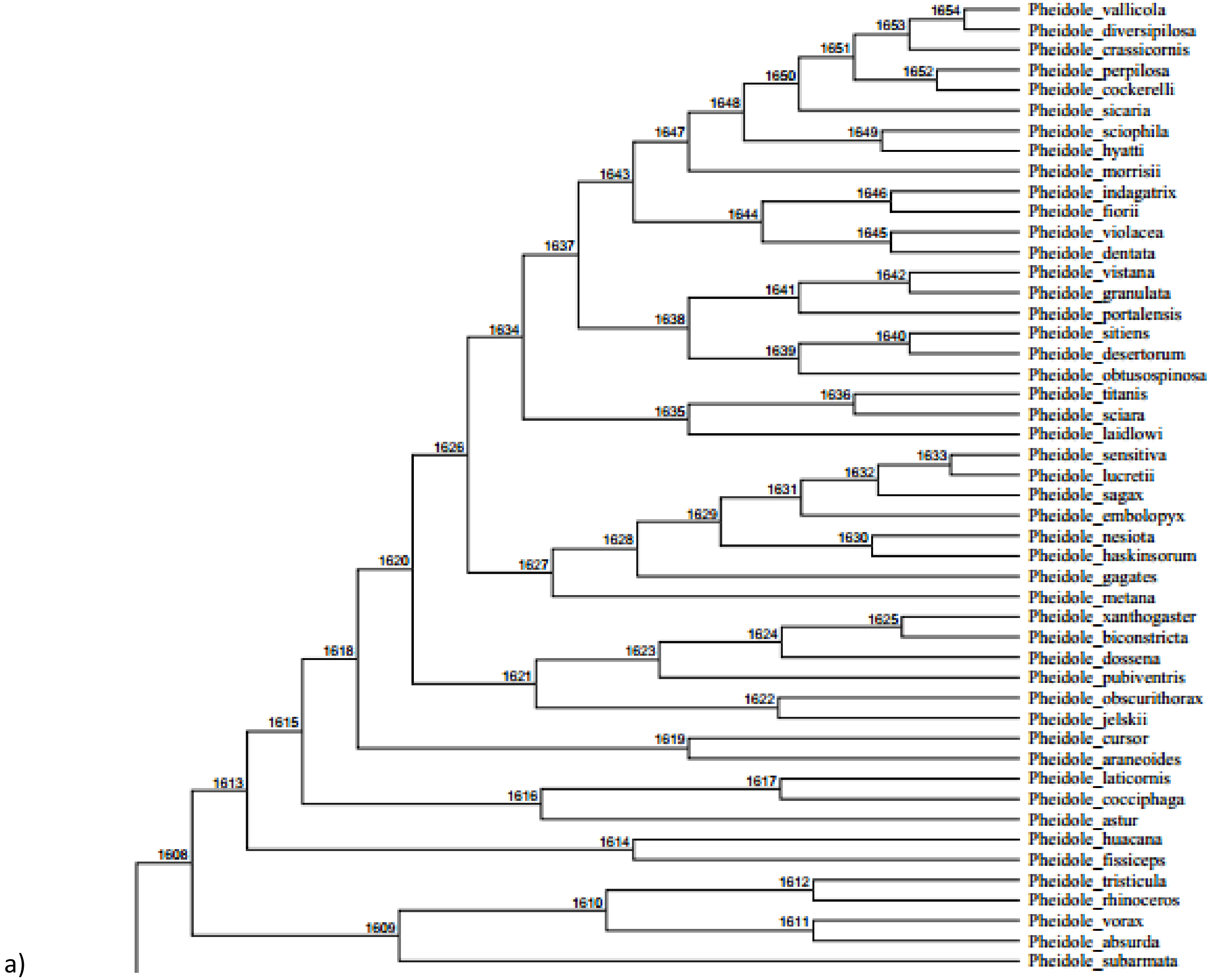
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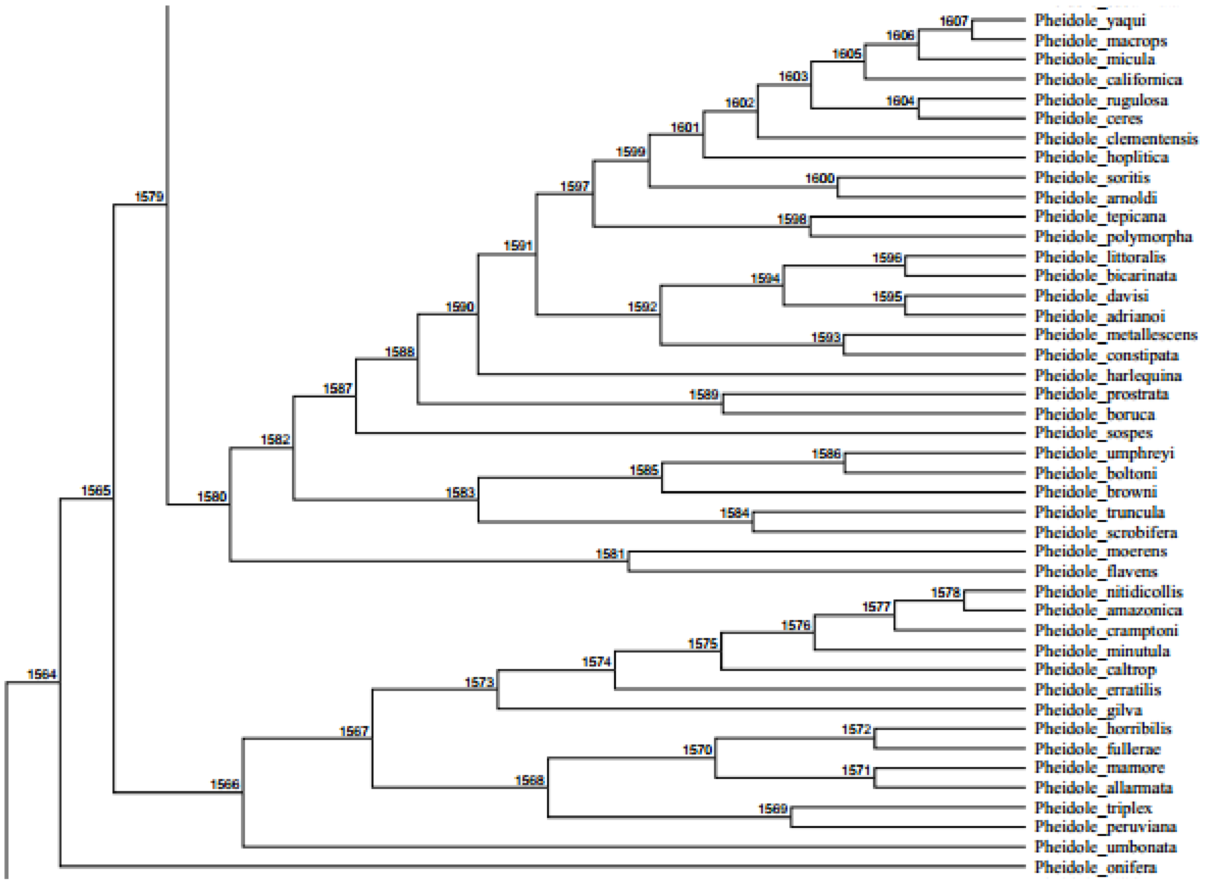
a)

b)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Pheidole_yaqui
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Pheidole_micula
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Pheidole_rugulosa
Pheidole_ceres
Pheidole_clementensis
Pheidole_hoplitica
Pheidole_soritis
Pheidole_arnoldi
Pheidole_tepicana
Pheidole_polymorpha
Pheidole_littoralis
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Pheidole_sospes
Pheidole_umphreyi
Pheidole_boltoni
Pheidole_browni
Pheidole_truncula
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Pheidole_moerens
Pheidole_flavens
Pheidole_nitidicollis
Pheidole_amazonica
Pheidole_cramptoni
Pheidole_minutula
Pheidole_caltrop
Pheidole_erratilis
Pheidole_gilva
Pheidole_horribilis
Pheidole_fullerae
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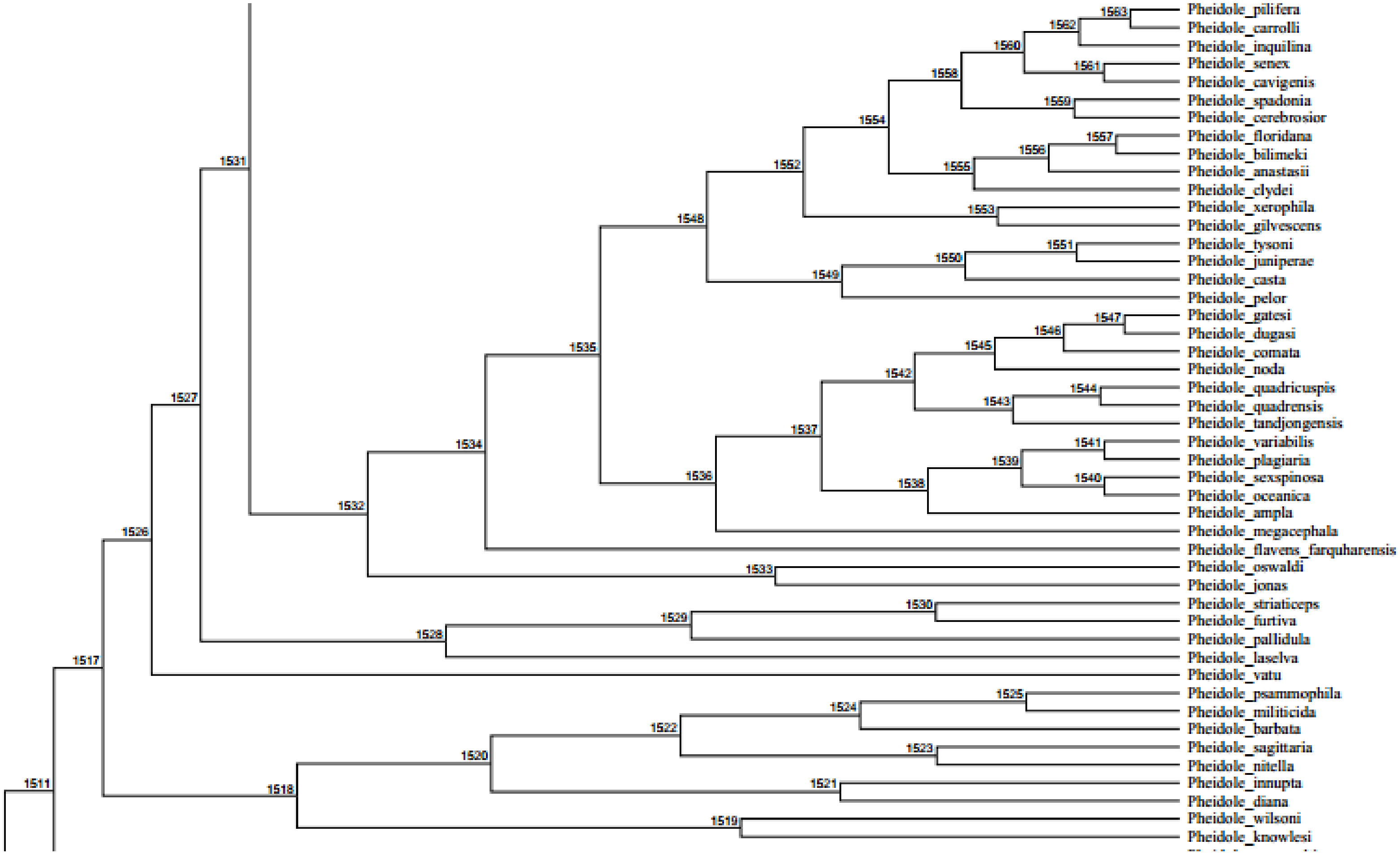
Pheidole_triplex
Pheidole_peruviana
Pheidole_umbonata
Pheidole_onifera

c)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Pheidole_cerebrosior
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Pheidole_juniperae
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Pheidole_casta
Pheidole_pelor
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Pheidole_dugasi
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Pheidole_tandjongensis
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Pheidole_jonas
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Pheidole_laselva
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Pheidole_diana
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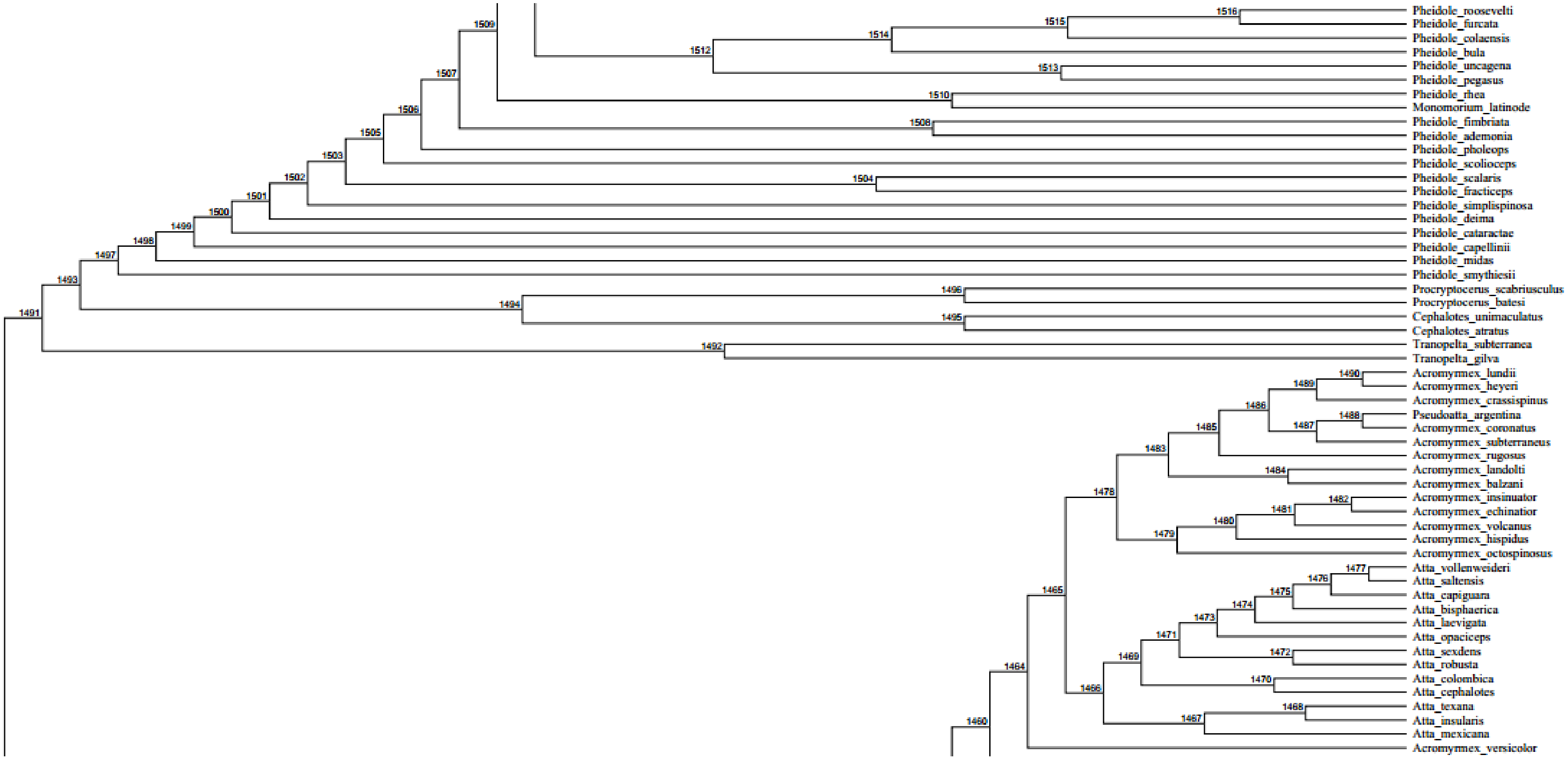
Pheidole_knowlesi

d)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Monomorium_latinode
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Pheidole_fimbriata
Pheidole_ademonia
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Pheidole_pholeops
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Pheidole_scolioceps
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Pheidole_fracticeps
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Pheidole_simplispinosa
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Pheidole_deima
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Pheidole_cataractae
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Pheidole_capellinii
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Pheidole_midas
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Pheidole_smythiesii
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Procryptocerus_scabriusculus
Procryptocerus_batesi
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Cephalotes_unimaculatus
Cephalotes_atratus
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Tranopelta_gilva
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Acromyrmex_lundii
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Acromyrmex_heyeri
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Acromyrmex_crassispinus
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Pseudoatta_argentina
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Acromyrmex_coronatus
Acromyrmex_subterraneus
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Acromyrmex_rugosus
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Acromyrmex_landolti
Acromyrmex_balzani
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Acromyrmex_insinuator
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Acromyrmex_echinatior
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Acromyrmex_hispidus
Acromyrmex_octospinosus
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Atta_capiguara
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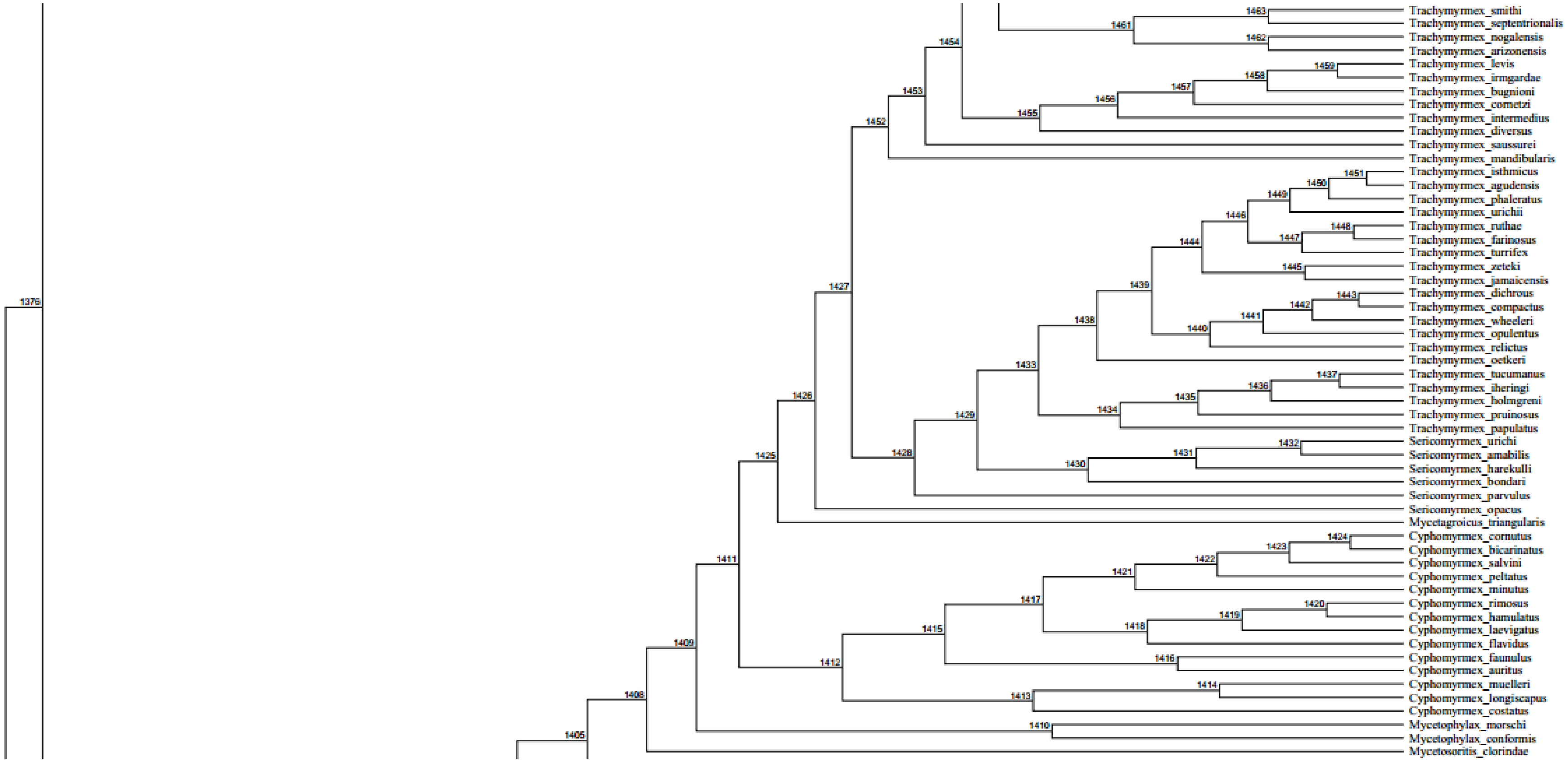
Acromyrmex_versicolor

e)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Trachymyrmex_smithi
Trachymyrmex_septentrionalis
Trachymyrmex_nogalensis
Trachymyrmex_arizonensis
Trachymyrmex_levis
Trachymyrmex_irmgardae
Trachymyrmex_bugnioni
Trachymyrmex_cornetzi
Trachymyrmex_intermedius
Trachymyrmex_diversus
Trachymyrmex_saussurei
Trachymyrmex_mandibularis
Trachymyrmex_isthmicus
Trachymyrmex_agudensis
Trachymyrmex_phaleratus
Trachymyrmex_urichii
Trachymyrmex_ruthae
Trachymyrmex_farinosus
Trachymyrmex_turrifex
Trachymyrmex_zeteki
Trachymyrmex_jamaicensis
Trachymyrmex_dichrous
Trachymyrmex_compactus
Trachymyrmex_wheeleri
Trachymyrmex_opulentus
Trachymyrmex_relictus
Trachymyrmex_oetkeri
Trachymyrmex_tucumanus
Trachymyrmex_iheringi
Trachymyrmex_holmgreni
Trachymyrmex_pruinosus
Trachymyrmex_papulatus
Sericomyrmex_urichi
Sericomyrmex_amabilis
Sericomyrmex_harekulli
Sericomyrmex_bondari
Sericomyrmex_parvulus
Sericomyrmex_opacus
Mycetagroicus_triangularis
Cyphomyrmex_cornutus
Cyphomyrmex_bicarinatus
Cyphomyrmex_salvini
Cyphomyrmex_peltatus
Cyphomyrmex_minutus
Cyphomyrmex_rimosus
Cyphomyrmex_hamulatus
Cyphomyrmex_laevigatus
Cyphomyrmex_flavidus
Cyphomyrmex_faunulus
Cyphomyrmex_auritus
Cyphomyrmex_muelleri
Cyphomyrmex_longiscapus
Cyphomyrmex_costatus
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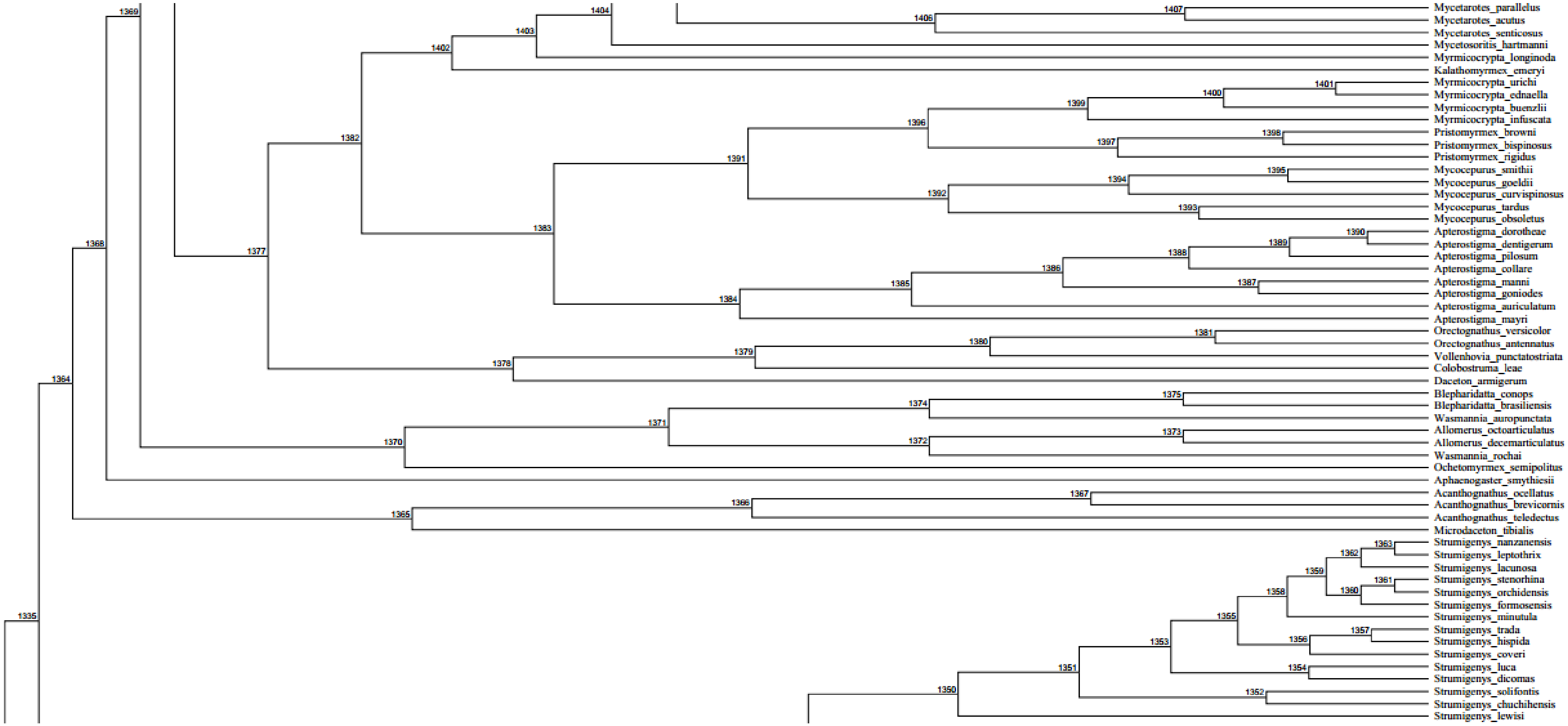
Mycetophylax_conformis
Mycetosoritis_clorindae

f)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Mycetosoritis_hartmanni
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Myrmicocrypta_urichi
Myrmicocrypta_ednaella
Myrmicocrypta_buenzlii
Myrmicocrypta_infuscata
Pristomyrmex_browni
Pristomyrmex_bispinosus
Pristomyrmex_rigidus
Mycocepurus_smithii
Mycocepurus_goeldii
Mycocepurus_curvispinosus
Mycocepurus_tardus
Mycocepurus_obsoletus
Apterostigma_dorotheae
Apterostigma_dentigerum
Apterostigma_pilosum
Apterostigma_collare
Apterostigma_manni
Apterostigma_goniodes
Apterostigma_auriculatum
Apterostigma_mayri
Orectognathus_versicolor
Orectognathus_antennatus
Vollenhovia_punctatostriata
Colobostruma_leae
Daceton_armigerum
Blepharidatta_conops
Blepharidatta_brasiliensis
Wasmannia_auropunctata
Allomerus_octoarticulatus
Allomerus_decemarticulatus
Wasmannia_rochai
Ochetomyrmex_semipolitus
Aphaenogaster_smythiesii
Acanthognathus_ocellatus
Acanthognathus_brevicornis
Acanthognathus_teledectus
Microdaceton_tibialis
Strumigenys_nanzanensis
Strumigenys_leptothrix
Strumigenys_lacunosa
Strumigenys_stenorhina
Strumigenys_orchidensis
Strumigenys_formosensis
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Strumigenys_hispida
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Strumigenys_luca
Strumigenys_dicomas
Strumigenys_solifontis
Strumigenys_chuchihensis
Strumigenys_lewisi
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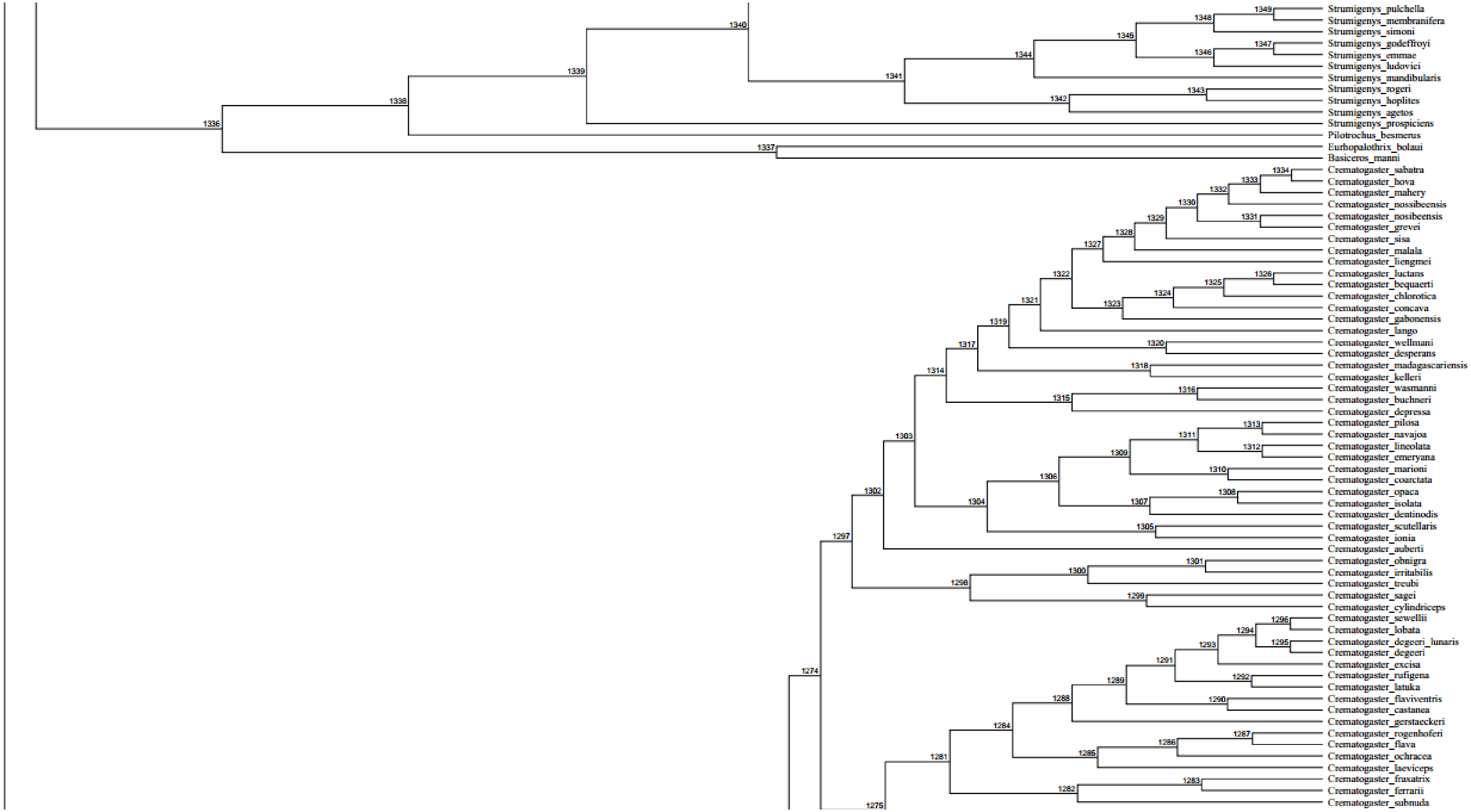
g)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Strumigenys_mandibularis
Strumigenys_rogeri
Strumigenys_hoplites
Strumigenys_agetos
Strumigenys_prospiciens
Pilotrochus_besmerus
Eurhopalothrix_bolaui
Basiceros_manni
Crematogaster_sabatra
Crematogaster_hova
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Crematogaster_nossibeensis
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Crematogaster_grevei
Crematogaster_sisa
Crematogaster_malala
Crematogaster_liengmei
Crematogaster_luctans
Crematogaster_bequaerti
Crematogaster_chlorotica
Crematogaster_concava
Crematogaster_gabonensis
Crematogaster_lango
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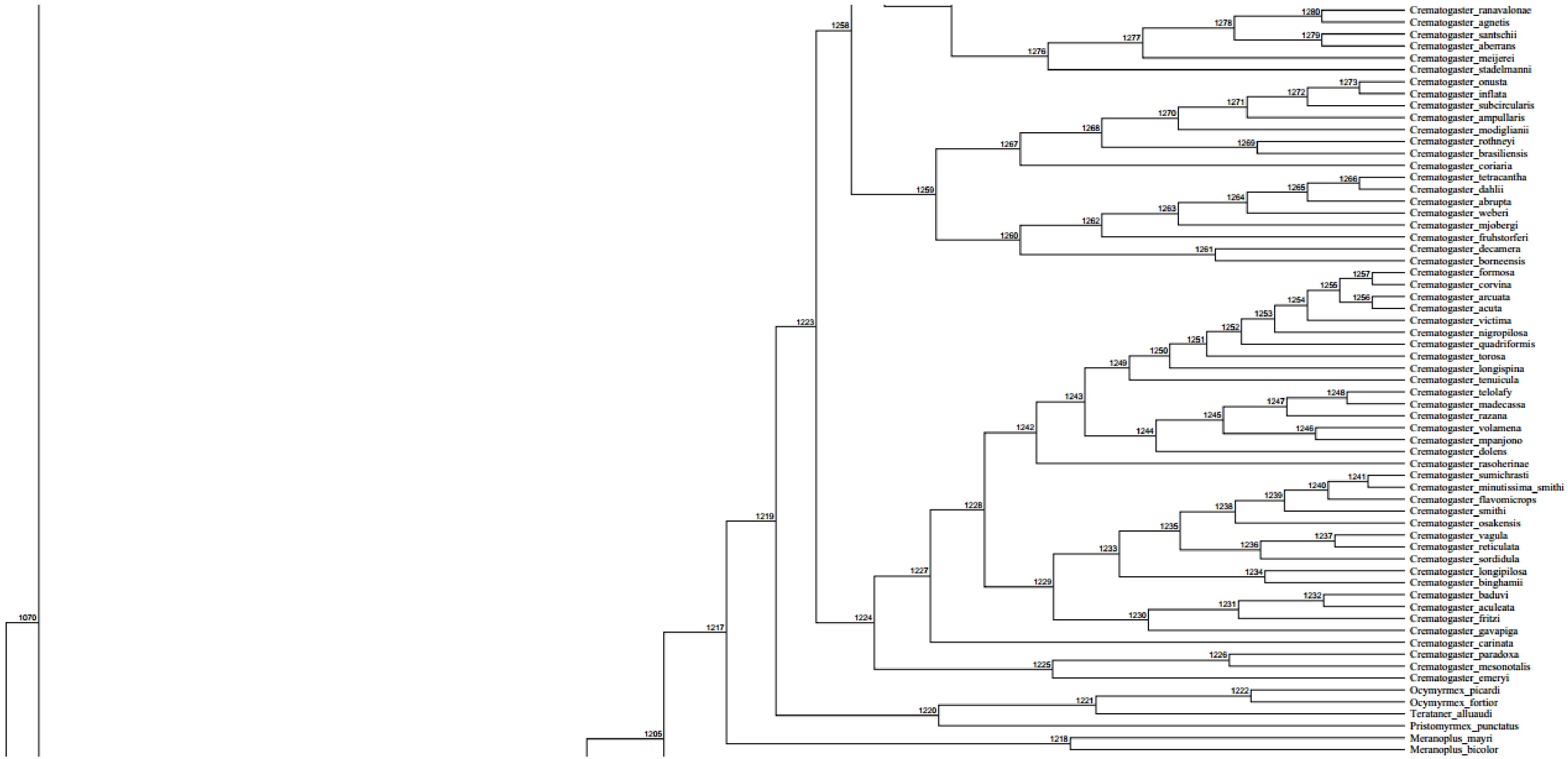

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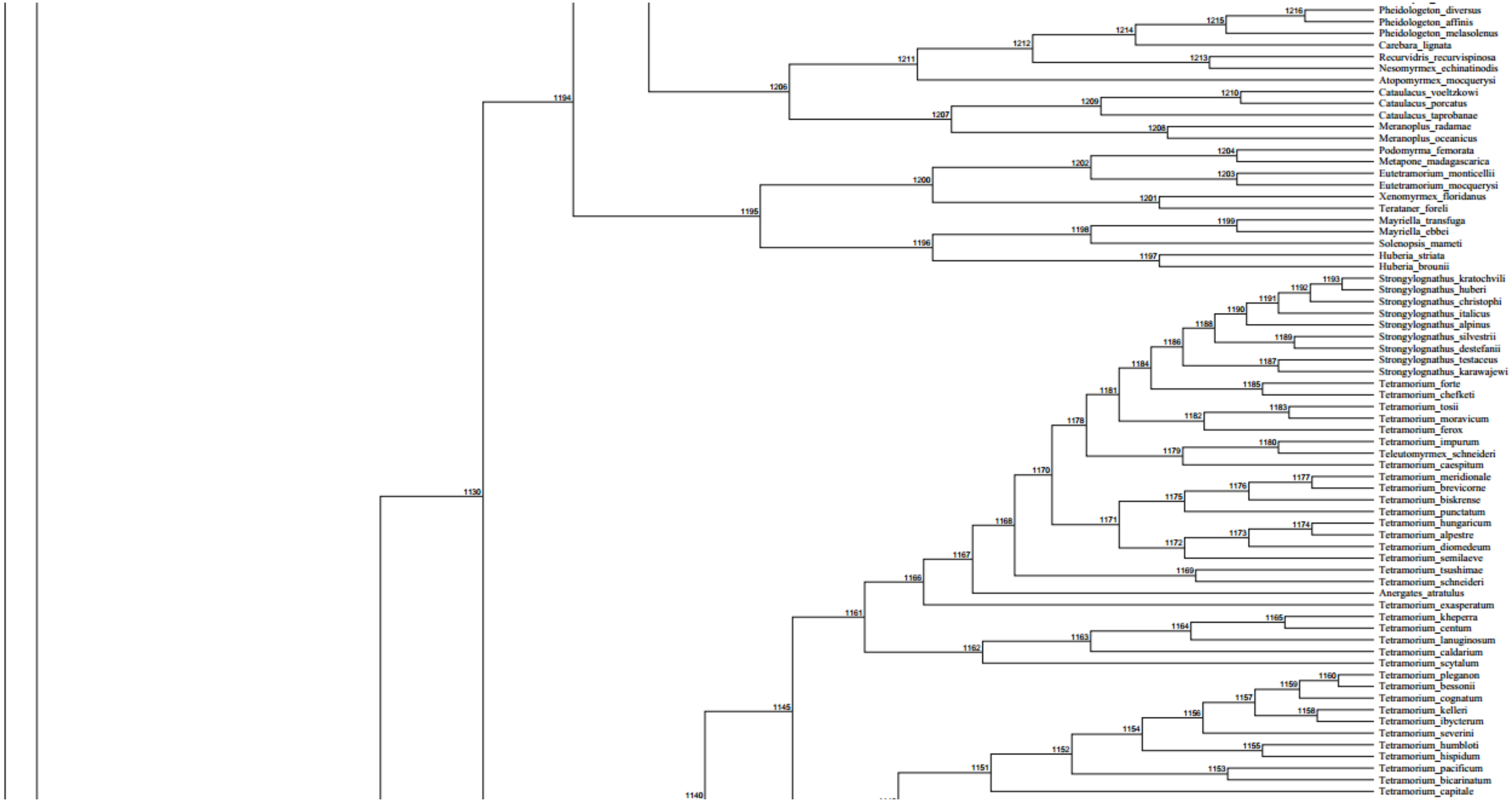
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Terataner_foreli
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Mayriella_ebbei
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Huberia_brounii
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Strongylognathus_alpinus
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Strongylognathus_destefanii
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Tetramorium_brevicorne
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Tetramorium_bessonii
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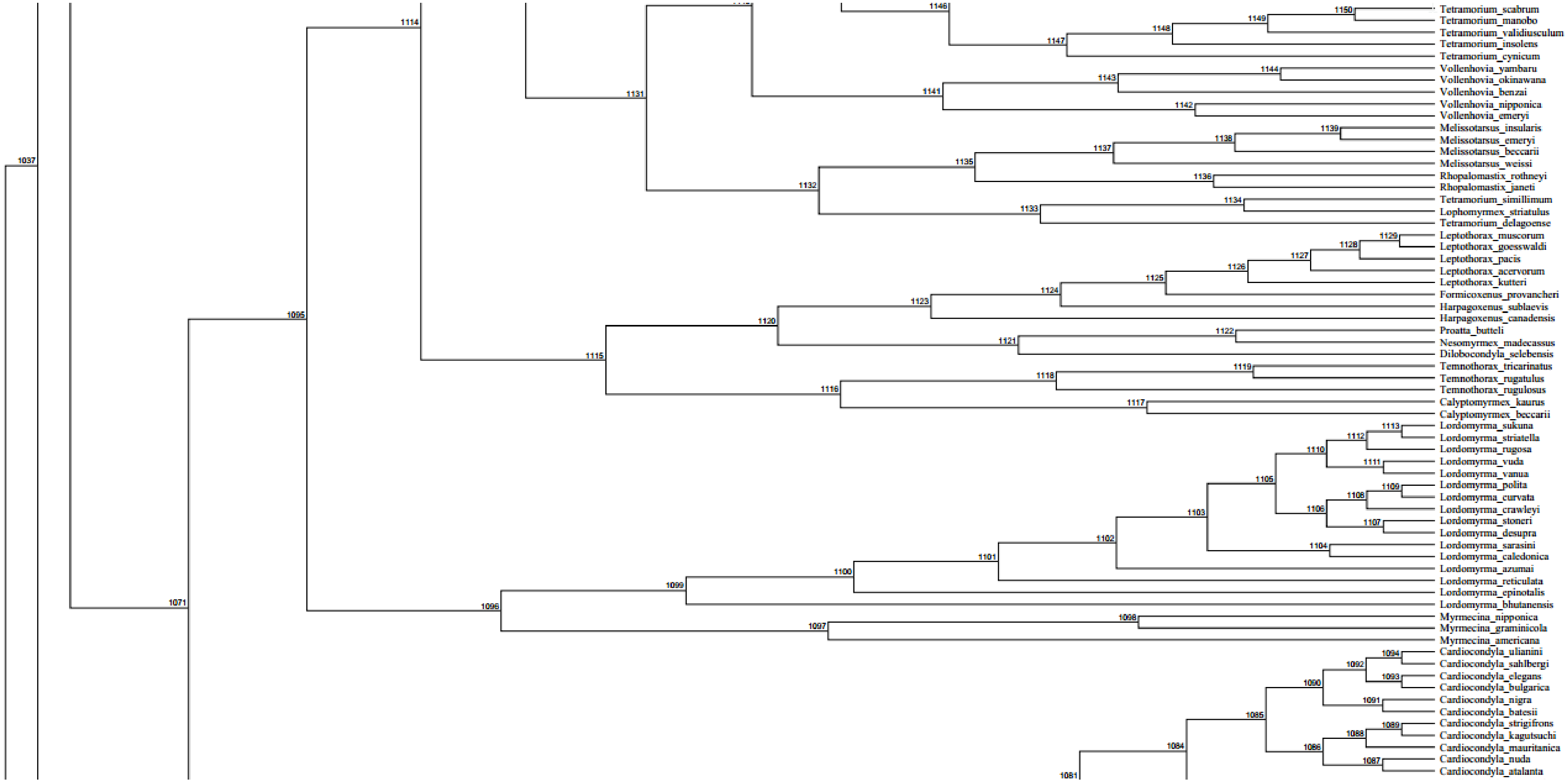
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Leptothorax_goesswaldi
Leptothorax_pacis
Leptothorax_acervorum
Leptothorax_kutteri
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Harpagoxenus_sublaevis
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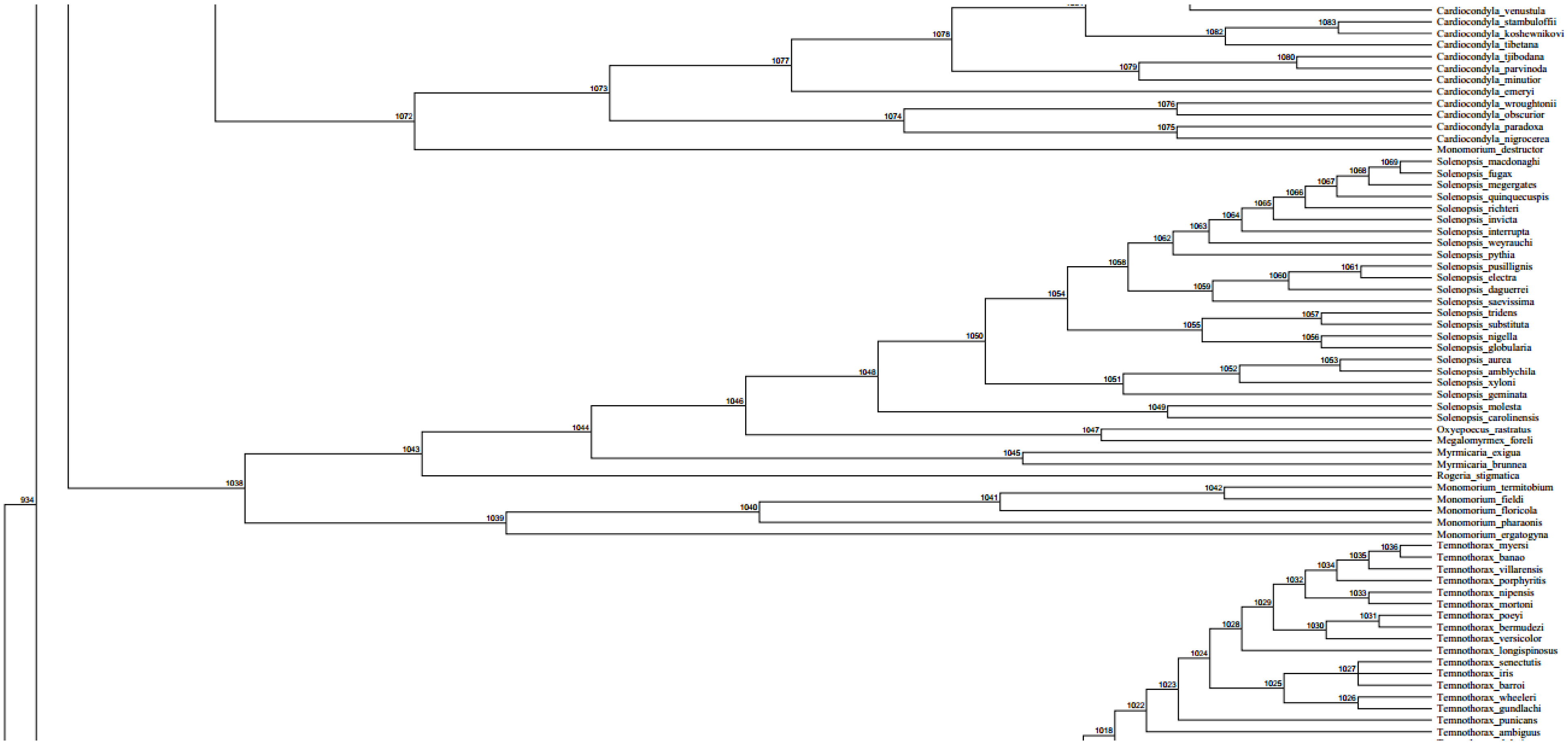
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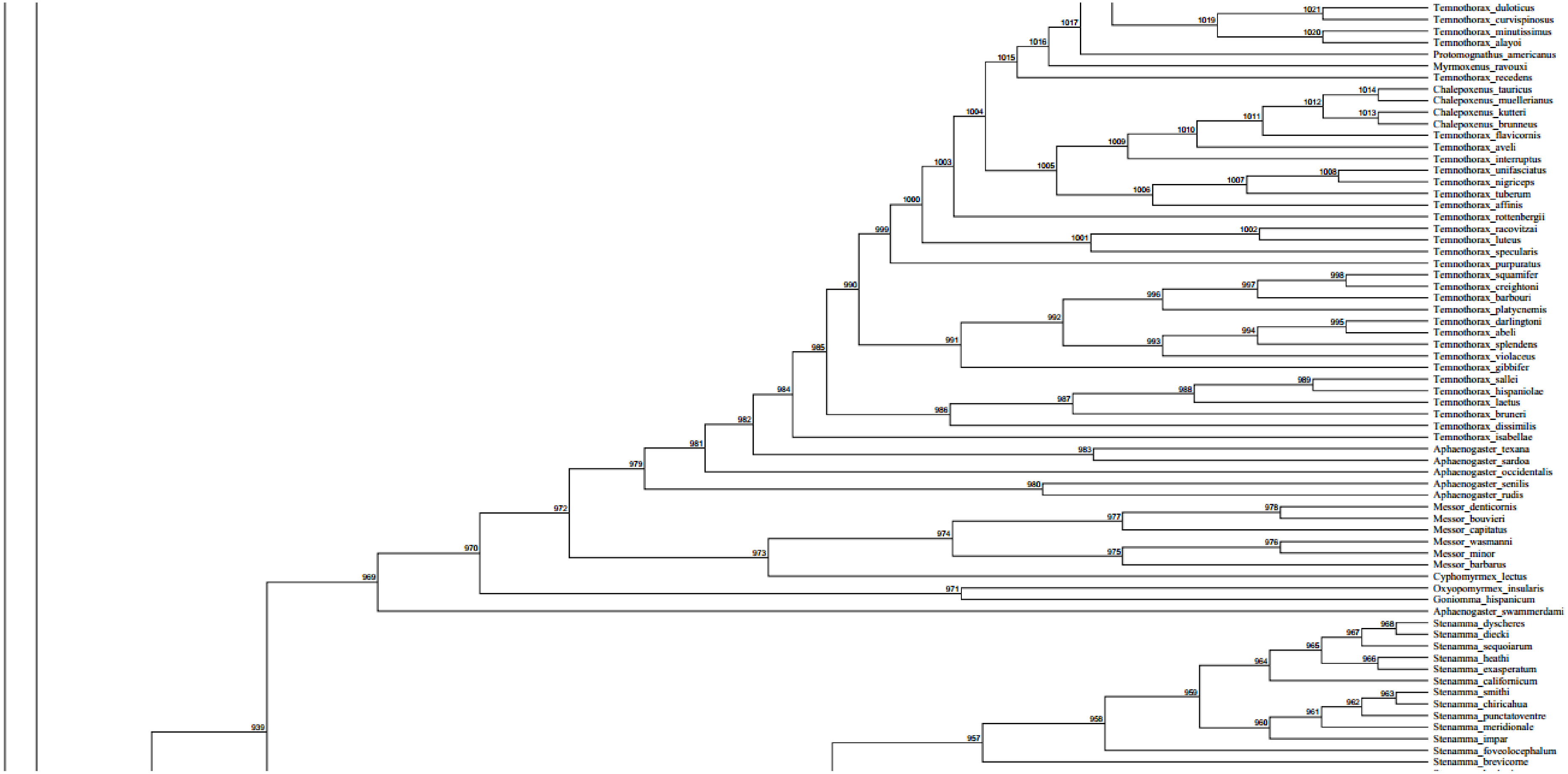
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Temnothorax_recedens
Chalepoxenus_tauricus
Chalepoxenus_muellerianus
Chalepoxenus_kutteri
Chalepoxenus_brunneus
Temnothorax_flavicornis
Temnothorax_aveli
Temnothorax_interruptus
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Temnothorax_nigriceps
Temnothorax_tuberum
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Temnothorax_rottenbergii
Temnothorax_racovitzai
Temnothorax_luteus
Temnothorax_specularis
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Temnothorax_squamifer
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Temnothorax_barbouri
Temnothorax_platycnemis
Temnothorax_darlingtoni
Temnothorax_abeli
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Aphaenogaster_sardoa
Aphaenogaster_occidentalis
Aphaenogaster_senilis
Aphaenogaster_rudis
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Messor_bouvieri
Messor_capitatus
Messor_wasmanni
Messor_minor
Messor_barbarus
Cyphomyrmex_lectus
Oxyopomyrmex_insularis
Goniomma_hispanicum
Aphaenogaster_swammerdami
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Stenamma_smithi
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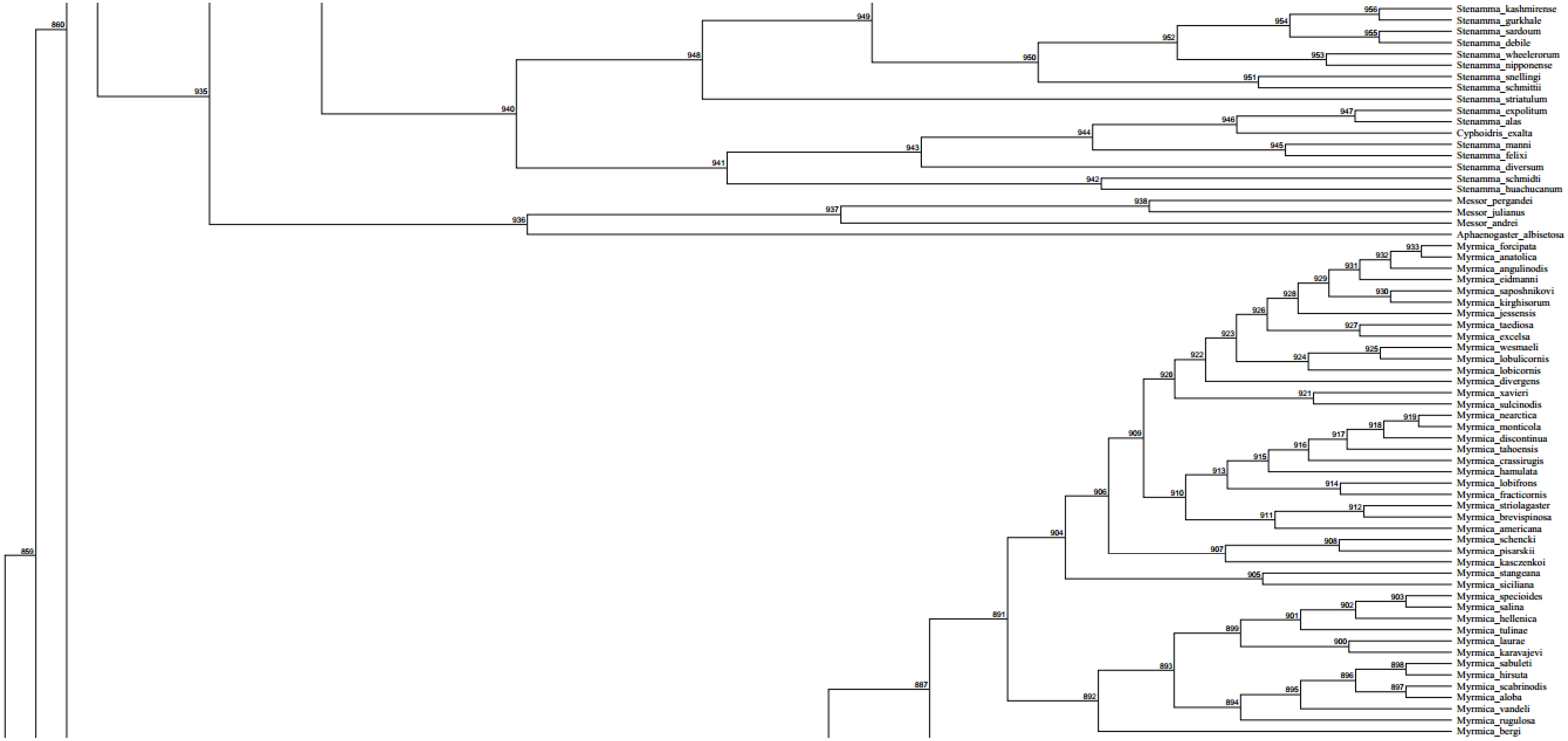
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Stenamma_schmittii
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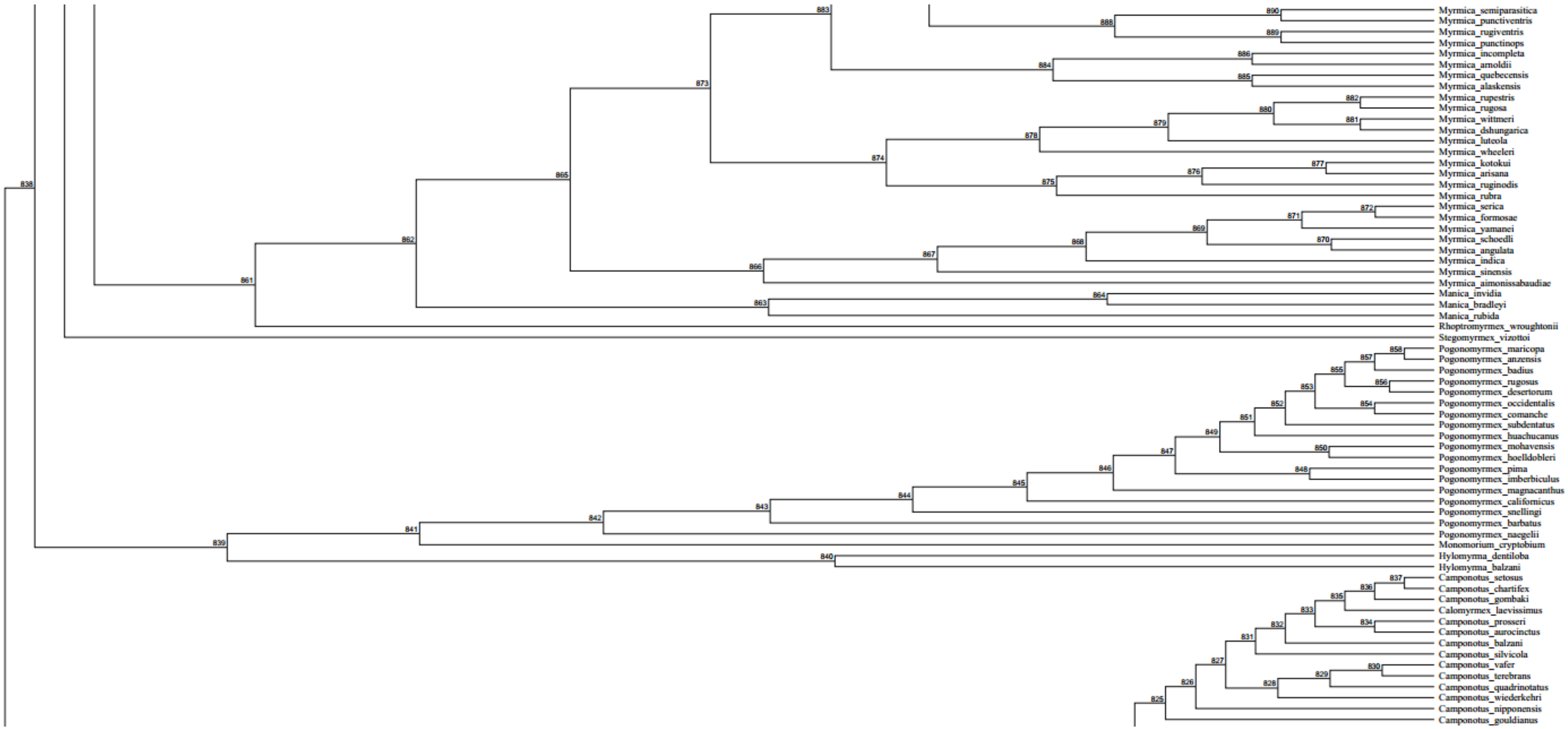
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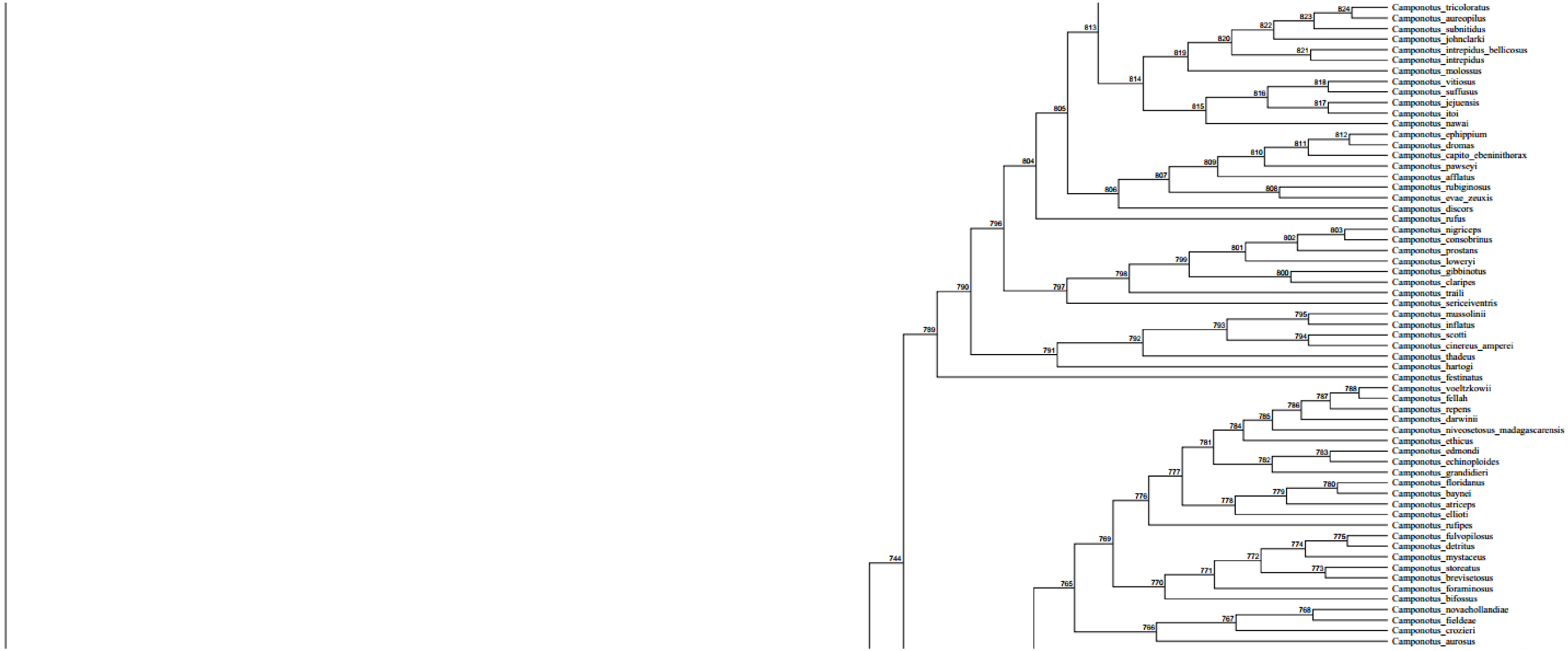
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Camponotus_capito_ebeninithorax
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Camponotus_afflatus
Camponotus_rubiginosus
Camponotus_evae_zeuxis
Camponotus_discors
Camponotus_rufus
Camponotus_nigriceps
Camponotus_consobrinus
Camponotus_prostans
Camponotus_loweryi
Camponotus_gibbinotus
Camponotus_claripes
Camponotus_traili
Camponotus_sericeiventris
Camponotus_mussolinii
Camponotus_inflatus
Camponotus_scotti
Camponotus_cinereus_amperei
Camponotus_thadeus
Camponotus_hartogi
Camponotus_festinatus
Camponotus_voeltzkowii
Camponotus_fellah
Camponotus_repens
Camponotus_darwinii
Camponotus_niveosetosus_madagascarensis
Camponotus_ethicus
Camponotus_edmondi
Camponotus_echinoploides
Camponotus_grandidieri
Camponotus_floridanus
Camponotus_baynei
Camponotus_atriceps
Camponotus_ellioti
Camponotus_rufipes
Camponotus_fulvopilosus
Camponotus_detritus
Camponotus_mystaceus
Camponotus_storeatus
Camponotus_brevisetosus
Camponotus_foraminosus
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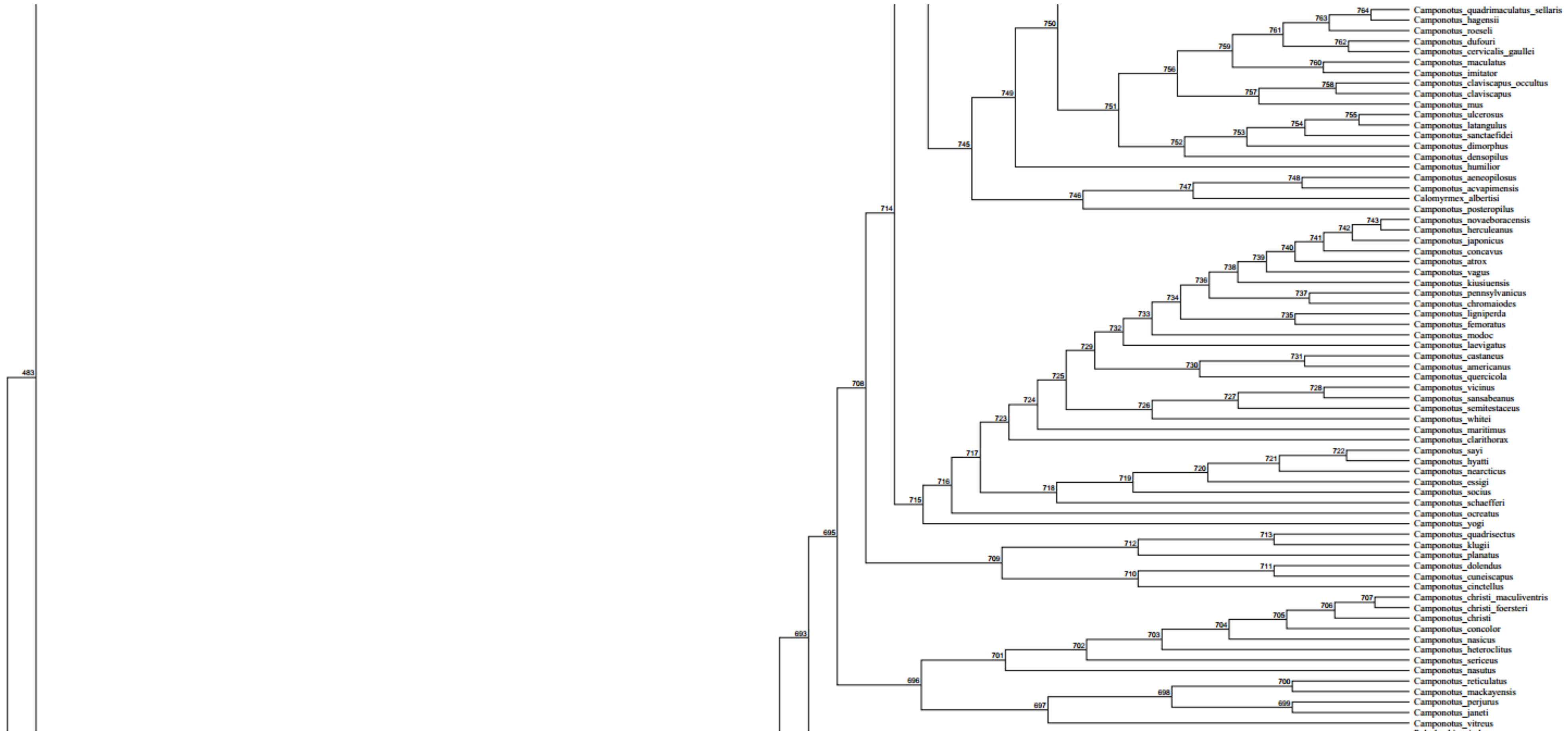
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Camponotus_quadrimaculatus_sellaris
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Camponotus_imitator
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Camponotus_claviscapus
Camponotus_mus
Camponotus_ulcerosus
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Camponotus_sanctaefidei
Camponotus_dimorphus
Camponotus_densopilus
Camponotus_humilior
Camponotus_aeneopilosus
Camponotus_acvapimensis
Calomyrmex_albertisi
Camponotus_posteropilus
Camponotus_novaeboracensis
Camponotus_herculeanus
Camponotus_japonicus
Camponotus_concavus
Camponotus_atrox
Camponotus_vagus
Camponotus_kiusiuensis
Camponotus_pennsylvanicus
Camponotus_chromaiodes
Camponotus_ligniperda
Camponotus_femoratus
Camponotus_modoc
Camponotus_laevigatus
Camponotus_castaneus
Camponotus_americanus
Camponotus_quercicola
Camponotus_vicinus
Camponotus_sansabeanus
Camponotus_semitestaceus
Camponotus_whitei
Camponotus_maritimus
Camponotus_clarithorax
Camponotus_sayi
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Camponotus_nearcticus
Camponotus_essigi
Camponotus_socius
Camponotus_schaefferi
Camponotus_ocreatus
Camponotus_yogi
Camponotus_quadrisectus
Camponotus_klugii
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Camponotus_cuneiscapus
Camponotus_cinctellus
Camponotus_christi_maculiventris
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Camponotus_nasutus
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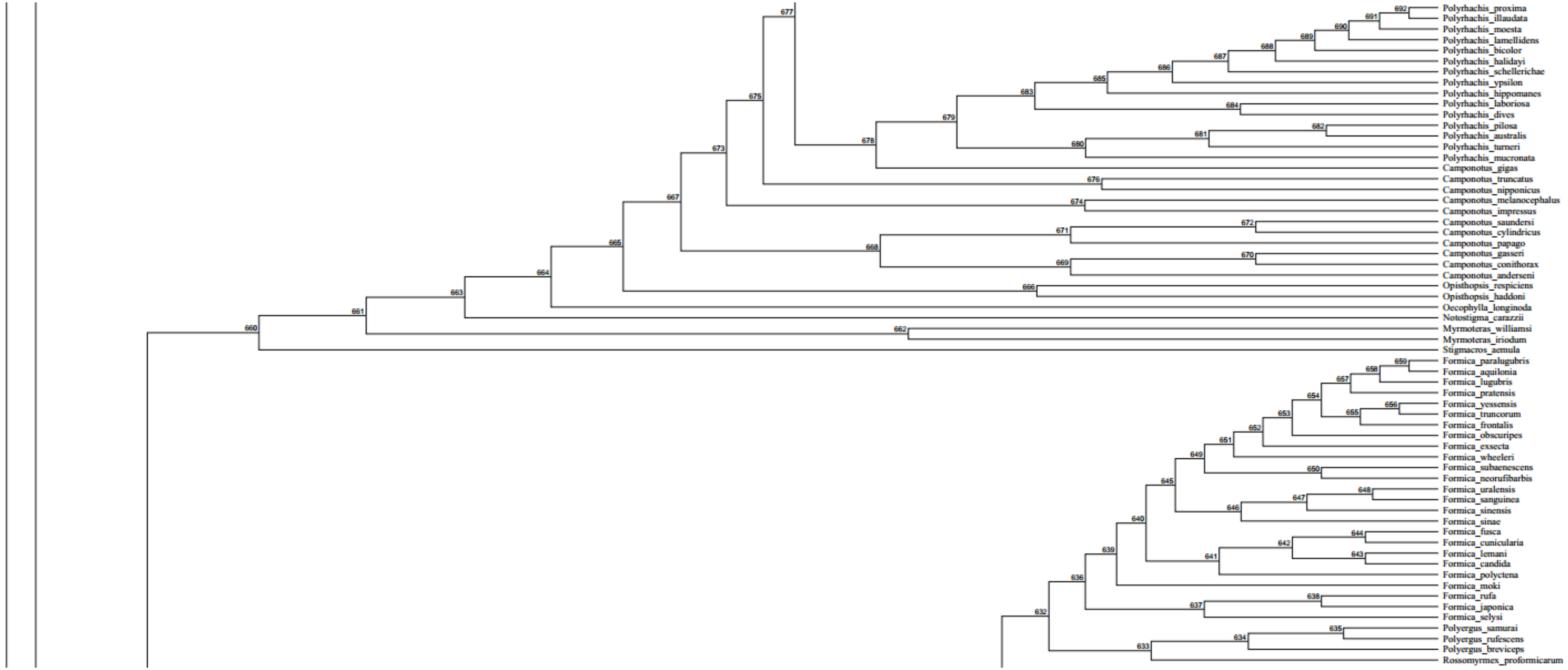
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Polyrhachis_illaudata
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Polyrhachis_bicolor
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Polyrhachis_schellerichae
Polyrhachis_ypsilon
Polyrhachis_hippomanes
Polyrhachis_laboriosa
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Polyrhachis_pilosa
Polyrhachis_australis
Polyrhachis_turneri
Polyrhachis_mucronata
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Camponotus_truncatus
Camponotus_nipponicus
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Camponotus_saundersi
Camponotus_cylindricus
Camponotus_papago
Camponotus_gasseri
Camponotus_conithorax
Camponotus_anderseni
Opisthopsis_respiciens
Opisthopsis_haddoni
Oecophylla_longinoda
Notostigma_carazzii
Myrmoteras_williamsi
Myrmoteras_iriodum
Stigmacros_aemula
Formica_paralugubris
Formica_aquilonia
Formica_lugubris
Formica_pratensis
Formica_yessensis
Formica_truncorum
Formica_frontalis
Formica_obscuripes
Formica_exsecta
Formica_wheeleri
Formica_subaenescens
Formica_neorufibarbis
Formica_uralensis
Formica_sanguinea
Formica_sinensis
Formica_sinae
Formica_fusca
Formica_cunicularia
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Formica_candida
Formica_polyctena
Formica_moki
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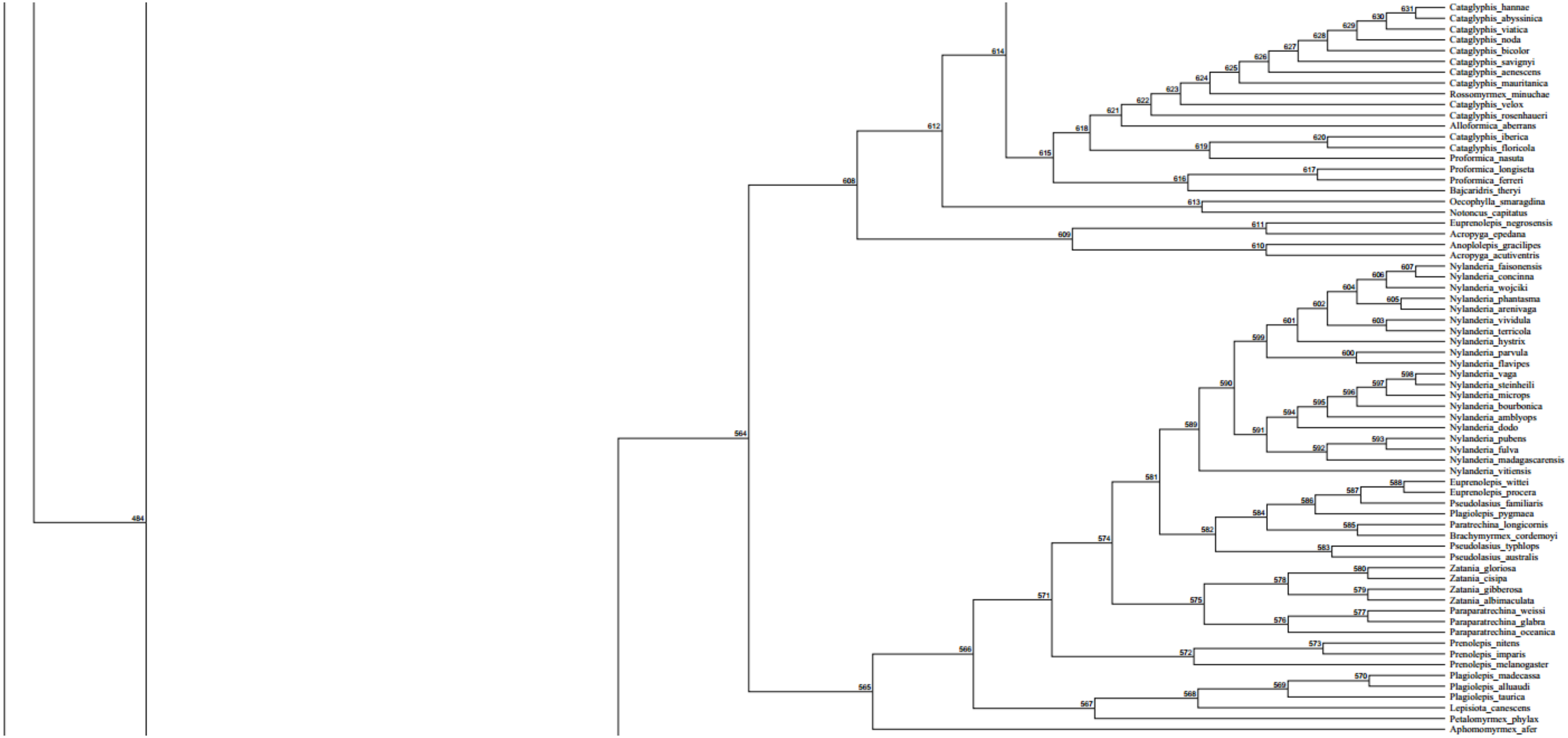
Rossomyrmex_proformicarum

r)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Cataglyphis_mauritanica
Rossomyrmex_minuchae
Cataglyphis_velox
Cataglyphis_rosenhaueri
Alloformica_aberrans
Cataglyphis_iberica
Cataglyphis_floricola
Proformica_nasuta
Proformica_longiseta
Proformica_ferreri
Bajcaridris_theryi
Oecophylla_smaragdina
Notoncus_capitatus
Euprenolepis_negrosensis
Acropyga_epedana
Anoplolepis_gracilipes
Acropyga_acutiventris
Nylanderia_faisonensis
Nylanderia_concinna
Nylanderia_wojciki
Nylanderia_phantasma
Nylanderia_arenivaga
Nylanderia_vividula
Nylanderia_terricola
Nylanderia_hystrix
Nylanderia_parvula
Nylanderia_flavipes
Nylanderia_vaga
Nylanderia_steinheili
Nylanderia_microps
Nylanderia_bourbonica
Nylanderia_amblyops
Nylanderia_dodo
Nylanderia_pubens
Nylanderia_fulva
Nylanderia_madagascarensis
Nylanderia_vitiensis
Euprenolepis_wittei
Euprenolepis_procera
Pseudolasius_familiaris
Plagiolepis_pygmaea
Paratrechina_longicornis
Brachymyrmex_cordemoyi
Pseudolasius_typhlops
Pseudolasius_australis
Zatania_gloriosa
Zatania_cisipa
Zatania_gibberosa
Zatania_albimaculata
Paraparatrechina_weissi
Paraparatrechina_glabra
Paraparatrechina_oceanica
Prenolepis_nitens
Prenolepis_imparis
Prenolepis_melanogaster
Plagiolepis_madecassa
Plagiolepis_alluaudi
Plagiolepis_taurica
Lepisiota_canescens
Petalomyrmex_phylax
Aphomomyrmex_afer
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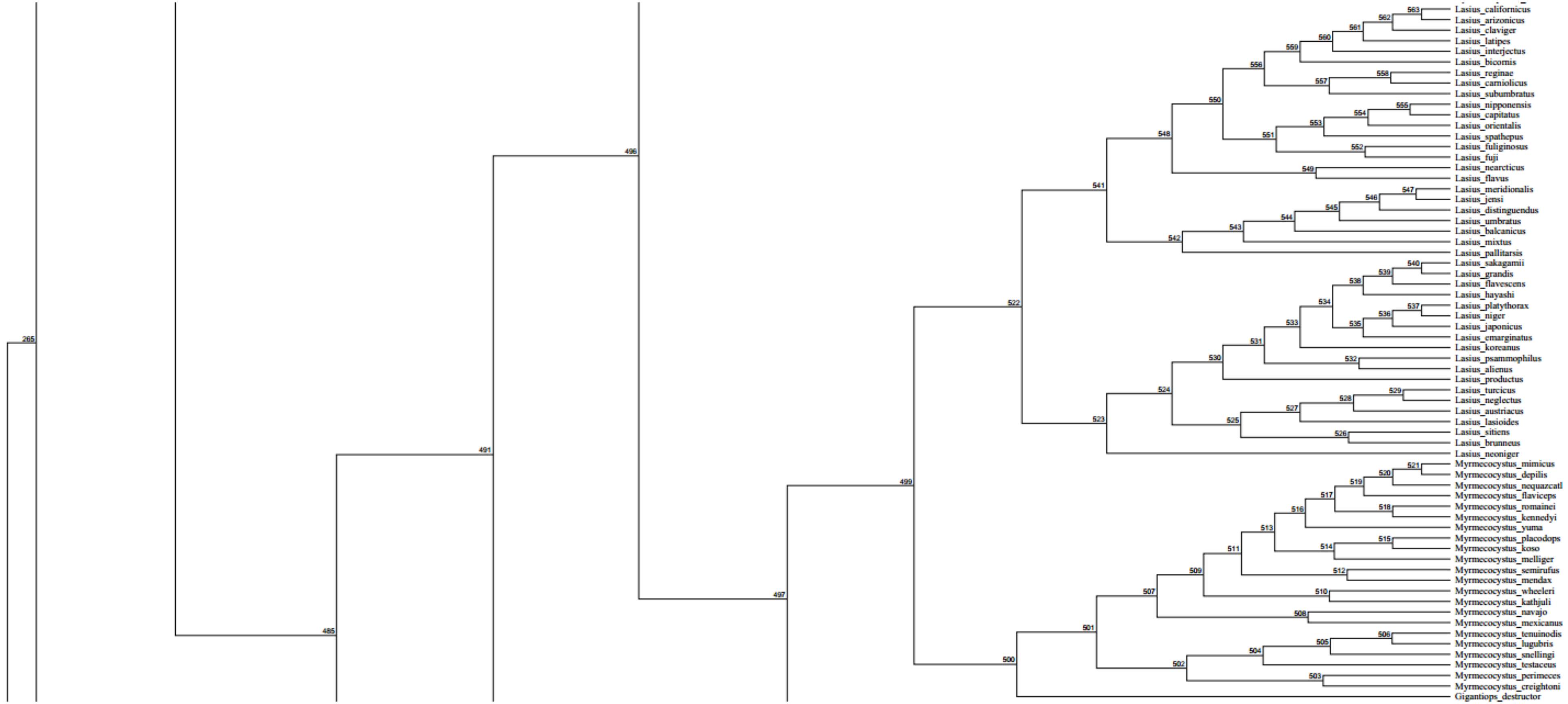
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Lasius_reginae
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Lasius_subumbratus
Lasius_nipponensis
Lasius_capitatus
Lasius_orientalis
Lasius_spathepus
Lasius_fuliginosus
Lasius_fuji
Lasius_nearcticus
Lasius_flavus
Lasius_meridionalis
Lasius_jensi
Lasius_distinguendus
Lasius_umbratus
Lasius_balcanicus
Lasius_mixtus
Lasius_pallitarsis
Lasius_sakagamii
Lasius_grandis
Lasius_flavescens
Lasius_hayashi
Lasius_platythorax
Lasius_niger
Lasius_japonicus
Lasius_emarginatus
Lasius_koreanus
Lasius_psammophilus
Lasius_alienus
Lasius_productus
Lasius_turcicus
Lasius_neglectus
Lasius_austriacus
Lasius_lasioides
Lasius_sitiens
Lasius_brunneus
Lasius_neoniger
Myrmecocystus_mimicus
Myrmecocystus_depilis
Myrmecocystus_nequazcatl
Myrmecocystus_flaviceps
Myrmecocystus_romainei
Myrmecocystus_kennedyi
Myrmecocystus_yuma
Myrmecocystus_placodops
Myrmecocystus_koso
Myrmecocystus_melliger
Myrmecocystus_semirufus
Myrmecocystus_mendax
Myrmecocystus_wheeleri
Myrmecocystus_kathjuli
Myrmecocystus_navajo
Myrmecocystus_mexicanus
Myrmecocystus_tenuinodis
Myrmecocystus_lugubris
Myrmecocystus_snellingi
Myrmecocystus_testaceus
Myrmecocystus_perimeces
Myrmecocystus_creightoni
Gigantiops_destructor
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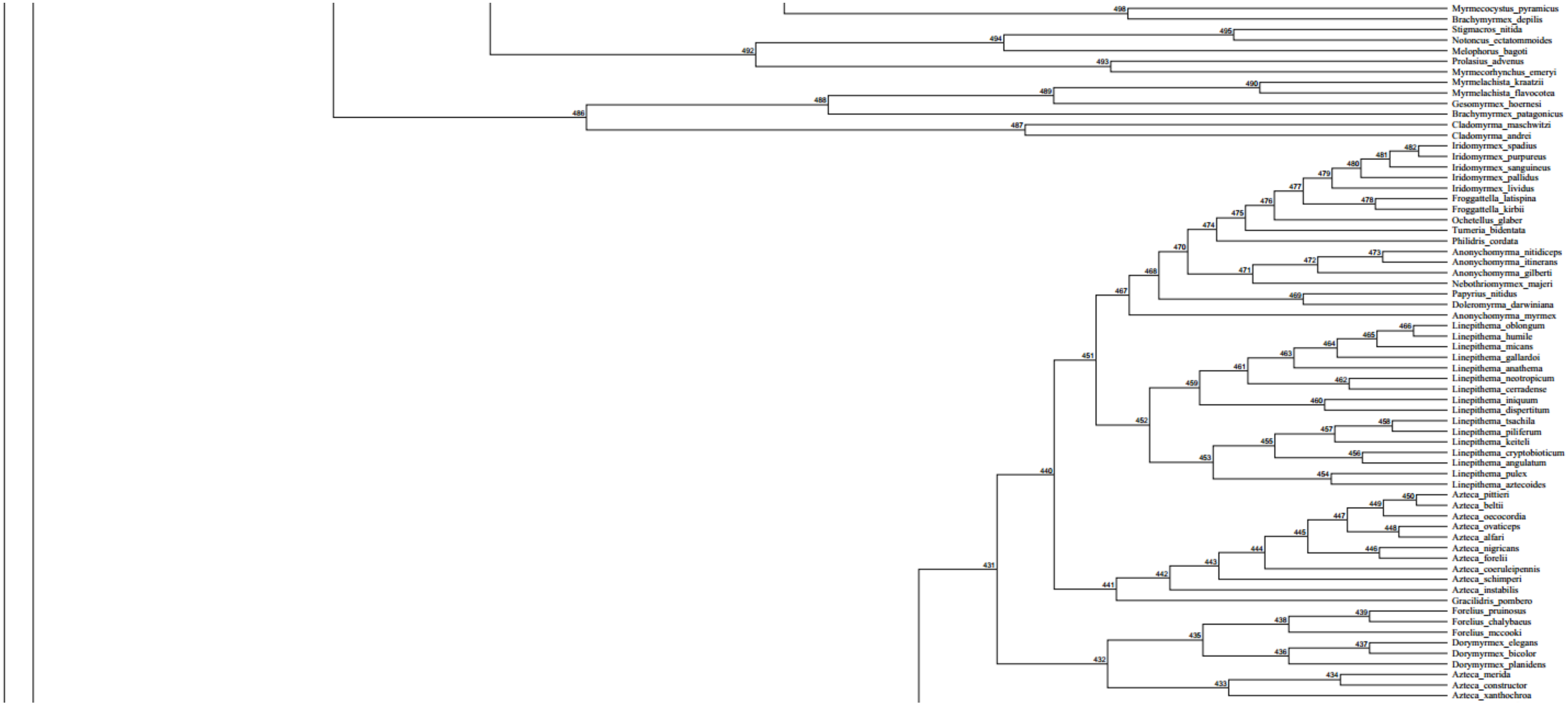
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Prolasius_advenus
Myrmecorhynchus_emeryi
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Myrmelachista_flavocotea
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Gesomyrmex_hoernesi
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Brachymyrmex_patagonicus
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Cladomyrma_maschwitzi
Cladomyrma_andrei
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Iridomyrmex_pallidus
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Iridomyrmex_lividus
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Froggattella_latispina
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Ochetellus_glaber
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Turneria_bidentata
Philidris_cordata
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Anonychomyrma_itinerans
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Nebothriomyrmex_majeri
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Papyrius_nitidus
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Linepithema_oblongum
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Linepithema_humile
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Linepithema_micans
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Linepithema_gallardoi
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Linepithema_neotropicum
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Linepithema_iniquum
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Azteca_oecocordia
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Azteca_ovaticeps
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Azteca_alfari
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Azteca_nigricans
Azteca_forelii
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Azteca_coeruleipennis
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Azteca_schimperi
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Azteca_instabilis
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Forelius_pruinosus
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Forelius_chalybaeus
Forelius_mccooki
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Dorymyrmex_elegans
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Azteca_constructor
Azteca_xanthochroa

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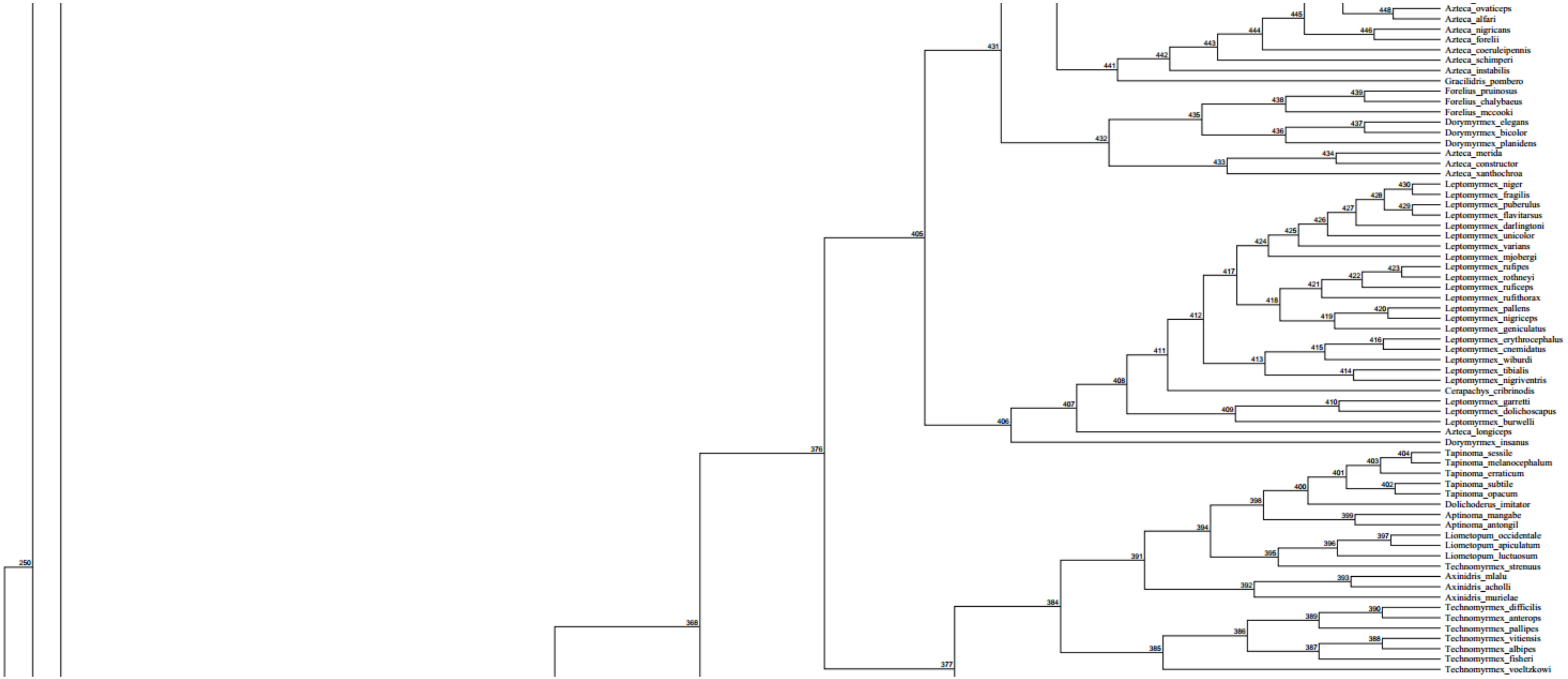
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Dorymyrmex_elegans
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Dorymyrmex_planidens
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Azteca_xanthochroa
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Leptomyrmex_puberulus
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Dorymyrmex_insanus
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Tapinoma_erraticum
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Tapinoma_opacum
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Dolichoderus_imitator
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Aptinoma_mangabe
Aptinoma_antongil
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Liometopum_occidentale
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Liometopum_apiculatum
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Liometopum_luctuosum
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Axinidris_mlalu
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Axinidris_acholli
Axinidris_murielae
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Technomyrmex_difficilis
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Technomyrmex_anterops
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Technomyrmex_pallipes
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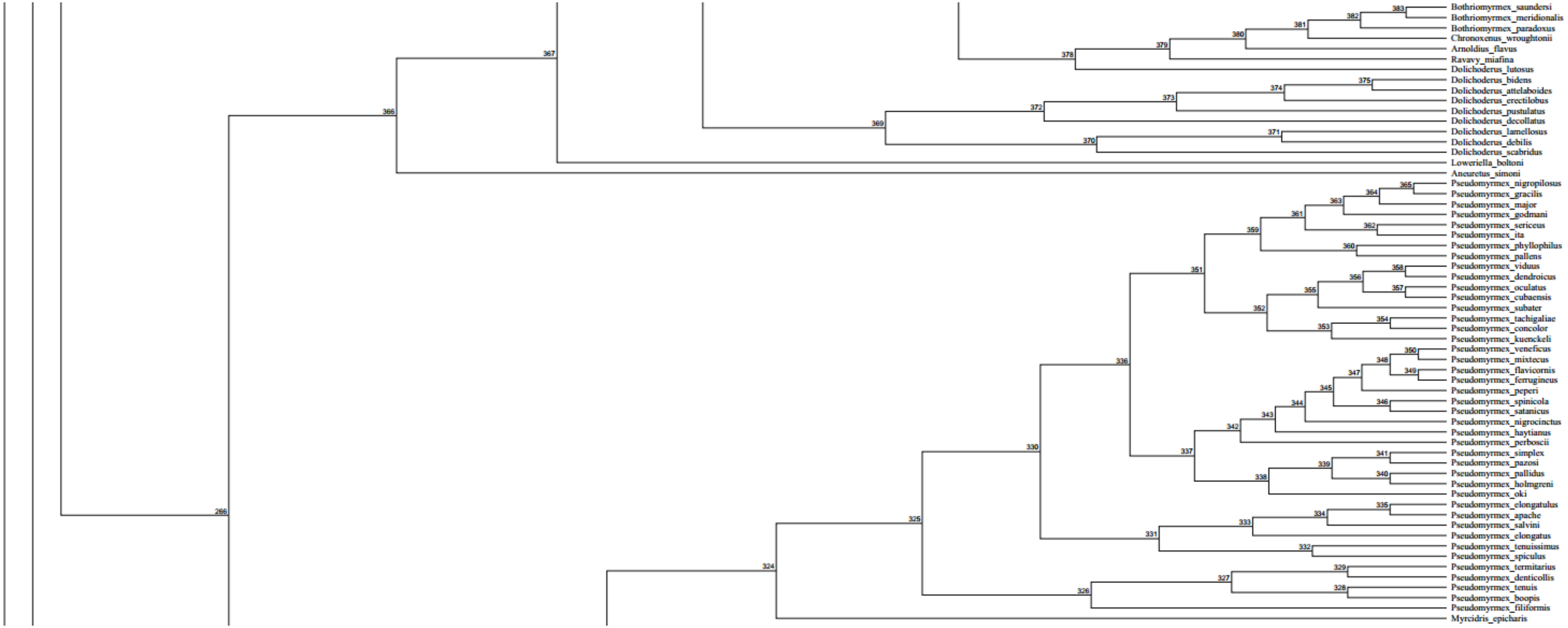
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Bothriomyrmex_meridionalis
Bothriomyrmex_paradoxus
Chronoxenus_wroughtonii
Arnoldius_flavus
Ravavy_miafina
Dolichoderus_lutosus
Dolichoderus_bidens
Dolichoderus_attelaboides
Dolichoderus_erectilobus
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Dolichoderus_debilis
Dolichoderus_scabridus
Loweriella_boltoni
Aneuretus_simoni
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Pseudomyrmex_sericeus
Pseudomyrmex_ita
Pseudomyrmex_phyllophilus
Pseudomyrmex_pallens
Pseudomyrmex_viduus
Pseudomyrmex_dendroicus
Pseudomyrmex_oculatus
Pseudomyrmex_cubaensis
Pseudomyrmex_subater
Pseudomyrmex_tachigaliae
Pseudomyrmex_concolor
Pseudomyrmex_kuenckeli
Pseudomyrmex_veneficus
Pseudomyrmex_mixtecus
Pseudomyrmex_flavicornis
Pseudomyrmex_ferrugineus
Pseudomyrmex_peperi
Pseudomyrmex_spinicola
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Pseudomyrmex_haytianus
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Pseudomyrmex_simplex
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Pseudomyrmex_pallidus
Pseudomyrmex_holmgreni
Pseudomyrmex_oki
Pseudomyrmex_elongatulus
Pseudomyrmex_apache
Pseudomyrmex_salvini
Pseudomyrmex_elongatus
Pseudomyrmex_tenuissimus
Pseudomyrmex_spiculus
Pseudomyrmex_termitarius
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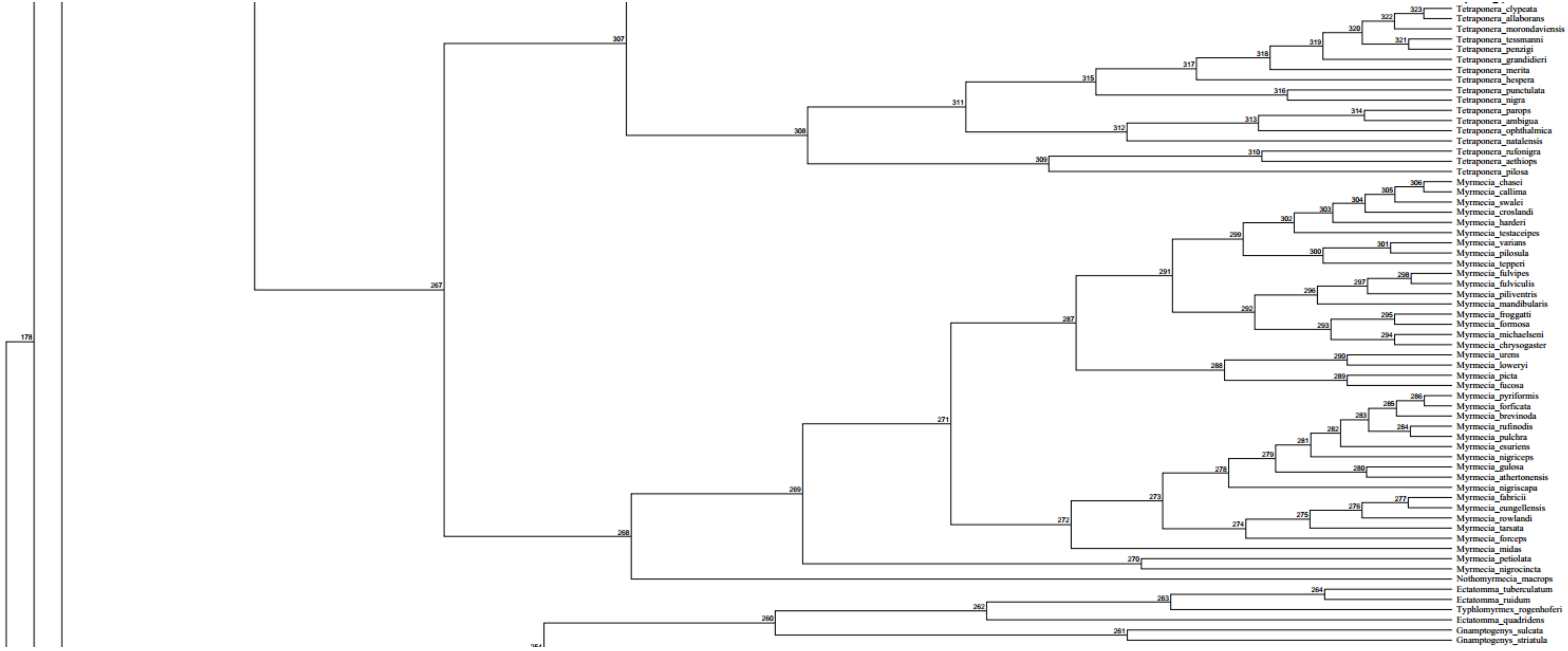
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Tetraponera_parops
Tetraponera_ambigua
Tetraponera_ophthalmica
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Tetraponera_aethiops
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Myrmecia_callima
Myrmecia_swalei
Myrmecia_croslandi
Myrmecia_harderi
Myrmecia_testaceipes
Myrmecia_varians
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Myrmecia_tepperi
Myrmecia_fulvipes
Myrmecia_fulviculis
Myrmecia_piliventris
Myrmecia_mandibularis
Myrmecia_froggatti
Myrmecia_formosa
Myrmecia_michaelseni
Myrmecia_chrysogaster
Myrmecia_urens
Myrmecia_loweryi
Myrmecia_picta
Myrmecia_fucosa
Myrmecia_pyriformis
Myrmecia_forficata
Myrmecia_brevinoda
Myrmecia_rufinodis
Myrmecia_pulchra
Myrmecia_esuriens
Myrmecia_nigriceps
Myrmecia_gulosa
Myrmecia_athertonensis
Myrmecia_nigriscapa
Myrmecia_fabricii
Myrmecia_eungellensis
Myrmecia_rowlandi
Myrmecia_tarsata
Myrmecia_forceps
Myrmecia_midas
Myrmecia_petiolata
Myrmecia_nigrocincta
Nothomyrmecia_macrops
Ectatomma_tuberculatum
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Typhlomyrmex_rogenhoferi
Ectatomma_quadridens
Gnamptogenys_sulcata
Gnamptogenys_striatula

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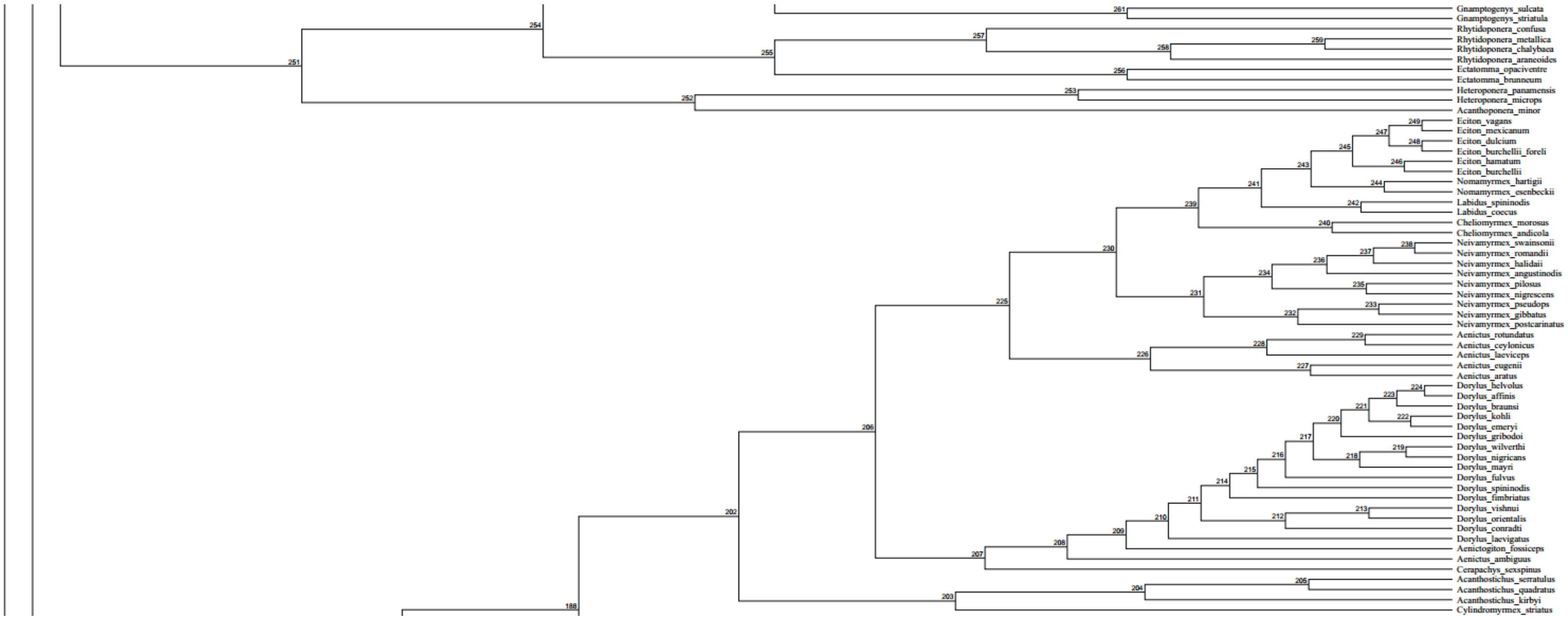
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Eciton_mexicanum
Eciton_dulcium
Eciton_burchellii_foreli
Eciton_hamatum
Eciton_burchellii
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Nomamyrmex_esenbeckii
Labidus_spininodis
Labidus_coecus
Cheliomyrmex_morosus
Cheliomyrmex_andicola
Neivamyrmex_swainsonii
Neivamyrmex_romandii
Neivamyrmex_halidaii
Neivamyrmex_angustinodis
Neivamyrmex_pilosus
Neivamyrmex_nigrescens
Neivamyrmex_pseudops
Neivamyrmex_gibbatus
Neivamyrmex_postcarinatus
Aenictus_rotundatus
Aenictus_ceylonicus
Aenictus_laeviceps
Aenictus_eugenii
Aenictus_aratus
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Dorylus_affinis
Dorylus_braunsi
Dorylus_kohli
Dorylus_emeryi
Dorylus_gribodoi
Dorylus_wilverthi
Dorylus_nigricans
Dorylus_mayri
Dorylus_fulvus
Dorylus_spininodis
Dorylus_fimbriatus
Dorylus_vishnui
Dorylus_orientalis
Dorylus_conradti
Dorylus_laevigatus
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Aenictus_ambiguus
Cerapachys_sexspinus
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Cylindromyrmex_striatus
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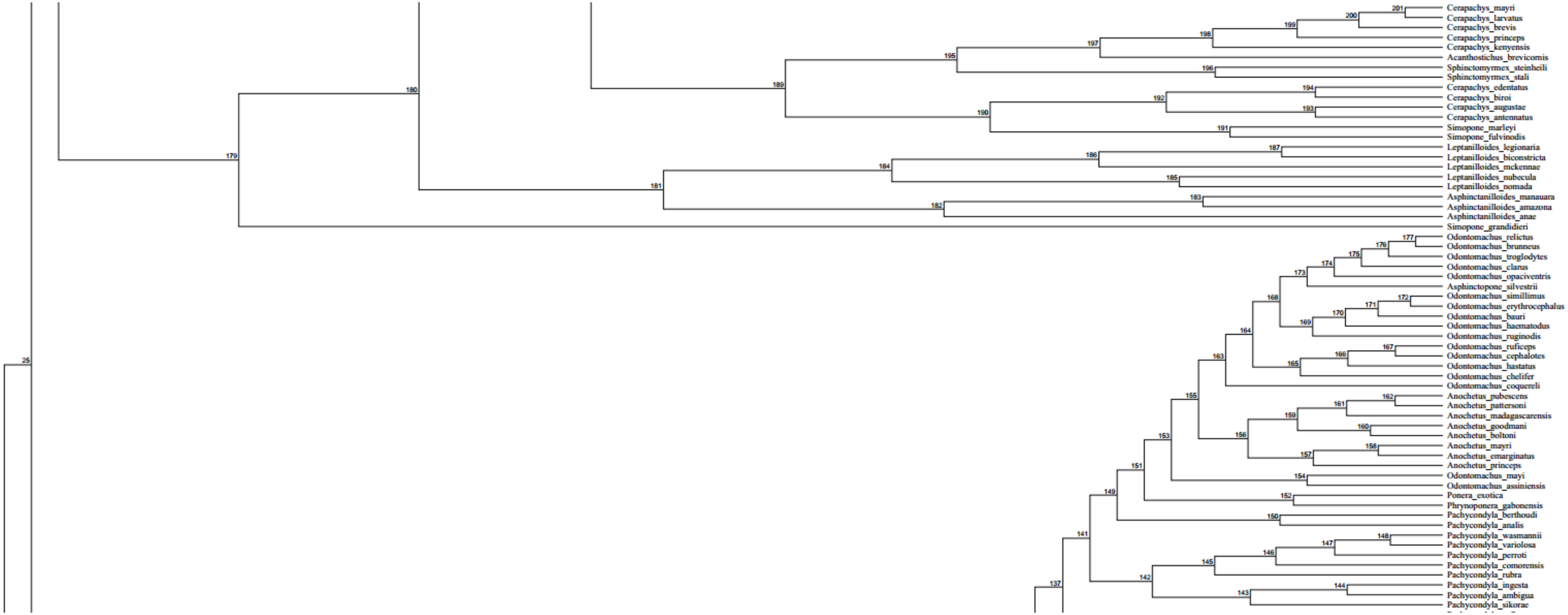
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Odontomachus_troglodytes
Odontomachus_clarus
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Asphinctopone_silvestrii
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Odontomachus_erythrocephalus
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Odontomachus_ruginodis
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Odontomachus_cephalotes
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Odontomachus_chelifer
Odontomachus_coquereli
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Anochetus_pattersoni
Anochetus_madagascarensis
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Anochetus_boltoni
Anochetus_mayri
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Odontomachus_assiniensis
Ponera_exotica
Phrynoponera_gabonensis
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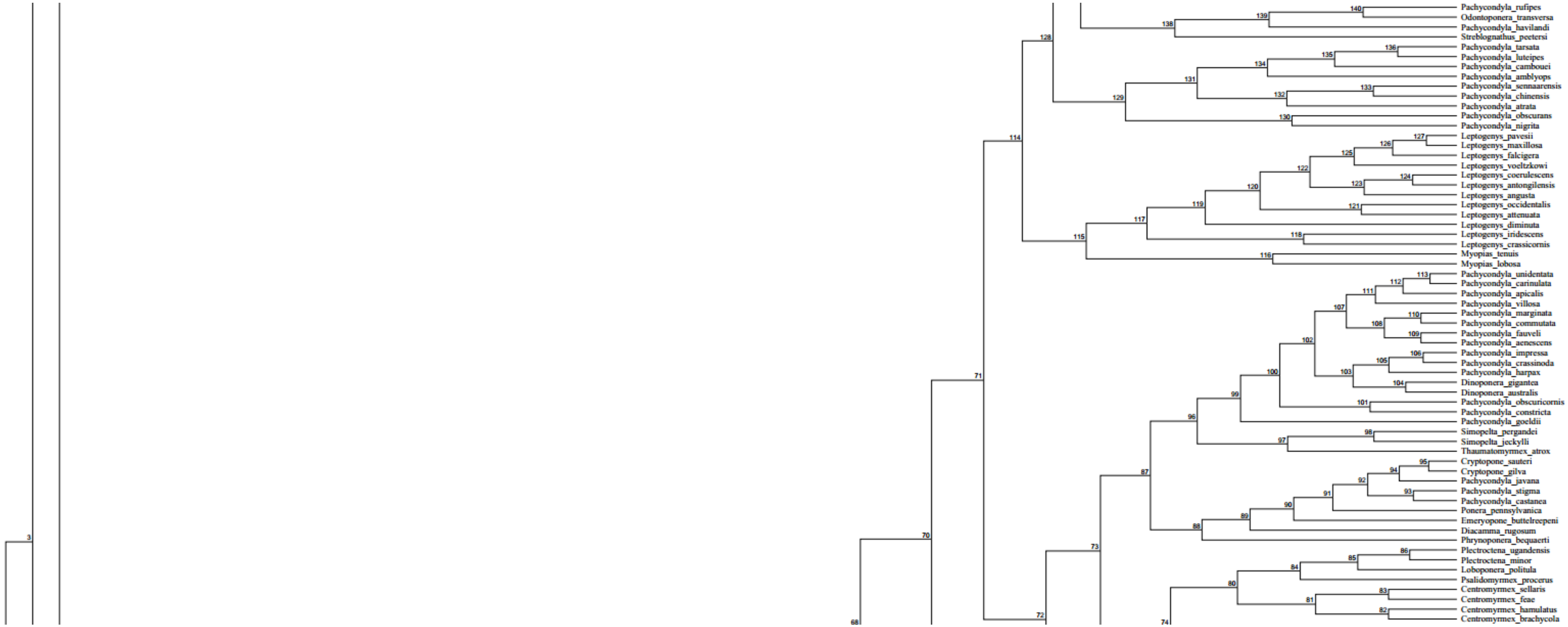
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Pachycondyla_rufipes
Odontoponera_transversa
Pachycondyla_havilandi
Streblognathus_peetersi
Pachycondyla_tarsata
Pachycondyla_luteipes
Pachycondyla_cambouei
Pachycondyla_amblyops
Pachycondyla_sennaarensis
Pachycondyla_chinensis
Pachycondyla_atrata
Pachycondyla_obscurans
Pachycondyla_nigrita
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Leptogenys_maxillosa
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Leptogenys_coerulescens
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Pachycondyla_fauveli
Pachycondyla_aenescens
Pachycondyla_impressa
Pachycondyla_crassinoda
Pachycondyla_harpax
Dinoponera_gigantea
Dinoponera_australis
Pachycondyla_obscuricornis
Pachycondyla_constricta
Pachycondyla_goeldii
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Simopelta_jeckylli
Thaumatomyrmex_atrox
Cryptopone_sauteri
Cryptopone_gilva
Pachycondyla_javana
Pachycondyla_stigma
Pachycondyla_castanea
Ponera_pennsylvanica
Emeryopone_buttelreepeni
Diacamma_rugosum
Phrynoponera_bequaerti
Plectroctena_ugandensis
Plectroctena_minor
Loboponera_politula
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Centromyrmex_sellaris
Centromyrmex_feae
Centromyrmex_hamulatus
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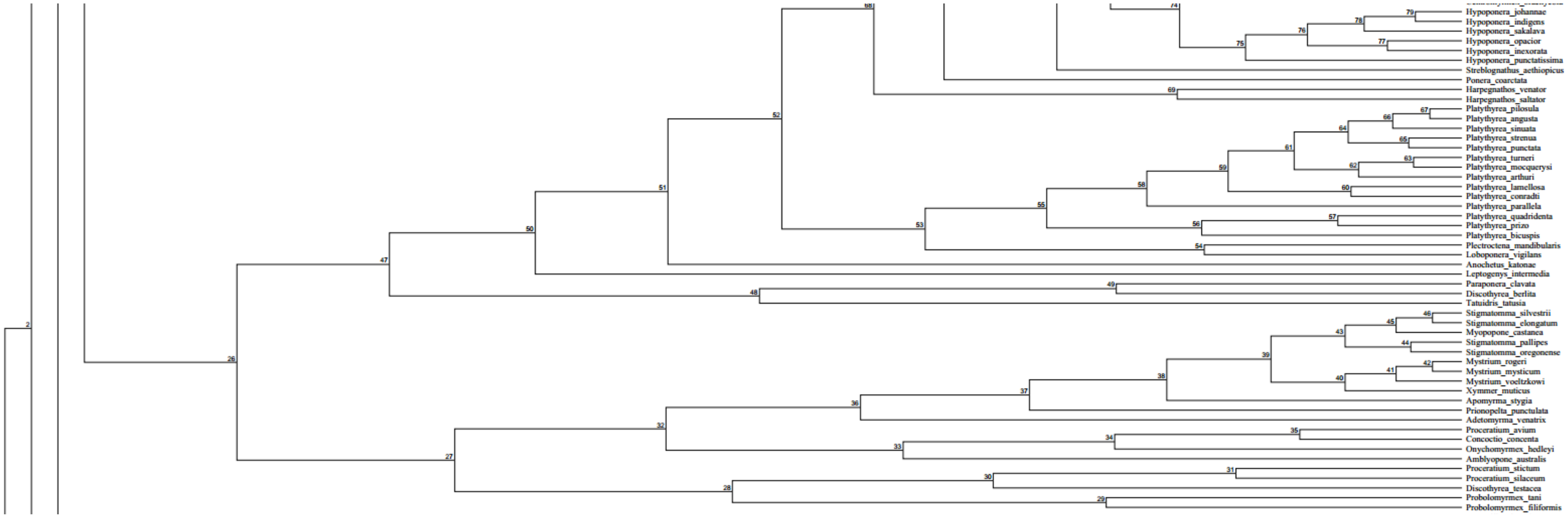
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Hypoponera_punctatissima
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Ponera_coarctata
Harpegnathos_venator
Harpegnathos_saltator
Platythyrea_pilosula
Platythyrea_angusta
Platythyrea_sinuata
Platythyrea_strenua
Platythyrea_punctata
Platythyrea_turneri
Platythyrea_mocquerysi
Platythyrea_arthuri
Platythyrea_lamellosa
Platythyrea_conradti
Platythyrea_parallela
Platythyrea_quadridenta
Platythyrea_prizo
Platythyrea_bicuspis
Plectroctena_mandibularis
Loboponera_vigilans
Anochetus_katonae
Leptogenys_intermedia
Paraponera_clavata
Discothyrea_berlita
Tatuidris_tatusia
Stigmatomma_silvestrii
Stigmatomma_elongatum
Myopopone_castanea
Stigmatomma_pallipes
Stigmatomma_oregonense
Mystrium_rogeri
Mystrium_mysticum
Mystrium_voeltzkowi
Xymmer_muticus
Apomyrma_stygia
Prionopelta_punctulata
Adetomyrma_venatrix
Proceratium_avium
Concoctio_concenta
Onychomyrmex_hedleyi
Amblyopone_australis
Proceratium_stictum
Proceratium_silaceum
Discothyrea_testacea
Probolomyrmex_tani
Probolomyrmex_filiformis
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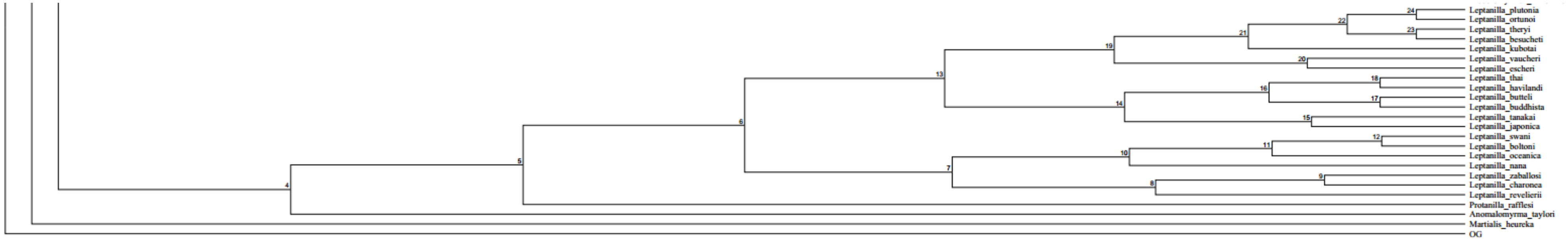

Figure A1.1 A species-level supertree of 1656 species as described in chapter 2 in 28 parts. Node numbers correspond to those in table A2.3. Branch lengths are arbitray.

Table A1.4 rQS scores for the complete genus-level supertree of the ants. Node refers to the numbered nodes in figure A2.2. The rQS algorithm prunes the supertree to match a source tree, and measures the degree of agreement between the two trees. This is repeated for each node and each source tree to generate a mean rQS score for each node. Positive rQS scores indicate support for a node, showing that more source trees agreed on the placement of that node than disagreed.

Node	rQS	Node	rQS	Node	rQS	Node	rQS
1	1	87	-0.12	173	0	259	0
2	1	88	0.06	174	0	260	0.068
3	0.992	89	0.06	175	0	261	-0.038
4	0.925	90	0.09	176	0.008	262	0.015
5	0.925	91	0.173	177	0.023	263	0.008
6	0.767	92	0.158	178	0.038	264	0.008
7	0.737	93	0.15	179	0.128	265	0.008
8	0.624	94	0.12	180	0.008	266	0.008
9	0.586	95	0.165	181	0.008	267	0.008
10	0.639	96	0.068	182	0.015	268	-0.03
11	-0.241	97	0.068	183	0.083	269	0.023
12	-0.323	98	-0.188	184	0.098	270	0
13	-0.083	99	0.023	185	-0.008	271	-0.008
14	-0.053	100	0.12	186	-0.015	272	0
15	-0.053	101	-0.045	187	-0.06	273	0.008
16	-0.053	102	-0.308	188	-0.06	274	0
17	-0.023	103	-0.308	189	-0.045	275	0.008
18	-0.03	104	-0.008	190	0.008	276	0.045
19	0.045	105	0.015	191	-0.015	277	0.068
20	0.038	106	0.023	192	0.008	278	0.045
21	0.03	107	0.023	193	-0.023	279	0.023
22	-0.045	108	0.038	194	0.008	280	0.008
23	0.015	109	0.038	195	0.075	281	0.023
24	0.023	110	0	196	0.023	282	0.075
25	0.015	111	0.03	197	0.008	283	0.075
26	0.008	112	-0.045	198	0.023	284	-0.075
27	0.015	113	-0.06	199	0.023	285	-0.045
28	0.038	114	-0.391	200	0.008	286	-0.045
29	0	115	-0.376	201	0.06	287	-0.075
30	-0.015	116	0.068	202	0.03	288	-0.06
31	-0.278	117	-0.308	203	0.075	289	0.015
32	-0.271	118	-0.316	204	0.06	290	0.075
33	-0.271	119	-0.316	205	0.015	291	0.06
34	-0.331	120	-0.278	206	-0.068	292	0.09
35	-0.331	121	0.008	207	0.09	293	0.09
36	-0.331	122	-0.293	208	0.143	294	0.083
37	-0.338	123	-0.293	209	0.135	295	0.038
38	-0.353	124	-0.278	210	0.135	296	-0.015
39	-0.053	125	-0.248	211	0.135	297	0.023
40	-0.06	126	-0.09	212	0.135	298	0.008
41	-0.068	127	0.023	213	0	299	-0.023

42	-0.03	128	0.023	214	-0.008	300	0.008
43	0	129	0.211	215	-0.09	301	-0.008
44	0.008	130	0.015	216	-0.03	302	0.015
45	-0.045	131	0.038	217	0.015	303	-0.068
46	-0.038	132	0.015	218	-0.075	304	-0.03
47	0	133	0	219	-0.045	305	-0.023
48	-0.015	134	0.015	220	-0.045	306	-0.008
49	0.008	135	-0.286	221	-0.045	307	0.008
50	-0.045	136	-0.301	222	0.015	308	-0.023
51	-0.038	137	-0.233	223	0.038	309	-0.045
52	-0.038	138	0.008	224	0.038	310	0.015
53	-0.053	139	-0.053	225	-0.008	311	0.015
54	-0.068	140	-0.068	226	0.015	312	0
55	-0.03	141	0	227	-0.06	313	0.045
56	-0.008	142	-0.053	228	-0.023	314	0.03
57	0	143	0.015	229	-0.053	315	0.015
58	0	144	0.226	230	0.023	316	0.008
59	0	145	0.218	231	0	317	-0.06
60	0.023	146	0.218	232	-0.045	318	0
61	0.023	147	0.218	233	0.015	319	0.03
62	0.038	148	0.218	234	0	320	0.023
63	0.023	149	0.218	235	0.06	321	-0.06
64	0.03	150	0.195	236	0.06	322	-0.008
65	0.015	151	0.195	237	0.015	323	-0.038
66	-0.008	152	0.195	238	0.128	324	-0.038
67	0.015	153	0.195	239	0.143	325	-0.038
68	0.045	154	0.195	240	0.06	326	-0.015
69	0.03	155	0.195	241	0.098	327	0.008
70	0.03	156	0.195	242	0.105	328	0.015
71	0.015	157	0.195	243	0.008	329	0.015
72	0.008	158	0.195	244	-0.038	330	-0.015
73	0	159	0.18	245	-0.023	331	-0.023
74	-0.008	160	0.008	246	0.008	332	0.008
75	-0.03	161	0.023	247	0	333	-0.023
76	-0.03	162	-0.008	248	-0.008	334	0.045
77	0	163	0.045	249	-0.023	335	0.045
78	-0.015	164	0.06	250	0.038	336	0.015
79	-0.023	165	0.12	251	0.113	337	0.045
80	0.045	166	0.09	252	0.03	338	0.045
81	-0.008	167	0.045	253	-0.015	339	0.03
82	-0.023	168	0.045	254	0.008	340	0.045
83	0.045	169	0.008	255	-0.06	341	0.023
84	-0.045	170	-0.008	256	-0.008	342	0.03
85	-0.128	171	0	257	0	343	0.038
86	-0.135	172	0.015	258	0.023	344	0.038

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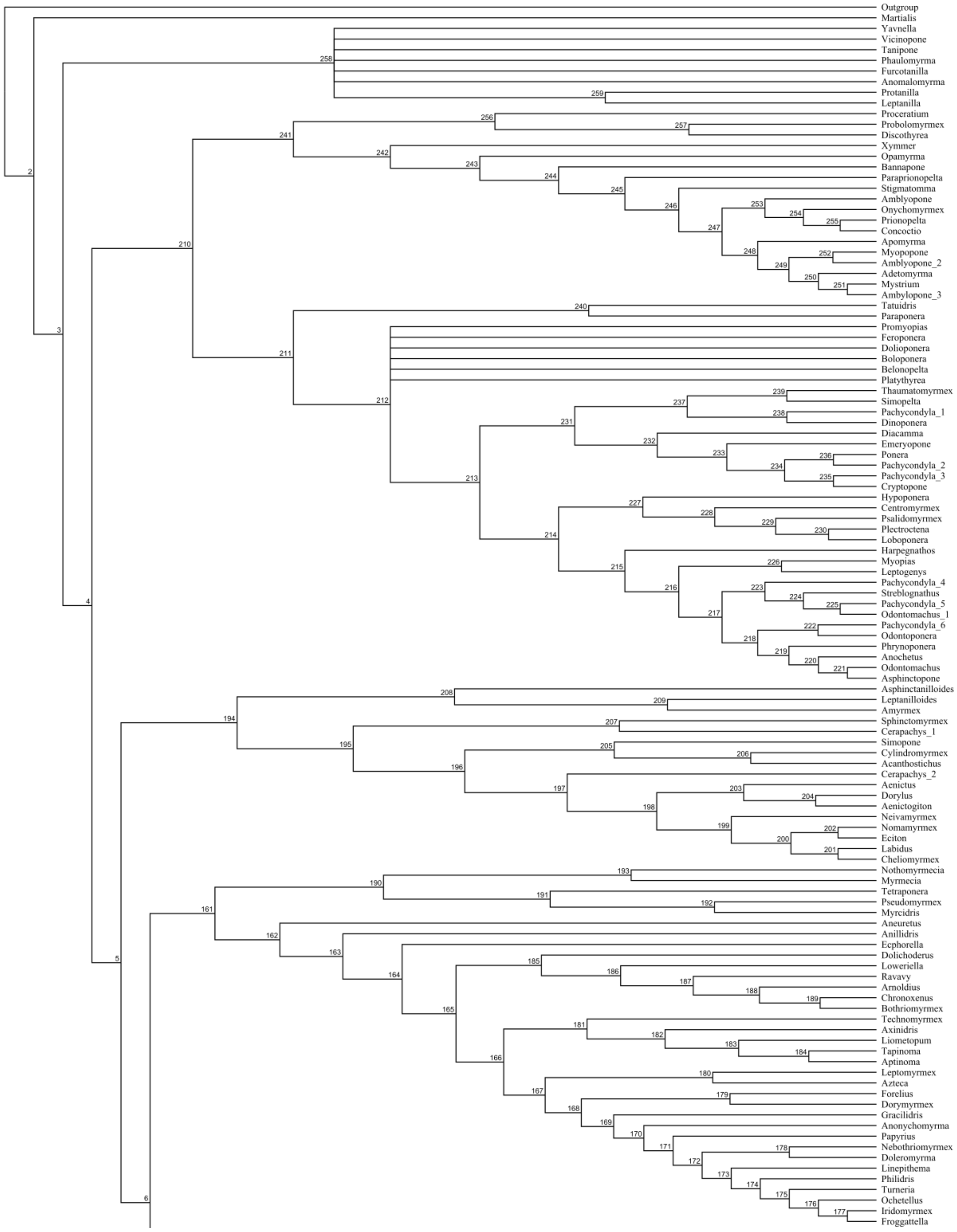
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Proceratium
Probolomyrmex
Discothyrea
Xymmer
Opamyrma
Bannapone
Paraprionopelta
Stigmatomma
Amblyopone
Onychomyrmex
Prionopelta
Concoctio
Apomyrma
Myopopone
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Adetomyrma
Mystrium
Amblylopone_3
Tatuidris
Paraponera
Promyopias
Feroponera
Dolioponera
Boloponera
Belonopelta
Platythyrea
Thaumatomyrmex
Simopelta
Pachycondyla_1
Dinoponera
Diacamma
Emeryopone
Ponera
Pachycondyla_2
Pachycondyla_3
Cryptopone
Hypoponera
Centromyrmex
Psalidomyrmex
Plectroctena
Loboponera
Harpegnathos
Myopias
Leptogenys
Pachycondyla_4
Streblognathus
Pachycondyla_5
Odontomachus_1
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Phrynoponera
Anochetus
Odontomachus
Asphinctopone
Asphinctanilloides
Leptanilloides
Amyrmex
Sphinctomyrmex
Cerapachys_1
Simopone
Cylindromyrmex
Acanthostichus
Cerapachys_2
Aenictus
Dorylus
Aenictogiton
Neivamyrmex
Nomamyrmex
Eciton
Labidus
Cheliomyrmex
Nothomyrmecia
Myrmecia
Tetraponera
Pseudomyrmex
Myrcidris
Aneuretus
Anillidris
Ecphorella
Dolichoderus
Loweriella
Ravavy
Arnoldius
Chronoxenus
Bothriomyrmex
Technomyrmex
Axinidris
Liometopum
Tapinoma
Aptinoma
Leptomyrmex
Azteca
Forelius
Dorymyrmex
Gracilidris
Anonychomyrma
Papyrius
Nebothriomyrmex
Doleromyrma
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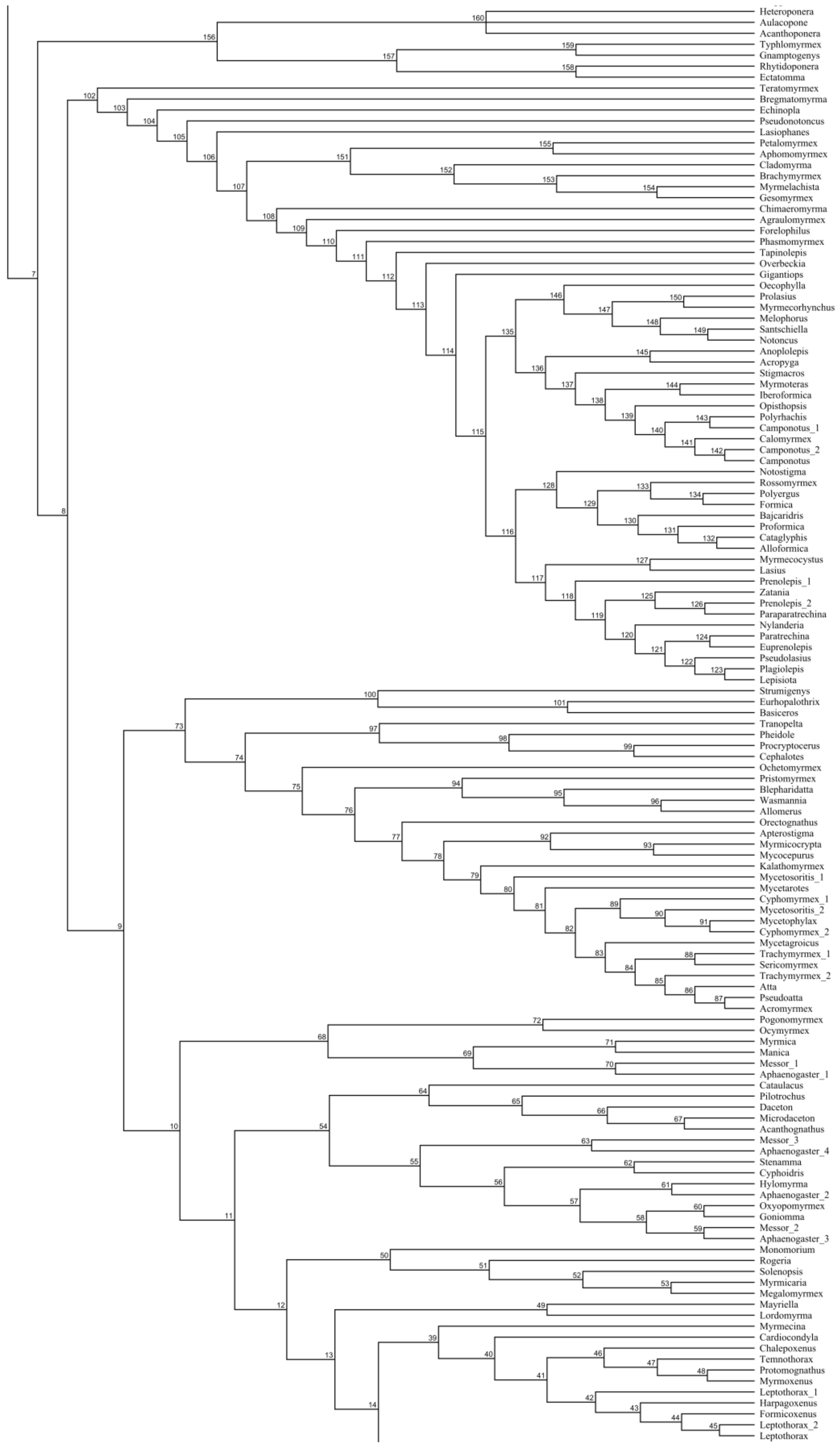
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Echinopla
Pseudonotoncus
Lasiophanes
Petalomyrmex
Aphomomyrmex
Cladomyrma
Brachymyrmex
Myrmelachista
Gesomyrmex
Chimaeromyrma
Agraulomyrmex
Forelophilus
Phasmomyrmex
Tapinolepis
Overbeckia
Gigantiops
Oecophylla
Prolasius
Myrmecorhynchus
Melophorus
Santschiella
Notoncus
Anoplolepis
Acropyga
Stigmacros
Myrmoteras
Iberoformica
Opisthopsis
Polyrhachis
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Camponotus_2
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Rossomyrmex
Polyergus
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Bajcaridris
Proformica
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Pristomyrmex
Blepharidatta
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Apterostigma
Myrmicocrypta
Mycocepurus
Kalathomyrmex
Mycetosoritis_1
Mycetarotes
Cyphomyrmex_1
Mycetosoritis_2
Mycetophylax
Cyphomyrmex_2
Mycetagroicus
Trachymyrmex_1
Sericomyrmex
Trachymyrmex_2
Atta
Pseudoatta
Acromyrmex
Pogonomyrmex
Ocymyrmex
Myrmica
Manica
Messor_1
Aphaenogaster_1
Cataulacus
Pilotrochus
Daceton
Microdaceton
Acanthognathus
Messor_3
Aphaenogaster_4
Stenamma
Cyphoidris
Hylomyrma
Aphaenogaster_2
Oxyopomyrmex
Goniomma
Messor_2
Aphaenogaster_3
Monomorium
Rogeria
Solenopsis
Myrmicaria
Megalomyrmex
Mayriella
Lordomyrma
Myrmecina
Cardiocondyla
Chalepoxenus
Temnothorax
Protomognathus
Myrmoxenus
Leptothorax_1
Harpagoxenus
Formicoxenus
Leptothorax_2
Leptothorax

c)

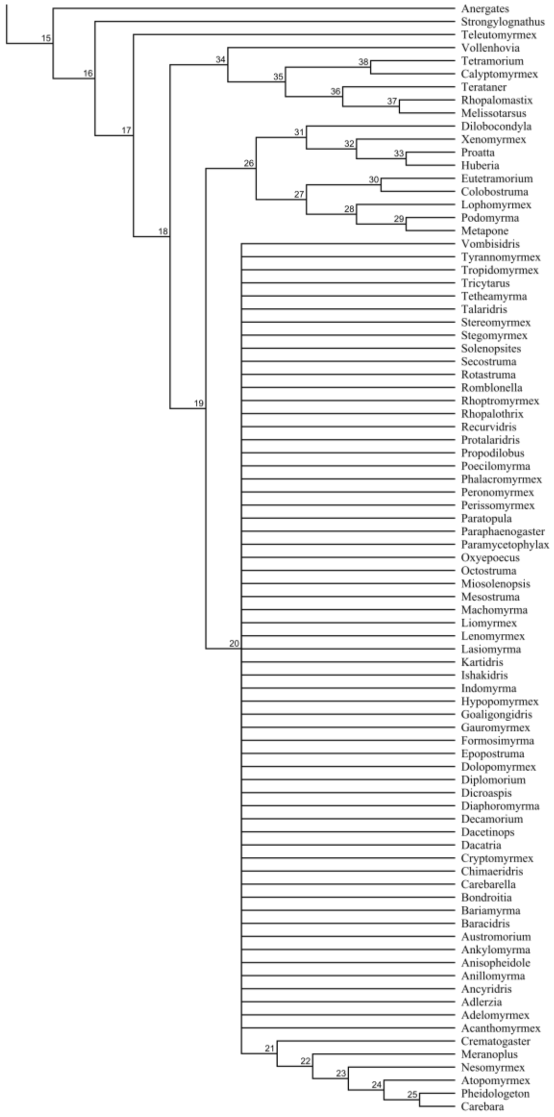

Figure A1.1 The genus-level supertree as described in Chapter 2. Node numbers correspond to those on table A2.4. Branch lengths are arbitrary. Genera that appear more than once reflect paraphyly in that genus (see Chapter 2).

Table A1.5 Morphological and social traits for a) 1957 species and b) 208 genera of ant. Mean values and central tendencies for each trait were established according to the protocol outlined in Chapter 2. All means are weighted by the sample size of the sources contributing to the mean. where se = study effort (the number of hits per genus from a Web of Knowledge search conducted in 2013); cs = mean colony size (number of workers at maturity); cs ss = sample size for colony size data (the sum of sample sizes reported by sources contributing to the mean value. Absent sample sizes were assumed to be one. This is true for all subsequent sample sizes); wk hw = mean worker head width across the widest part of the head capsule (mm); wk hw ss = sample size for worker head width data; q hw = mean queen head width across the widest part of the head capsule (mm); q hw ss = sample size for queen head width data; w pm = worker polymorphism (presence of absence of discrete worker castes); pg = polygyny; pa = polyandry and ref = reference(s). All references for these data are listed below the tables. Taxonomy follows the Bolton World Catalogue (www.antweb.org). – denotes missing data.

(a)

Genus	Species	se	cs	cs ss	wk hw	wk hw ss	q hw	q hw ss	w pm	pg	pa	ref
Acanthognathus	brevicornis	29	-	-	0.67	1	0.68	4	-	-	-	[1]
Acanthognathus	laevigatus	29	-	-	0.34	1	-	-	-	-	-	[2]
Acanthognathus	lentus	29	-	-	0.63	3	-	-	-	-	-	[1]
Acanthognathus	ocellatus	29	-	-	0.61	6	0.34	1	-	-	-	[1]
Acanthognathus	rudis	29	-	-	0.63	15	0.32	1	-	-	-	[1]
Acanthognathus	stipulosus	29	-	-	0.28	1	-	-	-	-	-	[1]
Acanthognathus	teledectus	29	-	-	0.3	1	-	-	-	-	-	[1]
Acanthomyrmex	crassispinus	15	-	-	1.33	194	-	-	Yes	-	-	[3]
Acanthomyrmex	ferox	15	30.42	84	1.86	52	2.44	23	Yes	No	-	[4-7]
Acanthomyrmex	minus	15	13.5	2	0.63	2	0.54	1	Yes	-	-	[8]
Acanthomyrmex	notabilis	15	40	1	-	-	-	-	Yes	-	-	[7]

Acanthomyrmex	padanensis	15	10	3	0.83	2	0.5	1	Yes	No	-	[8]
Acanthomyrmex	sulawesiensis	15	30	1	0.92	2	1.25	1	Yes	No	-	[8]
Acanthomyrmex	thailandensis	15	-	-	1.55	9	0.53	1	Yes	-	-	[9]
Acanthostichus	arizonensis	26	-	-	0.81	1	-	-	-	-	-	[10]
Acanthostichus	bentoni	26	-	-	1.1	8	-	-	-	-	-	[10]
Acanthostichus	brevicornis	26	-	-	1.35	112	1.01	1	-	-	-	[10-12]
Acanthostichus	concavinodis	26	-	-	0.98	1	-	-	-	-	-	[10]
Acanthostichus	emmae	26	-	-	-	-	1.03	1	-	-	-	[10]
Acanthostichus	fermoralis	26	-	-	0.65	1	-	-	-	-	-	[10]
Acanthostichus	hispaniolicus	26	-	-	0.92	3	-	-	-	-	-	[13]
Acanthostichus	kirbyi	26	-	-	1.07	1	-	-	-	-	-	[10]
Acanthostichus	laevigatus	26	-	-	0.98	1	-	-	-	-	-	[10]
Acanthostichus	laticornis	26	-	-	1.03	1	1.82	1	-	-	-	[10]
Acanthostichus	lattekei	26	-	-	1.14	1	-	-	-	-	-	[10]
Acanthostichus	longinodis	26	-	-	0.59	3	-	-	-	-	-	[12]
Acanthostichus	punctiscapus	26	-	-	0.72	1	-	-	-	-	-	[10]
Acanthostichus	quadratus	26	-	-	1.17	1	2.1	1	-	-	-	[10]
Acanthostichus	quirozi	26	-	-	0.71	1	-	-	-	-	-	[10]
Acanthostichus	serratulus	26	-	-	0.84	1	-	-	-	-	-	[10]
Acanthostichus	texanus	26	-	-	0.9	1	0.94	1	-	-	-	[10]
Acanthostichus	truncatus	26	-	-	1.18	1	-	-	-	-	-	[10]
Acromyrmex	balzani	923	-	-	-	-	-	-	-	No	-	[14]
Acromyrmex	coronatus	923	17596	1	-	-	-	-	Yes	-	-	[15]
Acromyrmex	echinatior	923	-	-	-	-	-	-	-	Yes	Yes	[16-18]
Acromyrmex	landolti	923	1000	1	-	-	-	-	-	-	-	[19]
Acromyrmex	niger	923	-	-	-	-	-	-	-	No	-	[14]

Acromyrmex	octospinosus	923	1814.03	29	1.95	1	-	-	Yes	Yes	Yes	[17-27]
Acromyrmex	rugosus	923	519	8	-	-	-	-	-	Yes	-	[28, 29]
Acromyrmex	subterraneus	923	-	-	0.98	125	-	-	-	Yes	-	[24, 30-32]
Acromyrmex	versicolor	923	-	-	-	-	-	-	-	Yes	-	[33, 34]
Acromyrmex	volcanus	923	-	-	-	-	-	-	No	-	-	[26]
Acropyga	bakwele	81	-	-	0.44	1	-	-	-	-	-	[35]
Acropyga	butteli	81	-	-	0.58	6	0.69	3	-	-	-	[36]
Acropyga	epedana	81	167	2	-	-	0.6	6	-	Yes	-	[37, 38]
Acropyga	nipponensis	81	-	-	0.47	5	-	-	-	-	-	[36]
Adelomyrmex	anxiocalor	12	-	-	0.71	5	-	-	-	-	-	[39]
Adelomyrmex	betoi	12	-	-	0.3	1	-	-	-	-	-	[39]
Adelomyrmex	bispeculum	12	46.5	2	0.57	3	-	-	-	No	-	[39]
Adelomyrmex	brenesi	12	-	-	0.35	2	-	-	-	-	-	[39, 40]
Adelomyrmex	coco	12	-	-	0.59	2	-	-	-	-	-	[39]
Adelomyrmex	cristiani	12	-	-	0.28	1	-	-	-	-	-	[39]
Adelomyrmex	dentivagans	12	-	-	0.65	6	-	-	-	-	-	[39]
Adelomyrmex	foveolatus	12	-	-	0.25	1	-	-	-	-	-	[39]
Adelomyrmex	marginodus	12	-	-	0.47	5	-	-	-	-	-	[39]
Adelomyrmex	metzabok	12	-	-	0.61	6	-	-	-	-	-	[39]
Adelomyrmex	minimus	12	-	-	0.25	1	-	-	-	-	-	[39]
Adelomyrmex	nortenyo	12	-	-	0.67	4	-	-	-	-	-	[39]
Adelomyrmex	paratristani	12	11	1	0.63	10	-	-	-	Yes	-	[39]
Adelomyrmex	quetzal	12	-	-	0.69	6	-	-	-	-	-	[39]
Adelomyrmex	silvestrii	12	-	-	0.55	1	-	-	-	-	-	[39]
Adelomyrmex	striatus	12	-	-	-	-	-	-	Yes	-	-	[39]

Adelomyrmex	tristani	12	-	-	0.54	2	-	-	-	-	-	[39]
Aenictus	abelliei	134	-	-	0.42	1	-	-	-	-	-	[41]
Aenictus	acerbus	134	-	-	0.64	26	-	-	-	-	-	[42]
Aenictus	aratus	134	-	-	0.74	36	-	-	-	-	-	[42]
Aenictus	binghami	134	-	-	0.86	10	-	-	-	-	-	[43]
Aenictus	carolianus	134	-	-	0.62	10	-	-	-	-	-	[44]
Aenictus	changmaiensis	134	-	-	0.38	1	-	-	-	-	-	[45]
Aenictus	decolor	134	-	-	0.59	8	1.1	4	-	-	-	[46]
Aenictus	dentatus	134	100000	1	0.81	15	-	-	-	-	Yes	[43, 47, 48]
Aenictus	diclops	134	-	-	0.79	18	-	-	-	-	-	[42]
Aenictus	doydeei	134	-	-	0.57	10	-	-	-	-	-	[43]
Aenictus	eugenii	134	-	-	-	-	1.62	1	-	-	-	[49]
Aenictus	fuchuanensis	134	-	-	0.68	10	-	-	-	-	-	[43]
Aenictus	glabratus	134	-	-	0.51	7	-	-	-	-	-	[50]
Aenictus	gracilis	134	65657.89	38	0.57	1	-	-	Yes	-	-	[44, 51, 52]
Aenictus	henanensis	134	-	-	0.53	5	-	-	-	-	-	[53]
Aenictus	hodgsoni	134	-	-	0.66	6	-	-	-	-	-	[43]
Aenictus	hottai	134	-	-	0.96	11	-	-	-	-	-	[54, 55]
Aenictus	jarujini	134	-	-	0.75	20	-	-	-	-	-	[56]
Aenictus	laeviceps	134	72222.22	18	-	-	-	-	Yes	-	Yes	[47, 51, 52, 57]
Aenictus	latifemoratus	134	-	-	0.84	6	-	-	-	-	-	[54, 56]
Aenictus	lifuiae	134	-	-	0.49	5	1.53	1	-	-	-	[58]
Aenictus	minutulus	134	-	-	0.35	1	-	-	-	-	-	[54]

Aenictus	nesiotis	134	-	-	0.67	30	-	-	-	-	-	[42]
Aenictus	nishimurai	134	-	-	0.42	11	-	-	-	-	-	[43, 45]
Aenictus	pachycerus	134	-	-	-	-	1.32	1	-	-	-	[59]
Aenictus	pangantihoni	134	-	-	0.72	10	-	-	-	-	-	[44]
Aenictus	paradentatus	134	-	-	0.87	9	-	-	-	-	-	[48]
Aenictus	pfeifferi	134	-	-	0.83	10	-	-	-	-	-	[44]
Aenictus	philiporum	134	-	-	0.63	20	-	-	-	-	-	[42]
Aenictus	prolixus	134	-	-	0.5	26	-	-	-	-	-	[42]
Aenictus	silvestrii	134	-	-	0.84	4	-	-	-	-	-	[56]
Aenictus	thailandianus	134	-	-	0.63	1	-	-	-	-	-	[45]
Aenictus	turneri	134	-	-	0.51	74	-	-	-	-	-	[42]
Aenictus	yamanei	134	-	-	0.67	10	-	-	-	-	-	[55]
Amblyopone	australis	111	50	2	-	-	-	-	-	Yes	-	[11, 60]
Amblyopone	pallipes	111	10	1	-	-	-	-	-	-	-	[61]
Amblyopone	sylvestrii	111	16.21	14	-	-	-	-	-	Yes	-	[62]
Anergates	atratulus	52	-	-	-	-	-	-	-	Yes	-	[63]
Aneuretus	simoni	21	40	1	-	-	-	-	-	-	-	[19]
Ankylomyrma	coronacantha	2	-	-	1.4	4	-	-	No	-	-	[64]
Anochetus	bequaerti	88	-	-	-	-	-	-	-	No	-	[65]
Anochetus	boltoni	88	-	-	1.75	20	-	-	-	-	-	[66]
Anochetus	elegans	88	-	-	1.78	3	-	-	-	-	-	[67]
Anochetus	faurei	88	-	-	-	-	-	-	-	No	-	[65]
Anochetus	goodmani	88	-	-	1.68	15	1.57	5	-	-	-	[66]
Anochetus	grandidieri	88	-	-	0.89	20	0.94	5	-	-	-	[66]
Anochetus	katonae	88	-	-	-	-	-	-	-	No	-	[65]
Anochetus	madagascarensis	88	-	-	1.36	20	1.52	5	-	-	-	[66]

Anochetus	maryatiae	88	-	-	1.29	2	-	-	-	-	-	[68]
Anochetus	miserabilis	88	-	-	1.69	7	1.74	2	-	-	-	[69]
Anochetus	pattersoni	88	-	-	1.28	8	1.29	1	-	-	-	[66]
Anochetus	vallensis	88	-	-	1.19	1	1.22	2	-	-	-	[67]
Anonychomyrma	nitidiceps	26	-	-	-	-	-	-	-	Yes	-	[70]
Anoplolepis	gracilipes	309	3599.06	80	-	-	-	-	-	Yes	-	[70-73]
Anoplolepis	sp_indet	309	-	-	0.28	1	-	-	-	-	-	[74]
Aphaenogaster	aktaci	590	-	-	1.08	56	-	-	-	-	-	[75]
Aphaenogaster	albiceotosus	590	350	1	-	-	-	-	-	-	-	[19]
Aphaenogaster	albisetosa	590	-	-	-	-	-	-	-	No	-	[76]
Aphaenogaster	araneoides	590	111.5	2	-	-	-	-	-	No	-	[77, 78]
Aphaenogaster	ashmeadi	590	104.52	23	-	-	-	-	-	Yes	-	[79]
Aphaenogaster	cockerelli	590	6294	7	-	-	-	-	-	Yes	Yes	[38, 76, 80-82]
Aphaenogaster	famelica	590	-	-	1	10	0.83	1	-	-	-	[83]
Aphaenogaster	flemingi	590	300	1	-	-	-	-	-	-	-	[61]
Aphaenogaster	floridana	590	151.64	36	-	-	-	-	-	Yes	-	[79]
Aphaenogaster	japonica	590	-	-	0.35	1	-	-	-	-	-	[83]
Aphaenogaster	lamellidens	590	300	1	-	-	-	-	-	-	-	[61]
Aphaenogaster	maculifrons	590	-	-	0.96	100	1.18	25	-	-	-	[75]
Aphaenogaster	punctaticeps	590	-	-	0.97	2	-	-	-	-	-	[84]
Aphaenogaster	radchenkoi	590	-	-	0.69	100	1.17	5	-	-	-	[75]
Aphaenogaster	rudis	590	335.23	73	-	-	-	-	-	No	-	[85, 86]
Aphaenogaster	senilis	590	950.64	109	0.62	2	-	-	Yes	No	No	[87-91]
Aphaenogaster	smythiesi	590	300.87	69	-	-	-	-	-	No	No	[92, 93]
Aphaenogaster	tinauti	590	-	-	1.18	30	1.2	5	-	-	-	[94]

Aphaenogaster	treatae	590	130.71	21	-	-	-	-	-	Yes	-	[79]
Aphomomyrmex	afer	17	-	-	0.44	2087	-	-	-	-	-	[95]
Apterostigma	collare	77	35.36	72	-	-	-	-	No	Yes	Yes	[18, 96-98]
Apterostigma	mayri	77	20	25	-	-	-	-	-	No	No	[22]
Apterostigma	megacephala	77	-	-	0.74	3	-	-	-	-	-	[99]
Aptinoma	mangabe	2	-	-	-	-	0.59	1	-	-	-	[100]
Asphinctanilloides	anae	6	-	-	0.37	16	-	-	-	-	-	[101]
Asphinctanilloides	manuara	6	-	-	0.35	1	-	-	-	-	-	[101]
Asphinctopone	differens	5	-	-	0.66	1	-	-	-	-	-	[102]
Asphinctopone	pilosa	5	-	-	0.86	1	-	-	-	-	-	[103]
Asphinctopone	silvestrii	5	-	-	0.64	20	-	-	-	-	-	[102]
Atopomyrmex	cryptoceroides	11	-	-	-	-	-	-	Yes	-	-	[64]
Atopomyrmex	mocquerysi	11	-	-	1.59	85	-	-	Yes	-	-	[64]
Atta	cephalotes	1722	10000000	1	1.85	1	-	-	Yes	No	Yes	[104-108]
Atta	colombica	1722	50000	5	1.85	3	-	-	Yes	No	Yes	[18, 22, 107-110]
Atta	sexdens	1722	7000	1	1.3	5	-	-	Yes	Yes	Yes	[107, 111-115]
Atta	texana	1722	-	-	-	-	-	-	-	Yes	-	[116, 117]
Atta	vollenweideri	1722	3500000	1	-	-	-	-	-	-	-	[118]
Axinidris	denticulata	7	-	-	0.71	1	-	-	-	-	-	[119]
Axinidris	denticulatum	7	-	-	0.79	1	-	-	-	-	-	[120]
Axinidris	ghanensis	7	-	-	0.76	2	-	-	-	-	-	[119, 120]

Axinidris	hylekoites	7	-	-	0.35	8	0.74	1	-	-	-	[119, 120]
Axinidris	kakamegensis	7	-	-	0.97	2	-	-	-	-	-	[119, 120]
Axinidris	mlalu	7	-	-	0.74	1	-	-	-	-	-	[119]
Axinidris	murielae	7	-	-	-	-	0.78	1	-	-	-	[120]
Axinidris	namib	7	-	-	0.81	1	-	-	-	-	-	[119]
Axinidris	nigripes	7	-	-	0.97	2	-	-	-	-	-	[119, 120]
Azteca	alfari	317	-	-	-	-	-	-	-	No	-	[70]
Azteca	chartifex	317	-	-	-	-	-	-	-	No	-	[70]
Azteca	trailii	317	-	-	-	-	-	-	-	No	-	[70]
Azteca	trigona	317	-	-	-	-	-	-	-	Yes	-	[70]
Baracidris	meketra	2	-	-	0.33	5	0.2	1	No	-	-	[64]
Baracidris	sitra	2	-	-	0.22	1	-	-	-	-	-	[64]
Basiceros	conjugans	22	-	-	0.55	4	0.55	1	-	Yes	-	[121]
Basiceros	manni	22	31.67	3	1.37	10	0.69	1	-	Yes	-	[122]
Basiceros	scambognatha	22	-	-	-	-	0.63	1	-	-	-	[123]
Basiceros	scambognathus	22	-	-	0.57	1	1.01	3	-	-	-	[124]
Belonopelta	deletrix	8	10	1	-	-	-	-	-	No	-	[41]
Blepharidatta	brasiliensis	10	132	13	-	-	-	-	-	Yes	-	[125]
Blepharidatta	conops	10	190.74	119	-	-	-	-	No	Yes	-	[126, 127]
Bothriomyrmex	paradoxus	52	-	-	0.52	5	0.54	4	-	-	-	[128]
Brachymyrmex	admotus	171	-	-	0.45	98	0.56	8	-	-	-	[129, 130]

Brachymyrmex	brevicornis	171	-	-	0.38	52	0.49	16	-	-	-	[129, 130]
Brachymyrmex	depilis	171	200	1	-	-	-	-	-	No	Yes	[61, 131]
Brachymyrmex	gaucho	171	-	-	0.63	16	-	-	-	-	-	[129, 130]
Camponotus	adenensis	5444	-	-	1.2	1	-	-	-	-	-	[74]
Camponotus	aethiops	5444	2500	1	-	-	-	-	-	-	-	[19]
Camponotus	aktaci	5444	-	-	1.17	50	-	-	-	-	-	[132]
Camponotus	anatolicus	5444	-	-	0.91	50	-	-	-	-	-	[132]
Camponotus	anderseni	5444	-	-	1	1	-	-	-	-	-	[133]
Camponotus	annetteae	5444	-	-	1.4	1	-	-	-	-	-	[133]
Camponotus	arabicus	5444	-	-	1.57	2	1.3	1	-	-	-	[74]
Camponotus	armenius	5444	-	-	2.01	1	-	-	-	-	-	[134]
Camponotus	aureopilus	5444	-	-	1.87	2	-	-	-	-	-	[135]
Camponotus	candiotes	5444	-	-	-	-	1.46	22	-	-	-	[136]
Camponotus	carbo	5444	-	-	1.15	1	-	-	-	-	-	[137]
Camponotus	casteneus	5444	350	1	-	-	-	-	-	-	-	[61]
Camponotus	christi	5444	2356	2	-	-	-	-	-	Yes	-	[138, 139]
Camponotus	cingulatus	5444	-	-	-	-	-	-	-	No	-	[70]
Camponotus	concavus	5444	-	-	2.17	1	-	-	-	-	-	[140]
Camponotus	conithorax	5444	-	-	1.8	1	-	-	-	-	-	[133]
Camponotus	cyrtomyrmodes	5444	-	-	1.41	4	-	-	-	-	-	[135]
Camponotus	densopilus	5444	-	-	2.22	5	-	-	-	-	-	[135]
Camponotus	detritus	5444	-	-	-	-	-	-	-	Yes	-	[70]
Camponotus	empedocles	5444	-	-	1.68	1	-	-	-	-	-	[74]

Camponotus	eperiamorum	5444	-	-	1.4	3	2.1	4	-	-	-	[141]
Camponotus	erythrocephalus	5444	-	-	0.88	3	-	-	-	-	-	[141]
Camponotus	essigi	5444	-	-	1.01	114	-	-	-	-	-	[142, 143]
Camponotus	fayfaensis	5444	-	-	0.55	2	-	-	-	-	-	[74]
Camponotus	fellah	5444	-	-	2.25	1	-	-	-	-	-	[74]
Camponotus	femoratus	5444	-	-	-	-	-	-	-	Yes	-	[70]
Camponotus	fergusoni	5444	-	-	1	2	-	-	-	-	-	[144]
Camponotus	festinatus	5444	-	-	-	-	-	-	-	No	-	[76]
Camponotus	flavicomans	5444	-	-	1.16	6	-	-	-	-	-	[141]
Camponotus	floridanus	5444	1426.55	42	-	-	-	-	Yes	Yes	No	[61, 80, 145-147]
Camponotus	gallagheri	5444	-	-	1.42	1	-	-	-	-	-	[137]
Camponotus	gasseri	5444	-	-	1.25	1	-	-	-	-	-	[133]
Camponotus	gigas	5444	2375.5	4	-	-	-	-	-	No	-	[70, 148-151]
Camponotus	gombaki	5444	-	-	1.58	40	2.27	8	-	-	-	[146, 152]
Camponotus	herculeanus	5444	5771.72	9	-	-	-	-	-	Yes	-	[70, 139, 153, 154]
Camponotus	hirtus	5444	-	-	1.03	50	-	-	-	-	-	[132]
Camponotus	honazienisis	5444	-	-	0.96	42	-	-	-	-	-	[132]
Camponotus	howensis	5444	-	-	1.48	1	-	-	-	-	-	[133]
Camponotus	impressus	5444	250	1	-	-	-	-	-	No	-	[61, 70]
Camponotus	janeti	5444	-	-	1.33	1	-	-	-	-	-	[133]
Camponotus	janforrestae	5444	-	-	1.6	1	-	-	-	-	-	[133]

Camponotus	jizani	5444	-	-	1	2	-	-	-	-	-	[74]
Camponotus	kersteni	5444	-	-	2.75	1	-	-	-	-	-	[74]
Camponotus	kiusiuensis	5444	-	-	-	-	-	-	-	No	-	[70]
Camponotus	laevigatus	5444	1250	2	-	-	-	-	-	-	-	[139]
Camponotus	ligniperda	5444	3.5	1	-	-	-	-	-	Yes	Yes	[70, 153-155]
Camponotus	longifacies	5444	-	-	0.61	2	-	-	-	-	-	[144]
Camponotus	mackayensis	5444	-	-	1.08	1	-	-	-	-	-	[133]
Camponotus	macrocephalus	5444	-	-	1.33	1	-	-	-	-	-	[133]
Camponotus	marianensis	5444	-	-	1.07	13	-	-	-	-	-	[141]
Camponotus	modoc	5444	18405	21	-	-	-	-	-	Yes	-	[139]
Camponotus	mussolinii	5444	-	-	1.73	4	-	-	-	-	-	[135]
Camponotus	nawai	5444	-	-	-	-	-	-	-	Yes	-	[156]
Camponotus	nearcticus	5444	70	1	-	-	-	-	-	-	-	[61]
Camponotus	nipponicus	5444	-	-	-	-	-	-	-	No	-	[70]
Camponotus	novaboracensis	5444	10833.33	3	-	-	-	-	-	-	-	[139]
Camponotus	papago	5444	-	-	0.49	2	0.63	1	-	-	-	[157]
Camponotus	pawseyi	5444	-	-	1.13	2	-	-	-	-	-	[144]
Camponotus	peleliuensis	5444	-	-	1.1	6	-	-	-	-	-	[141]
Camponotus	pennsylvanicus	5444	2083.13	8	-	-	-	-	-	No	-	[19, 70, 139]
Camponotus	pitjantjatarae	5444	-	-	1.13	2	-	-	-	-	-	[144]
Camponotus	planatus	5444	-	-	-	-	-	-	-	Yes	-	[70, 158]
Camponotus	posteropilus	5444	-	-	2.02	4	-	-	-	-	-	[135]
Camponotus	robechii	5444	-	-	1.29	7	-	-	-	-	-	[134]
Camponotus	royi	5444	-	-	0.84	2	-	-	-	-	-	[159]

Camponotus	rudis	5444	-	-	0.79	2	-	-	-	-	-	[144]
Camponotus	ruseni	5444	-	-	1.06	14	-	-	-	-	-	[160]
Camponotus	sanguinifrons	5444	-	-	0.93	1	-	-	-	-	-	[133]
Camponotus	scotti	5444	-	-	0.9	2	-	-	-	-	-	[144]
Camponotus	senex	5444	-	-	-	-	-	-	Yes	-	-	[40]
Camponotus	sericeiventris	5444	-	-	2.65	14	-	-	-	-	-	[161, 162]
Camponotus	sericeus	5444	300	1	-	-	-	-	-	-	-	[163]
Camponotus	simpsoni	5444	-	-	0.75	2	-	-	-	-	-	[144]
Camponotus	socius	5444	335	1	-	-	-	-	-	-	-	[79]
Camponotus	sp.	5444	-	-	-	-	-	-	-	No	-	[70]
Camponotus	sp_4	5444	1126	1	-	-	-	-	-	No	-	[164]
Camponotus	subpilus	5444	-	-	1.76	63	-	-	-	-	-	[135]
Camponotus	texens	5444	-	-	1.39	40	2.3	8	-	-	-	[146, 152]
Camponotus	textor	5444	-	-	-	-	-	-	Yes	-	-	[40]
Camponotus	thadeus	5444	-	-	1.83	4	-	-	-	-	-	[135]
Camponotus	truncatus	5444	50	1	-	-	-	-	-	-	-	[19]
Camponotus	vicinus	5444	24825.67	9	-	-	-	-	-	-	-	[139]
Camponotus	vitreus	5444	-	-	1.2	1	-	-	-	-	-	[133]
Camponotus	xanthopilus	5444	-	-	1.06	2	-	-	-	-	-	[135]
Camponotus	xerxes	5444	-	-	2.25	1	-	-	-	-	-	[74]
Camponotus	yamaokai	5444	-	-	1.14	80	1.24	20	-	Yes	-	[165-167]
Capmonotus	discolor	5444	70	1	-	-	-	-	-	-	-	[61]
Cardiocondyla	batesii	235	-	-	-	-	-	-	-	-	Yes	[168]
Cardiocondyla	emeryi	235	50	1	-	-	-	-	-	Yes	-	[61, 70]

Cardiocondyla	mauritanica	235	-	-	0.46	283	0.49	17	-	-	-	[169]
Cardiocondyla	nuda	235	50	1	-	-	-	-	-	Yes	-	[61, 70]
Cardiocondyla	wroughtonii	235	50	1	-	-	-	-	-	Yes	-	[61, 70, 170]
Carebara	abuhurayri	41	-	-	0.29	8	-	-	No	-	-	[171]
Carebara	arabica	41	-	-	-	-	-	-	Yes	-	-	[171]
Carebara	nevermanni	41	180	1	-	-	-	-	-	-	-	[19]
Carebara	overbecki	41	400	1	-	-	-	-	-	-	-	[19]
Cataglyphis	acutinodis	894	-	-	0.66	1	-	-	-	-	-	[137]
Cataglyphis	albicans	894	-	-	-	-	-	-	-	No	-	[70]
Cataglyphis	asiriensis	894	-	-	0.83	2	-	-	-	-	-	[74]
Cataglyphis	bicolor	894	2000	1	-	-	-	-	-	No	-	[19, 70]
Cataglyphis	cursor	894	924.5	2404	1.3	2404	-	-	-	No	Yes	[131, 172, 173]
Cataglyphis	emmae	894	-	-	-	-	0.73	2	-	-	-	[74]
Cataglyphis	flavobrunnea	894	-	-	1.08	3	-	-	-	-	-	[137]
Cataglyphis	hannae	894	-	-	-	-	1.69	5	-	-	-	[174]
Cataglyphis	harteni	894	-	-	0.76	1	-	-	-	-	-	[137]
Cataglyphis	iberica	894	335.88	250	-	-	-	-	-	No	-	[70, 175, 176]
Cataglyphis	isis	894	-	-	-	-	0.94	1	-	-	-	[74]
Cataglyphis	minima	894	-	-	0.47	4	0.81	2	-	-	-	[74]
Cataglyphis	nigra	894	-	-	2.98	93	3	28	-	-	-	[74, 177]
Cataglyphis	pubescens	894	-	-	1.01	9	-	-	-	-	-	[178]
Cataglyphis	sabulosa	894	185.19	870	-	-	-	-	-	-	-	[179]
Cataglyphis	shuaibensis	894	-	-	0.66	1	-	-	-	-	-	[137]

Cataglyphis	stigmata	894	-	-	1.37	7	-	-	-	-	-	[178]
Cataglyphis	urens	894	-	-	1.33	2	-	-	-	-	-	[74]
Cataglyphis	velox	894	-	-	1.69	4	-	-	-	-	-	[180]
Cataulacus	catuvolcus	57	-	-	-	-	-	-	-	No	-	[70]
Cataulacus	guineenensis	57	-	-	-	-	-	-	-	Yes	-	[70]
Cataulacus	mckeyi	57	248	75	-	-	-	-	-	Yes	-	[181, 182]
Centromyrmex	alfaroi	21	-	-	-	-	-	-	-	Yes	-	[102, 183]
Centromyrmex	angolensis	21	-	-	0.89	60	1	8	-	-	-	[102, 183]
Centromyrmex	bequaerti	21	329.44	8	1.35	138	2.04	10	Yes	Yes	-	[11, 102, 183, 184]
Centromyrmex	decessor	21	-	-	1.27	22	1.43	4	-	-	-	[102, 183]
Centromyrmex	ereptor	21	-	-	0.8	6	-	-	-	-	-	[102, 183]
Centromyrmex	fugator	21	-	-	0.78	4	0.78	2	-	-	-	[102, 183]
Centromyrmex	longiventris	21	-	-	0.67	8	-	-	-	-	-	[102, 183]
Centromyrmex	praedator	21	-	-	0.99	2	-	-	-	-	-	[102, 183]
Centromyrmex	raptor	21	-	-	1.97	10	1.88	2	-	-	-	[102, 183]
Centromyrmex	secutor	21	-	-	1.04	20	-	-	-	-	-	[102, 183]

Centromyrmex	sellaris	21	-	-	1.02	30	1.12	2	-	-	-	[102, 183]
Cephalotes	atratus	299	6037	2	2.17	200	-	-	-	No	-	[70, 185-187]
Cephalotes	christopherseni	299	4000	1	2.04	1	-	-	Yes	Yes	-	[187]
Cephalotes	depressus	299	-	-	1.17	200	-	-	Yes	-	-	[186]
Cephalotes	minutus	299	-	-	1.33	1	-	-	Yes	No	-	[70, 187]
Cephalotes	persimilis	299	-	-	0.9	200	-	-	Yes	-	-	[186]
Cephalotes	pusillus	299	35.56	9	1.18	200	-	-	Yes	No	-	[186, 188]
Cephalotes	varians	299	1000	1	-	-	-	-	-	-	-	[19]
Cerapachys	biroi	95	405.36	14	0.44	411	-	-	-	Yes	-	[189-192]
Cerapachys	eguchii	95	-	-	0.63	12	-	-	-	-	-	[193]
Cerapachys	paradoxus	95	-	-	0.55	6	-	-	-	-	-	[193]
Cerapachys	sauteri	95	-	-	1.16	3	1.23	3	-	-	-	[8]
Cerapachys	sexspinus	95	-	-	0.61	2	-	-	-	-	-	[193]
Cerapachys	turneri	95	-	-	-	-	-	-	-	Yes	-	[189]
Cerapachys	wittmeri	95	-	-	0.35	1	-	-	-	-	-	[74]
Chalepoxenus	brunneus	45	-	-	-	-	-	-	-	Yes	-	[194]
Chalepoxenus	kutteri	45	-	-	0.5	16	0.58	8	-	-	-	[195]
Chalepoxenus	spinosus	45	-	-	-	-	0.35	1	-	-	-	[196]
Cheliomyrmex	andicola	22	-	-	1.8	1	-	-	-	-	-	[197]
Cheliomyrmex	morosus	22	-	-	-	-	-	-	Yes	-	-	[198, 199]
Chimaeridris	boltoni	1	-	-	0.59	2	-	-	-	-	-	[200]
Chimaeridris	burckhardti	1	-	-	0.23	1	-	-	-	-	-	[200]

Cladomyrma	andrei	28	-	-	0.89	30	1.13	29	-	-	-	[201, 202]
Cladomyrma	aurochaetae	28	-	-	0.57	6	1.25	4	-	-	-	[202]
Cladomyrma	crypteroniae	28	-	-	0.9	16	1.43	8	-	-	-	[202]
Cladomyrma	dianeae	28	-	-	0.85	16	1.15	8	-	-	-	[202]
Cladomyrma	hewitti	28	-	-	0.85	12	1.34	6	-	-	-	[202]
Cladomyrma	hobbyi	28	-	-	0.67	16	0.97	8	-	-	-	[202]
Cladomyrma	maryatiae	28	-	-	0.77	16	1.1	8	-	-	-	[202]
Cladomyrma	maschwitzi	28	-	-	0.63	45	1.01	9	-	-	-	[201, 202]
Cladomyrma	nudidorsalis	28	-	-	0.7	11	1.22	2	-	-	-	[202]
Cladomyrma	petalae	28	-	-	0.83	52	1.22	22	-	No	-	[201-203]
Cladomyrma	scopulosa	28	-	-	-	-	-	-	-	Yes	-	[203]
Cladomyrma	sp	28	15000	1	-	-	-	-	-	Yes	-	[202]
Cladomyrma	yongi	28	-	-	0.62	16	0.96	1	-	-	-	[202]
Creamtogaster	ashmeadi	1225	10000	1	-	-	-	-	-	-	-	[61, 204]
Creamtogaster	lineaolata	1225	200	1	-	-	-	-	-	-	-	[61]
Crematogaster	ampullaris	1225	-	-	1.23	3	-	-	Yes	-	-	[205]
Crematogaster	ashmeadi	1225	-	-	-	-	-	-	-	Yes	-	[61, 204]
Crematogaster	atkinsoni	1225	500	1	-	-	-	-	-	-	-	[61]
Crematogaster	aurita	1225	-	-	1.4	6	-	-	Yes	-	-	[205, 206]
Crematogaster	bouvardi	1225	-	-	0.81	4	-	-	No	-	-	[207]
Crematogaster	brevis	1225	-	-	0.71	2	-	-	No	-	-	[207]
Crematogaster	crinosa	1225	100	4	-	-	-	-	-	No	-	[208]
Crematogaster	cylindriceps	1225	-	-	0.54	9	0.73	5	No	Yes	-	[209]

Crematogaster	difformis	1225	-	-	1.08	6	-	-	Yes	-	-	[205]
Crematogaster	grevei	1225	-	-	0.86	12	1.3	3	-	-	-	[210]
Crematogaster	hova-complex	1225	-	-	0.97	58	1.79	16	Yes	-	-	[210]
Crematogaster	impressa	1225	-	-	-	-	-	-	-	No	-	[70]
Crematogaster	inflata	1225	-	-	0.97	3	-	-	-	-	-	[206]
Crematogaster	kojimai	1225	-	-	0.66	12	-	-	No	-	-	[207]
Crematogaster	laevis	1225	-	-	-	-	-	-	-	No	-	[70]
Crematogaster	limata	1225	-	-	-	-	-	-	-	Yes	-	[70]
Crematogaster	luctans	1225	-	-	-	-	-	-	-	Yes	-	[211]
Crematogaster	madecassa	1225	-	-	0.55	23	0.95	11	-	-	-	[212]
Crematogaster	mahery	1225	-	-	1.15	11	-	-	-	-	-	[210]
Crematogaster	malala	1225	-	-	0.99	10	-	-	-	-	-	[210]
Crematogaster	masukoi	1225	-	-	0.48	3	-	-	Yes	-	-	[213]
Crematogaster	matsumurai	1225	-	-	0.87	8	-	-	-	-	-	[214]
Crematogaster	minutissima	1225	309.5	82	-	-	-	-	-	No	-	[61, 215]
Crematogaster	modiglianii	1225	-	-	0.86	47	-	-	Yes	-	-	[213]
Crematogaster	mpanjono	1225	-	-	0.56	4	0.74	1	-	-	-	[212]
Crematogaster	msp._2	1225	500	34	-	-	-	-	-	Yes	-	[216]
Crematogaster	mucronata	1225	-	-	0.98	3	-	-	No	-	-	[205]
Crematogaster	myops	1225	-	-	0.47	3	-	-	Yes	-	-	[213]
Crematogaster	nawai	1225	-	-	0.83	3	-	-	-	-	-	[214]
Crematogaster	nigriceps	1225	-	-	0.9	2	-	-	-	-	-	[217]
Crematogaster	nosibeensis	1225	-	-	0.95	13	1.68	3	-	-	-	[210]
Crematogaster	onusta	1225	-	-	0.94	3	-	-	No	-	-	[205]
Crematogaster	overbecki	1225	-	-	0.32	1	-	-	No	-	-	[207]

Crematogaster	physothorax	1225	-	-	1.14	6	-	-	No	-	-	[205, 206]
Crematogaster	pygmaea	1225	-	-	0.3	1	0.67	1	-	Yes	-	[218]
Crematogaster	rasoherinae	1225	-	-	0.62	38	0.85	10	-	-	-	[212]
Crematogaster	razana	1225	-	-	0.44	3	0.55	1	-	-	-	[212]
Crematogaster	reticulata	1225	-	-	0.45	3	-	-	Yes	-	-	[219]
Crematogaster	sabatra	1225	-	-	1.23	10	-	-	-	-	-	[210]
Crematogaster	scutellaris	1225	-	-	-	-	-	-	-	No	-	[70]
Crematogaster	sewardi	1225	-	-	1.09	6	-	-	Yes	-	-	[205, 206]
Crematogaster	sisa	1225	-	-	1.02	10	-	-	-	-	-	[210]
Crematogaster	smithi	1225	-	-	0.61	112	0.93	10	-	-	-	[220]
Crematogaster	striatula	1225	-	-	-	-	-	-	-	Yes	-	[70]
Crematogaster	sumicrasti	1225	1000	1	-	-	-	-	-	-	-	[19]
Crematogaster	tanakai	1225	-	-	0.83	1	-	-	-	-	-	[205]
Crematogaster	telolafy	1225	-	-	0.52	16	-	-	-	-	-	[212]
Crematogaster	teranishii	1225	-	-	0.89	5	-	-	-	-	-	[214]
Crematogaster	treubi	1225	-	-	0.63	17	-	-	No	-	-	[207]
Crematogaster	vacca	1225	-	-	1.36	3	-	-	Yes	-	-	[205]
Crematogaster	vagula	1225	-	-	0.79	3	-	-	-	-	-	[214]
Crematogaster	volamena	1225	-	-	0.79	20	0.86	1	-	-	-	[212]
Crematogaster	walshi	1225	-	-	0.83	6	-	-	No	-	-	[207]
Crematogaster	yamanei	1225	-	-	1.43	3	-	-	Yes	-	-	[205]
Crematogaster	yappi	1225	-	-	0.7	6	-	-	No	-	-	[207]
Cyphoidris	exalta	2	-	-	0.43	2	-	-	No	-	-	[64]
Cyphoidris	parissa	2	-	-	0.38	1	-	-	No	-	-	[64]

Cyphoidris	spinosa	2	-	-	0.86	10	-	-	No	-	-	[64]
Cyphoidris	werneri	2	-	-	0.77	15	-	-	No	-	-	[64]
Cyphomyrmex	bicornis	116	-	-	0.38	1	-	-	-	-	-	[221]
Cyphomyrmex	cornutus	116	2021.75	8	-	-	-	-	-	Yes	-	[222, 223]
Cyphomyrmex	costatus	116	40.37	54	0.54	9	0.62	5	-	No	No	[22, 98, 221]
Cyphomyrmex	dentatus	116	-	-	0.68	10	-	-	-	Yes	-	[221]
Cyphomyrmex	foxi	116	-	-	0.84	6	-	-	-	-	-	[221]
Cyphomyrmex	hamulatus	116	-	-	0.65	4	-	-	-	-	-	[221]
Cyphomyrmex	kirbyi	116	-	-	0.73	11	-	-	-	-	-	[221]
Cyphomyrmex	laevigatus	116	-	-	0.87	12	-	-	-	-	-	[221]
Cyphomyrmex	longiscapus	116	24.85	346	0.62	98	0.69	27	-	Yes	Yes	[18, 98, 221, 224, 225]
Cyphomyrmex	minutus	116	137.5	2	-	-	-	-	-	-	-	[61, 226]
Cyphomyrmex	muelleri	116	39.71	148	0.63	78	0.7	23	-	Yes	-	[225]
Cyphomyrmex	peltatus	116	-	-	0.65	28	0.76	3	-	-	-	[221]
Cyphomyrmex	rimosus	116	64.64	107	-	-	-	-	-	Yes	No	[22, 61, 226, 227]
Cyphomyrmex	salvini	116	-	-	0.76	18	-	-	-	-	-	[221]
Cyphomyrmex	transversus	116	-	-	0.72	68	0.82	9	-	-	-	[221]
Cyphomyrmex	vorticis	116	-	-	0.68	3	-	-	-	-	-	[221]
Cyphomyrmex	wheeleri	116	-	-	0.67	6	-	-	-	-	-	[221]
Dacatria	templaris	2	-	-	0.34	1	-	-	-	-	-	[228]
Daceton	armigerum	28	168811.65	10	1.3	149	-	-	Yes	Yes	-	[229-231]

Daceton	boltoni	28	-	-	2.62	30	-	-	-	-	-	[229]
Diacamma	australe	190	37.19	48	-	-	-	-	-	No	-	[232-235]
Diacamma	ceylonense	190	246.52	79	2.06	22	-	-	-	Yes	No	[81, 232, 236-242]
Diacamma	cyaneiventre	190	461.51	168	-	-	-	-	-	No	No	[232, 236, 243, 244]
Diacamma	indicum	190	46	2	-	-	-	-	-	No	-	[240, 245]
Diacamma	rugosum	190	247.17	12	-	-	-	-	No	No	-	[234, 246-249]
Diacamma	sp	190	104.03	65	-	-	-	-	-	No	No	[232, 241, 250, 251]
Diacamma	sp,_1	190	88	24	-	-	-	-	-	-	-	[252]
Diacamma	sp.	190	105.35	191	-	-	-	-	-	No	No	[232, 253-256]
Diacamma	sp._	190	62.16	19	-	-	-	-	-	No	No	[257-261]
Diacamma	sp._from_Nigrili	190	9.5	2	-	-	-	-	-	-	-	[240]
Diacamma	sp_	190	86	1	-	-	-	-	-	No	-	[81]
Dilobocondyla	bangalorica	8	42.5	4	0.85	10	0.53	1	-	No	-	[262]
Dinoponera	australis	139	35.5	10	5.18	240	-	-	-	No	-	[81, 232, 263-266]
Dinoponera	gigantea	139	75.6	10	-	-	-	-	-	No	-	[148, 232, 267]
Dinoponera	lucida	139	15.57	21	-	-	-	-	-	No	-	[268-270]

Dinoponera	quadriceps	139	88.46	199	-	-	-	-	No	Yes	No	[19, 81, 232, 255, 265, 266, 269, 271-277]
Dolichoderus	laminatus	290	125	1	-	-	-	-	-	-	-	[226]
Dolichoderus	laurae	290	-	-	-	-	1.36	1	-	-	-	[278]
Dolichoderus	quadripunctatus	290	-	-	-	-	-	-	-	No	-	[70]
Dolichoderus	spurious	290	-	-	-	-	1.76	1	-	-	-	[278]
Dorylus	emeryi	223	-	-	1.96	1	-	-	-	-	-	[279]
Dorylus	gribodoi	223	-	-	1.84	1	4.58	1	Yes	-	-	[279]
Dorylus	laevigatus	223	325000	2	1.22	450	0.92	1	Yes	-	Yes	[47, 189, 280-283]
Dorylus	nigricans	223	5666666.67	3	1.24	699	-	-	-	No	Yes	[16, 47, 279, 280, 284-286]
Dorylus	vishnui	223	-	-	1.28	100	-	-	Yes	-	-	[281, 283]
Dorylus	wilverthi	223	15833333.33	3	-	-	-	-	-	No	-	[118, 163, 280, 284]
Dorymyrmex	bicornis	149	5000	1	-	-	-	-	-	-	-	[19]
Dorymyrmex	bossutus	149	1000	1	-	-	-	-	-	-	-	[61]
Dorymyrmex	burneri	149	1000	1	-	-	-	-	-	-	-	[61]
Dorymyrmex	elegans	149	1000	1	-	-	-	-	-	-	-	[61]
Dorymyrmex	grandulus	149	1000	1	-	-	-	-	-	-	-	[61]
Dorymyrmex	insanus	149	-	-	-	-	-	-	-	Yes	-	[70]

Dorymyrmex	reginicula	149	1000	1	-	-	-	-	-	-	-	[61]
Echinopla	cherapunjiensis	14	-	-	0.95	1	-	-	-	-	-	[287]
Eciton	burchellii	345	593928.57	14	2.02	2	-	-	Yes	No	Yes	[19, 47, 57, 163, 189, 197, 288-302]
Eciton	hamatum	345	113154.3	10	-	-	-	-	Yes	-	-	[19, 57, 288, 295, 303, 304]
Eciton	rapax	345	275000	1	-	-	-	-	No	-	-	[19, 305]
Ectatomma	confine	374	-	-	1.36	4	-	-	-	-	-	[306]
Ectatomma	edentatum	374	49.93	29	5.17	1	6.56	1	-	Yes	-	[307, 308]
Ectatomma	opaciventre	374	71.2	5	-	-	-	-	-	No	-	[309]
Ectatomma	parasiticum	374	-	-	-	-	1.79	66	-	-	-	[310]
Ectatomma	planidens	374	38.4	10	-	-	-	-	-	Yes	-	[311]
Ectatomma	ruidum	374	89.5	263	1.37	3	1.37	165	-	Yes	Yes	[306, 312-321]
Ectatomma	tuberculatum	374	164.49	321	-	-	-	-	No	Yes	No	[269, 314, 322-332]
Ectatomma	vizottoi	374	94.75	8	-	-	-	-	-	Yes	-	[333]
Eotapinoma	macalpini	4	-	-	0.26	1	-	-	-	-	-	[334]
Epopostruma	inornata	14	-	-	0.29	1	-	-	-	-	-	[335]
Euprenolepis	echinata	11	-	-	0.34	1	-	-	-	-	-	[336]
Euprenolepis	maschwitzi	11	-	-	0.87	3	-	-	-	-	-	[336]
Euprenolepis	negrosensis	11	-	-	0.4	1	0.6	1	-	-	-	[336]

Euprenolepis	procera	11	6375	2	1.13	11	0.55	1	-	-	-	[336, 337]
Euprenolepis	thrix	11	-	-	1.04	3	-	-	-	-	-	[336]
Euprenolepis	variegata	11	-	-	0.8	3	-	-	-	-	-	[336]
Euprenolepis	wittei	11	-	-	0.83	3	0.57	1	-	-	-	[336]
Euprenolepis	zeta	11	-	-	0.82	3	-	-	-	-	-	[336]
Eurhopalothrix	alopeciosa	20	-	-	0.29	1	-	-	-	-	-	[338]
Eurhopalothrix	australis	20	27	1	-	-	-	-	-	No	-	[339]
Eurhopalothrix	bolaui	20	-	-	0.34	1	-	-	-	-	-	[338]
Eurhopalothrix	cinnamea	20	-	-	0.71	5	-	-	-	-	-	[339]
Eurhopalothrix	depressa	20	-	-	0.86	4	0.44	2	-	-	-	[338]
Eurhopalothrix	dubia	20	-	-	0.82	10	-	-	-	-	-	[340]
Eurhopalothrix	elke	20	-	-	0.78	8	-	-	-	-	-	[340]
Eurhopalothrix	emeryi	20	-	-	0.62	2	-	-	-	-	-	[341]
Eurhopalothrix	floridanus	20	100	1	-	-	-	-	-	-	-	[61]
Eurhopalothrix	gravis	20	-	-	0.35	1	-	-	-	-	-	[338]
Eurhopalothrix	heliscata	20	262	2	1.07	47	0.61	1	No	Yes	-	[342]
Eurhopalothrix	hoplites	20	-	-	0.52	2	-	-	-	-	-	[341]
Eurhopalothrix	insidiatrix	20	-	-	0.71	3	-	-	-	-	-	[341]
Eurhopalothrix	platisquama	20	-	-	0.87	4	-	-	-	-	-	[340]
Eurhopalothrix	seguensis	20	-	-	0.41	1	-	-	-	-	-	[340]
Eutetramorium	mocquerysi	6	41.11	18	-	-	-	-	-	-	-	[343]
Feroponera	ferox	1	-	-	0.61	8	-	-	-	-	-	[102, 183]
Forelius	pruinosus	114	10000	1	-	-	-	-	-	-	-	[61]
Forelophilus	overbecki	2	-	-	0.44	2	0.69	1	-	-	-	[344]

Forelophilus	philippinensis	2	-	-	0.8	5	-	-	-	-	-	[344]
Forelophilus	stefanschoedli	2	-	-	0.99	5	-	-	-	-	-	[344]
Formica	aquilonia	6671	500000	8	-	-	-	-	-	Yes	Yes	[70, 131, 345-347]
Formica	archboldi	6671	-	-	-	-	-	-	-	Yes	-	[348]
Formica	archibaldi	6671	500	1	-	-	-	-	-	-	-	[61]
Formica	argentea	6671	-	-	-	-	-	-	-	Yes	No	[131]
Formica	bradleyi	6671	-	-	-	-	-	-	-	-	Yes	[131]
Formica	bruni	6671	34059.67	6	1.24	322	1.43	2	-	Yes	-	[70, 349, 350]
Formica	candida	6671	2000	10	-	-	-	-	-	-	-	[346]
Formica	cinerea	6671	10000	8	-	-	-	-	Yes	Yes	-	[70, 346, 351, 352]
Formica	cunicularia	6671	1100	1	-	-	-	-	-	-	-	[19]
Formica	dakotensis	6671	-	-	-	-	-	-	-	-	No	[131]
Formica	exsecta	6671	1137.79	170	1.36	2	1.72	2	Yes	Yes	Yes	[70, 131, 346, 349, 350, 352-356]
Formica	exsectoides	6671	-	-	-	-	-	-	-	Yes	-	[70, 357]
Formica	fennica	6671	-	-	1.26	2	1.52	2	-	-	-	[349, 350]
Formica	foreli	6671	-	-	1.22	2	1.36	2	Yes	-	-	[349, 350, 353, 358]
Formica	forsslundi	6671	-	-	-	-	1.25	2	-	-	-	[349, 350]

Formica	fukaii	6671	-	-	1.41	2	1.71	2	-	-	-	[349, 350]
Formica	fusca	6671	807.52	26	-	-	1.45	137	-	Yes	Yes	[19, 346, 359-364]
Formica	gynocrates	6671	-	-	1.56	1	2.06	1	-	-	-	[365]
Formica	integra	6671	-	-	1.42	179	-	-	-	Yes	-	[366]
Formica	lemani	6671	150	1	-	-	-	-	-	Yes	-	[367, 368]
Formica	longipilosa	6671	-	-	1.05	20	-	-	-	-	-	[369]
Formica	lugubris	6671	23442	11	-	-	-	-	Yes	Yes	-	[70, 352, 370-372]
Formica	manchu	6671	-	-	1.28	2	-	-	-	-	-	[349, 350]
Formica	mesasiatica	6671	-	-	1.41	2	1.72	2	-	-	-	[349, 350]
Formica	montana	6671	-	-	-	-	-	-	-	Yes	-	[373]
Formica	neorufibarbis	6671	225	1	1.13	84	-	-	-	Yes	-	[374-376]
Formica	obscuripes	6671	56000000	1	1.48	241	-	-	-	-	-	[377, 378]
Formica	occulta	6671	-	-	-	-	-	-	-	No	No	[379]
Formica	opaciventris	6671	-	-	-	-	-	-	-	Yes	Yes	[131]
Formica	pallidefulva	6671	726.04	48	-	-	-	-	-	Yes	-	[70, 380]
Formica	paralugubris	6671	-	-	-	-	-	-	-	Yes	-	[70]
Formica	pergandei	6671	-	-	-	-	-	-	-	Yes	Yes	[131]
Formica	perpilosa	6671	-	-	-	-	-	-	Yes	-	-	[381]
Formica	picea	6671	-	-	-	-	-	-	-	Yes	-	[382]

Formica	pisarskii	6671	-	-	1.22	2	-	-	-	-	-	[349, 350]
Formica	podzolica	6671	-	-	1.19	30	-	-	-	Yes	Yes	[70, 383-385]
Formica	polyctena	6671	1233333.33	15	1.63	256	-	-	-	Yes	-	[70, 346, 366, 372, 386]
Formica	pratensis	6671	100000	8	-	-	-	-	-	Yes	-	[70, 346, 372]
Formica	pressilabris	6671	388.71	38	1.22	2	1.29	2	Yes	Yes	-	[70, 349, 350, 353, 356]
Formica	ravida	6671	-	-	-	-	-	-	-	Yes	-	[70]
Formica	rufa	6671	116466.67	15	1.52	1087	-	-	-	Yes	Yes	[70, 131, 346, 366, 372, 387-389]
Formica	sanguinea	6671	-	-	-	-	-	-	Yes	Yes	Yes	[70, 131, 353, 390]
Formica	schaufussi	6671	600	1	-	-	-	-	-	-	-	[61]
Formica	selysi	6671	-	-	1.29	2	1.89	2	-	Yes	Yes	[243, 391-395]
Formica	sp._cf._argentea	6671	-	-	-	-	-	-	-	Yes	Yes	[379]
Formica	subintegra	6671	-	-	-	-	-	-	-	-	Yes	[131]
Formica	subnitens	6671	20118	1	-	-	-	-	-	-	-	[372]
Formica	suecica	6671	-	-	1.33	2	1.28	2	-	-	-	[349, 350]

Formica	talbotae	6671	-	-	-	-	1.11	32	-	-	-	[396, 397]
Formica	truncorum	6671	22865.32	141	-	-	-	-	Yes	Yes	Yes	[70, 346, 352, 355, 372, 398-403]
Formica	uralensis	6671	-	-	-	-	-	-	-	Yes	-	[70]
Formica	yessensis	6671	3285496.91	140	1.31	119	-	-	-	Yes	Yes	[70, 118, 131, 372, 404-407]
Gesomyrmex	tobiasi	13	-	-	0.75	1	-	-	-	-	-	[408]
Gigantiops	destructor	26	57.35	42	-	-	-	-	-	No	-	[70, 175]
Gnamptogenys	bicolor	129	240	1	0.99	6	-	-	-	No	-	[409, 410]
Gnamptogenys	bisulca	129	-	-	0.75	41	-	-	-	-	-	[411, 412]
Gnamptogenys	caelata	129	-	-	0.38	3	-	-	-	-	-	[411]
Gnamptogenys	costata	129	60	1	-	-	-	-	-	Yes	-	[410]
Gnamptogenys	cribrata	129	27	7	0.51	15	0.58	3	No	Yes	-	[413]
Gnamptogenys	europaea	129	-	-	0.4	1	-	-	-	-	-	[414]
Gnamptogenys	flava	129	-	-	0.55	1	-	-	-	-	-	[415]
Gnamptogenys	hartmani	129	625	2	0.75	10	-	-	-	No	-	[411, 416]
Gnamptogenys	ingeborgae	129	15	1	0.76	15	0.6	5	-	No	-	[417]
Gnamptogenys	lineolata	129	-	-	1.09	10	-	-	-	-	-	[417]

Gnamptogenys	menadensis	129	139.06	124	-	-	-	-	-	Yes	-	[5, 81, 232, 264, 274, 410, 418-421]
Gnamptogenys	moelleri	129	98.31	16	-	-	-	-	-	Yes	-	[410, 422, 423]
Gnamptogenys	striatula	129	49.8	52	-	-	-	-	-	Yes	Yes	[232, 424-428]
Gnamptogenys	vriesi	129	-	-	2.2	1	2.15	1	-	-	-	[429]
Harpagoxenus	sublaevis	168	-	-	-	-	-	-	-	No	-	[430]
Harpegnathos	saltator	149	90.89	179	2.08	46	2.25	29	-	Yes	-	[81, 232, 266, 274, 410, 418, 431-438]
Heteroponera	relicta	35	80	1	-	-	-	-	-	No	-	[60]
Hupoponera	opaciceps	199	50	1	-	-	-	-	-	Yes	-	[322, 439, 440]
Hypoponera	abeillei	199	-	-	0.4	2	-	-	-	-	-	[441]
Hypoponera	angustata	199	-	-	0.31	28	-	-	-	-	-	[441]
Hypoponera	aprora	199	-	-	0.41	8	-	-	-	-	-	[441]
Hypoponera	austra	199	-	-	0.48	12	-	-	-	-	-	[441]
Hypoponera	blanda	199	-	-	0.36	15	-	-	-	-	-	[441]
Hypoponera	boerorum	199	-	-	0.58	6	-	-	-	-	-	[441]
Hypoponera	bulawayensis	199	-	-	0.41	2	-	-	-	-	-	[441]
Hypoponera	camerunensis	199	-	-	0.44	25	-	-	-	-	-	[441]
Hypoponera	coeca	199	-	-	0.4	75	-	-	-	-	-	[441]
Hypoponera	comis	199	-	-	0.49	8	-	-	-	-	-	[441]

Hypoponera	defessa	199	-	-	0.45	11	-	-	-	-	-	[441]
Hypoponera	dema	199	-	-	0.66	9	-	-	-	-	-	[441]
Hypoponera	dis	199	-	-	0.39	8	-	-	-	-	-	[441]
Hypoponera	dulcis	199	-	-	0.48	60	-	-	-	-	-	[441]
Hypoponera	eduardi	199	-	-	0.57	30	-	-	-	-	-	[441]
Hypoponera	exigua	199	-	-	0.53	10	-	-	-	-	-	[441]
Hypoponera	faex	199	-	-	0.72	1	-	-	-	-	-	[441]
Hypoponera	fatiga	199	-	-	0.38	59	-	-	-	-	-	[441]
Hypoponera	gibbinota	199	-	-	0.62	1	-	-	-	-	-	[441]
Hypoponera	hawkesi	199	-	-	0.48	4	-	-	-	-	-	[441]
Hypoponera	hebes	199	-	-	0.66	10	-	-	-	-	-	[441]
Hypoponera	ignavia	199	-	-	0.66	4	-	-	-	-	-	[441]
Hypoponera	importuna	199	-	-	0.55	14	-	-	-	-	-	[441]
Hypoponera	inaudax	199	-	-	0.35	60	-	-	-	-	-	[441]
Hypoponera	inexorata	199	50	1	-	-	-	-	-	-	-	[61]
Hypoponera	jeanneli	199	-	-	0.49	39	-	-	-	-	-	[441]
Hypoponera	jocosa	199	-	-	0.48	3	-	-	-	-	-	[441]
Hypoponera	juxta	199	-	-	0.43	1	-	-	-	-	-	[441]
Hypoponera	lassa	199	-	-	0.42	10	-	-	-	-	-	[441]
Hypoponera	lepida	199	-	-	0.43	30	-	-	-	-	-	[441]
Hypoponera	meridia	199	-	-	0.4	19	-	-	-	-	-	[441]
Hypoponera	mixta	199	-	-	0.58	12	-	-	-	-	-	[441]
Hypoponera	molesta	199	-	-	0.47	6	-	-	-	-	-	[441]
Hypoponera	natalensis	199	-	-	0.53	12	-	-	-	-	-	[441]
Hypoponera	nippona	199	-	-	-	-	-	-	-	No	-	[440]
Hypoponera	nivariana	199	-	-	0.46	1	-	-	-	-	-	[441]

Hypoponera	nubatama	199	-	-	0.56	191	0.61	60	-	Yes	-	[440, 442]
Hypoponera	obtunsa	199	-	-	0.4	5	-	-	-	-	-	[441]
Hypoponera	occidentalis	199	-	-	0.54	40	-	-	-	-	-	[441]
Hypoponera	odiosa	199	-	-	0.48	15	-	-	-	-	-	[441]
Hypoponera	opacior	199	17.93	119	-	-	-	-	-	Yes	-	[61, 322, 439, 440, 443-445]
Hypoponera	orba	199	-	-	0.4	2	-	-	-	-	-	[441]
Hypoponera	perparva	199	-	-	0.31	11	-	-	-	-	-	[441]
Hypoponera	producta	199	-	-	0.54	8	-	-	-	-	-	[441]
Hypoponera	pulchra	199	-	-	0.51	1	-	-	-	-	-	[441]
Hypoponera	punctatissima	199	29.18	52	0.52	85	0.54	23	-	Yes	Yes	[70, 440, 441, 446]
Hypoponera	quaestio	199	-	-	0.52	1	-	-	-	-	-	[441]
Hypoponera	ragusai	199	-	-	0.46	17	-	-	-	Yes	-	[439-441]
Hypoponera	regis	199	-	-	0.42	2	-	-	-	-	-	[441]
Hypoponera	sauteri	199	-	-	-	-	-	-	-	No	-	[440]
Hypoponera	segnis	199	-	-	0.55	20	-	-	-	-	-	[441]
Hypoponera	sinuosa	199	-	-	0.43	1	-	-	-	-	-	[441]
Hypoponera	sp	199	98	2	-	-	-	-	-	No	-	[60, 436]
Hypoponera	sp._(JFC*_11104)	199	69.39	18	-	-	-	-	-	Yes	-	[447]
Hypoponera	spei	199	-	-	0.68	20	-	-	-	-	-	[441]
Hypoponera	sulcatinasis	199	-	-	0.68	15	-	-	-	-	-	[441]
Hypoponera	surda	199	-	-	0.54	5	-	-	-	-	-	[441]
Hypoponera	tecta	199	-	-	0.48	1	-	-	-	-	-	[441]

Hypoponera	traegaordhi	199	-	-	0.43	1	-	-	-	-	-	[441]
Hypoponera	transvaalensis	199	-	-	0.74	1	-	-	-	-	-	[441]
Hypoponera	tristis	199	-	-	0.57	10	-	-	-	-	-	[441]
Hypoponera	ursa	199	-	-	0.51	1	-	-	-	-	-	[441]
Hypoponera	venusta	199	-	-	0.42	14	-	-	-	-	-	[441]
Iridomyrmex	purpureus	934	-	-	-	-	-	-	-	Yes	-	[70, 138]
Iridomyrmex	sanguineus	934	-	-	-	-	-	-	-	Yes	-	[70]
Iridomyrmex	viridiaeneus	934	-	-	-	-	-	-	-	Yes	-	[70]
Ishakidris	ascitaspis	2	-	-	0.53	1	-	-	-	-	-	[448]
Kalathomyrmex	emeryi	2	-	-	-	-	-	-	No	-	-	[449]
Kalathomyrmex	morschi	2	145	10	-	-	-	-	-	No	-	[450]
Kartidris	ashima	9	-	-	0.77	8	0.93	1	-	-	-	[451]
Labidus	coecus	121	-	-	-	-	-	-	-	No	-	[452]
Labidus	praedator	121	1500000	3	1.54	1	-	-	-	No	-	[19, 197, 452-454]
Lasius	alienatus	2018	-	-	-	-	-	-	-	No	-	[70]
Lasius	alienoflavus	2018	-	-	0.8	1	-	-	-	-	-	[455]
Lasius	alienus	2018	-	-	0.81	36	1.61	13	-	No	Yes	[131, 456, 457]
Lasius	atopus	2018	-	-	1.35	16	-	-	-	-	-	[458]
Lasius	bicornis	2018	-	-	1.06	1	1.25	1	-	-	-	[455]
Lasius	brunneus	2018	-	-	0.93	31	1.64	9	-	No	-	[456, 457]
Lasius	capitatus	2018	-	-	0.94	2	-	-	-	-	-	[459]
Lasius	carniolicus	2018	191.25	4	0.8	1	0.78	1	-	Yes	-	[455, 460]

Lasius	crinitus	2018	-	-	1.18	1	2	1	-	-	-	[455]
Lasius	draco	2018	-	-	1	1	-	-	-	-	-	[455]
Lasius	elevatus	2018	-	-	0.69	36	-	-	-	-	-	[461]
Lasius	emarginatus	2018	-	-	-	-	-	-	-	No	-	[456]
Lasius	flavus	2018	4385.78	27	-	-	-	-	-	Yes	Yes	[70, 131, 462-465]
Lasius	fuji	2018	-	-	1.02	2	1.42	1	-	-	-	[459]
Lasius	fuliginosus	2018	50000	1	1.39	112	1.58	7	-	-	-	[465, 466]
Lasius	hayashi	2018	-	-	0.77	2	1.74	1	-	-	-	[467]
Lasius	mikir	2018	-	-	1.16	1	-	-	-	-	-	[455]
Lasius	minutus	2018	-	-	-	-	-	-	-	Yes	-	[70]
Lasius	myops	2018	-	-	0.74	248	-	-	-	-	-	[468-471]
Lasius	myrmidon	2018	-	-	0.5	200	0.25	4	-	-	-	[468-471]
Lasius	neglectus	2018	-	-	0.75	63	1.34	17	-	Yes	No	[70, 456, 457, 466, 472]
Lasius	neoniger	2018	-	-	-	-	-	-	-	No	-	[70, 456]
Lasius	niger	2018	12799.85	10	1.06	2	1.89	2	-	No	Yes	[131, 153, 154, 455, 456, 465, 467, 473, 474]
Lasius	nipponensis	2018	-	-	1.4	115	1.47	10	-	-	-	[459, 466]
Lasius	nitidigaster	2018	-	-	-	-	1.6	17	-	-	-	[475]
Lasius	orientalis	2018	-	-	1.12	17	-	-	-	-	-	[459]

Lasius	plumopilosus	2018	-	-	0.93	6	0.97	8	-	-	-	[476]
Lasius	rabaudi	2018	-	-	-	-	1.72	1	-	-	-	[475]
Lasius	sakagami	2018	-	-	-	-	-	-	-	Yes	-	[70]
Lasius	sakagamii	2018	21898.27	105	0.68	2	1.71	1	-	Yes	-	[456, 465, 467]
Lasius	sp	2018	750	1	-	-	-	-	-	-	-	[477]
Lasius	spathepus	2018	-	-	-	-	1.02	1	-	-	-	[459]
Lasius	talpa	2018	-	-	0.77	1	1.34	1	-	-	-	[455]
Lasius	tercicus	2018	-	-	-	-	-	-	-	No	-	[472]
Lasius	viehmeyeri	2018	-	-	0.64	1	-	-	-	-	-	[478]
Lenomyrmex	colwelli	5	-	-	0.34	3	-	-	-	-	-	[40]
Lenomyrmex	costatus	5	-	-	0.32	1	-	-	-	-	-	[479]
Lenomyrmex	foveolatus	5	-	-	0.81	5	-	-	-	-	-	[479]
Lenomyrmex	inusitatus	5	-	-	0.32	34	0.33	2	-	-	-	[480]
Lenomyrmex	mandibularis	5	-	-	0.68	19	0.38	1	No	-	-	[479]
Lenomyrmex	wardi	5	-	-	0.29	7	0.29	1	-	-	-	[479]
Lepisiota	arabica	46	-	-	0.35	2	-	-	-	-	-	[74]
Lepisiota	arenaria	46	-	-	0.69	1	-	-	-	-	-	[137]
Lepisiota	bipartita	46	-	-	0.6	1	-	-	-	-	-	[137]
Lepisiota	canescens	46	-	-	0.61	3	-	-	-	-	-	[137]
Lepisiota	carbonaria	46	-	-	0.61	3	-	-	-	-	-	[137]
Lepisiota	dammama	46	-	-	0.31	1	-	-	-	-	-	[137]
Lepisiota	depilis	46	-	-	0.31	1	-	-	-	-	-	[137]
Lepisiota	dhofara	46	-	-	0.3	1	-	-	-	-	-	[137]
Lepisiota	erythraea	46	-	-	0.58	2	-	-	-	-	-	[137]
Lepisiota	gracilicornis	46	-	-	0.65	3	-	-	-	-	-	[137]

Lepisiota	harteni	46	-	-	0.29	1	-	-	-	-	-	[137]
Lepisiota	incisa	46	-	-	0.57	2	-	-	-	-	-	[137]
Lepisiota	karawajewi	46	-	-	0.61	1	-	-	-	-	-	[137]
Lepisiota	modesta	46	-	-	0.43	55	-	-	No	-	-	[481]
Lepisiota	nigra	46	-	-	0.64	2	-	-	-	-	-	[137]
Lepisiota	nigrescens	46	-	-	0.31	2	-	-	-	-	-	[137]
Lepisiota	obtusa	46	-	-	0.62	3	-	-	-	-	-	[137]
Lepisiota	opaciventris	46	-	-	0.65	3	-	-	-	Yes	-	[74, 137]
Lepisiota	riyadha	46	-	-	0.57	1	-	-	-	-	-	[137]
Lepisiota	sericea	46	-	-	0.32	1	-	-	-	-	-	[137]
Lepisiota	spinisquama	46	-	-	0.68	1	-	-	-	-	-	[137]
Lepisiota	validiuscula	46	-	-	0.61	1	-	-	-	-	-	[137]
Leptanilla	japonica	56	68.58	12	-	-	-	-	-	No	-	[62, 482, 483]
Leptanilla	ortunoi	56	-	-	0.23	1	-	-	-	-	-	[484]
Leptanilla	plutonia	56	-	-	0.25	1	-	-	-	-	-	[484]
Leptanilla	taiwanensis	56	-	-	0.25	10	0.31	1	-	-	-	[485]
Leptanilloides	caracola	13	-	-	0.31	1	-	-	-	-	-	[486]
Leptanilloides	improvisa	13	-	-	0.38	1	-	-	-	-	-	[101]
Leptanilloides	nubecula	13	-	-	-	-	0.58	4	-	-	-	[486]
Leptogenys	acutirostris	181	-	-	1.84	1	-	-	-	-	-	[487]
Leptogenys	amazonica	181	-	-	0.98	4	-	-	-	-	-	[488]
Leptogenys	amon	181	-	-	0.7	1	-	-	-	-	-	[487]
Leptogenys	amu	181	-	-	0.62	1	-	-	-	-	-	[488]
Leptogenys	angusta	181	-	-	1.34	1	-	-	-	-	-	[487]
Leptogenys	ankhesa	181	-	-	0.84	2	-	-	-	-	-	[487]

Leptogenys	antillana	181	-	-	0.69	3	-	-	-	-	-	[488]
Leptogenys	arcirostris	181	-	-	1.28	1	-	-	-	-	-	[487]
Leptogenys	arcuata	181	-	-	0.74	7	-	-	-	-	-	[488]
Leptogenys	arnoldi	181	-	-	0.98	6	-	-	-	-	-	[487]
Leptogenys	attenuata	181	-	-	0.98	8	-	-	-	-	-	[487]
Leptogenys	australis	181	-	-	0.6	2	-	-	-	-	-	[488]
Leptogenys	bifida	181	-	-	1.9	2	-	-	-	-	-	[488]
Leptogenys	bohlsi	181	-	-	1.11	10	-	-	-	-	-	[488]
Leptogenys	borneensis	181	7500	1	-	-	-	-	-	-	-	[489]
Leptogenys	bubastis	181	-	-	0.98	1	-	-	-	-	-	[487]
Leptogenys	buyssoni	181	-	-	1.06	1	-	-	-	-	-	[487]
Leptogenys	camerunensis	181	-	-	1.28	3	-	-	-	-	-	[487]
Leptogenys	carbonaria	181	-	-	1.45	3	-	-	-	-	-	[488]
Leptogenys	castanea	181	-	-	0.61	12	-	-	-	-	-	[487]
Leptogenys	chamela	181	-	-	2.1	1	-	-	-	-	-	[488]
Leptogenys	chinensis	181	367	1	-	-	-	-	-	-	-	[19]
Leptogenys	ciliata	181	-	-	1.18	1	-	-	-	-	-	[488]
Leptogenys	conradti	181	-	-	1.44	12	-	-	-	-	-	[487]
Leptogenys	consanguinea	181	-	-	0.76	6	0.73	1	-	-	-	[488]
Leptogenys	cordoba	181	-	-	0.64	4	-	-	-	-	-	[488]
Leptogenys	corniculans	181	-	-	0.53	1	-	-	-	-	-	[488]
Leptogenys	cracens	181	-	-	0.68	1	-	-	-	-	-	[488]
Leptogenys	crassinoda	181	-	-	0.97	2	-	-	-	-	-	[487]
Leptogenys	crudelis	181	-	-	0.79	5	0.96	1	-	-	-	[488]
Leptogenys	crustosa	181	-	-	1.23	4	-	-	-	-	-	[487]
Leptogenys	cryptica	181	-	-	0.45	4	-	-	-	-	-	[487]

Leptogenys	cuneata	181	-	-	1.1	5	-	-	-	-	-	[488]
Leptogenys	deborae	181	-	-	0.84	3	0.88	1	-	-	-	[488]
Leptogenys	diatra	181	-	-	0.62	1	-	-	-	-	-	[487]
Leptogenys	donisthorpei	181	-	-	1.22	6	-	-	-	-	-	[488]
Leptogenys	elegans	181	-	-	0.7	8	-	-	-	-	-	[487]
Leptogenys	elongata	181	-	-	1.06	8	1.12	2	-	-	-	[488]
Leptogenys	ergatogyna	181	-	-	1	4	1	1	-	-	-	[487]
Leptogenys	erugata	181	-	-	0.8	4	-	-	-	-	-	[488]
Leptogenys	erythraea	181	-	-	1.31	3	-	-	-	-	-	[487]
Leptogenys	excellens	181	-	-	0.72	2	-	-	-	-	-	[487]
Leptogenys	falcigera	181	-	-	1.39	8	-	-	-	-	-	[487]
Leptogenys	famelica	181	-	-	1.47	6	-	-	-	-	-	[488]
Leptogenys	ferrarii	181	-	-	0.65	5	-	-	-	-	-	[487]
Leptogenys	foraminosa	181	-	-	1.05	3	-	-	-	-	-	[488]
Leptogenys	foveonates	181	-	-	0.68	1	-	-	-	-	-	[488]
Leptogenys	furtiva	181	-	-	0.96	6	-	-	-	-	-	[487]
Leptogenys	gagates	181	-	-	0.75	4	-	-	-	-	-	[488]
Leptogenys	gaigei	181	-	-	0.84	7	-	-	-	-	-	[488]
Leptogenys	gatu	181	-	-	1.47	6	-	-	-	-	-	[488]
Leptogenys	glabra	181	-	-	0.7	1	-	-	-	-	-	[488]
Leptogenys	gorgona	181	-	-	0.49	3	-	-	-	-	-	[488]
Leptogenys	grandidieri	181	-	-	0.92	1	-	-	-	-	-	[487]
Leptogenys	guianensis	181	-	-	0.6	3	-	-	-	-	-	[488]
Leptogenys	guineesis	181	-	-	0.69	6	-	-	-	-	-	[487]
Leptogenys	havilandi	181	-	-	0.98	3	-	-	-	-	-	[487]
Leptogenys	honduriana	181	-	-	1.58	5	-	-	-	-	-	[488]

Leptogenys	honoria	181	-	-	0.76	1	-	-	-	-	-	[487]
Leptogenys	iheringi	181	-	-	0.74	2	0.85	1	-	-	-	[488]
Leptogenys	imperatrix	181	-	-	1.26	7	-	-	-	-	-	[488]
Leptogenys	ingens	181	-	-	2.28	8	-	-	-	-	-	[488]
Leptogenys	ixta	181	-	-	1.11	2	-	-	-	-	-	[488]
Leptogenys	jeanneli	181	-	-	1.72	1	-	-	-	-	-	[487]
Leptogenys	josephi	181	-	-	0.59	5	-	-	-	-	-	[488]
Leptogenys	khammouanensis	181	-	-	1.02	6	-	-	-	-	-	[490]
Leptogenys	khaura	181	-	-	0.39	2	-	-	-	-	-	[487]
Leptogenys	kiche	181	-	-	0.65	5	-	-	-	-	-	[488]
Leptogenys	kraepelini	181	14	1	-	-	-	-	-	Yes	-	[410]
Leptogenys	langi	181	-	-	0.55	5	0.7	1	-	-	-	[488]
Leptogenys	leiothorax	181	-	-	1.12	3	-	-	-	-	-	[487]
Leptogenys	linda	181	-	-	1.31	1	-	-	-	-	-	[488]
Leptogenys	linearis	181	-	-	0.36	5	-	-	-	-	-	[488]
Leptogenys	longiceps	181	-	-	0.71	7	-	-	-	-	-	[487]
Leptogenys	luederwaldti	181	-	-	0.81	5	1.21	1	-	-	-	[488]
Leptogenys	mactans	181	-	-	0.77	2	-	-	-	-	-	[487]
Leptogenys	manni	181	-	-	0.95	6	-	-	-	-	-	[488]
Leptogenys	mastax	181	-	-	0.68	7	0.69	4	-	-	-	[487]
Leptogenys	mavaca	181	-	-	0.51	2	-	-	-	-	-	[488]
Leptogenys	maxillosa	181	-	-	1.39	11	-	-	-	-	-	[487, 488]
Leptogenys	maya	181	-	-	2.05	5	1.85	1	-	-	-	[488]
Leptogenys	melena	181	-	-	0.59	4	-	-	-	-	-	[488]
Leptogenys	microps	181	-	-	0.49	2	-	-	-	-	-	[487]

Leptogenys	minima	181	-	-	0.57	1	-	-	-	-	-	[488]
Leptogenys	mjobergi	181	35	1	-	-	-	-	-	No	-	[60]
Leptogenys	montuosa	181	-	-	1.04	4	-	-	-	-	-	[488]
Leptogenys	nebra	181	-	-	1.2	1	-	-	-	-	-	[487]
Leptogenys	nigricans	181	-	-	0.98	5	-	-	-	-	-	[488]
Leptogenys	nitida	181	494.13	8	0.77	12	-	-	No	No	-	[60, 487, 491]
Leptogenys	nuserra	181	-	-	0.59	6	0.59	2	-	-	-	[487]
Leptogenys	oaxaca	181	-	-	1.85	1	-	-	-	-	-	[488]
Leptogenys	occidentalis	181	-	-	0.74	4	-	-	-	-	-	[487]
Leptogenys	orchidioides	181	-	-	0.8	4	0.81	2	-	Yes	-	[488]
Leptogenys	oswaldi	181	-	-	1.68	1	-	-	-	-	-	[487]
Leptogenys	panops	181	-	-	1.6	1	-	-	-	-	-	[488]
Leptogenys	paraensis	181	-	-	1.85	4	-	-	-	-	-	[488]
Leptogenys	parvula	181	11	1	-	-	-	-	-	No	-	[410]
Leptogenys	pavesii	181	-	-	1.34	6	-	-	-	-	-	[487]
Leptogenys	peninsularis	181	-	-	0.94	6	-	-	-	-	-	[488]
Leptogenys	peringueyi	181	-	-	0.9	1	-	-	-	-	-	[487]
Leptogenys	peruana	181	-	-	0.94	2	-	-	-	-	-	[488]
Leptogenys	peuqueti	181	30	1	-	-	-	-	-	Yes	-	[232]
Leptogenys	phylloba	181	-	-	1.15	2	-	-	-	-	-	[488]
Leptogenys	pinna	181	-	-	0.88	2	0.94	1	-	-	-	[488]
Leptogenys	piroskae	181	-	-	0.7	1	-	-	-	-	-	[487]
Leptogenys	pittieri	181	-	-	0.73	5	0.83	2	-	-	-	[488]
Leptogenys	princeps	181	-	-	0.9	1	-	-	-	-	-	[487]

Leptogenys	processionalis	181	20500	2	-	-	-	-	-	-	-	[489, 492]
Leptogenys	pubiceps_complex	181	-	-	1.32	9	-	-	-	-	-	[488]
Leptogenys	pucuna	181	-	-	0.83	1	-	-	-	-	-	[488]
Leptogenys	punctaticeps	181	-	-	1.06	7	-	-	-	-	-	[488]
Leptogenys	pusilla	181	-	-	0.49	4	-	-	-	-	-	[488]
Leptogenys	quadrata	181	-	-	0.61	4	-	-	-	-	-	[488]
Leptogenys	quiriguana	181	-	-	0.72	5	-	-	-	-	-	[488]
Leptogenys	quirozi	181	-	-	1.32	4	1.31	1	-	-	-	[488]
Leptogenys	rasila	181	-	-	0.6	2	-	-	-	-	-	[488]
Leptogenys	ravida	181	-	-	0.78	1	-	-	-	-	-	[487]
Leptogenys	reggae	181	-	-	0.8	1	-	-	-	-	-	[488]
Leptogenys	regis	181	-	-	1.65	2	-	-	-	-	-	[487]
Leptogenys	ridens	181	-	-	1.36	1	-	-	-	-	-	[487]
Leptogenys	ritae	181	4	1	0.55	8	0.57	2	-	Yes	-	[488]
Leptogenys	rufa	181	-	-	0.58	3	-	-	-	-	-	[488]
Leptogenys	santacruzi	181	-	-	1.04	3	-	-	-	-	-	[488]
Leptogenys	saussurei	181	-	-	1.98	1	-	-	-	-	-	[487]
Leptogenys	schwabi	181	135.75	2	1.15	12	-	-	-	Yes	-	[60, 232, 487]
Leptogenys	serrata	181	-	-	0.81	2	-	-	-	-	-	[488]
Leptogenys	sianka	181	-	-	1.35	4	-	-	-	-	-	[488]
Leptogenys	socorda	181	-	-	1.53	4	-	-	-	-	-	[488]
Leptogenys	sonora	181	-	-	1.45	1	-	-	-	-	-	[488]
Leptogenys	sp._1	181	21350	5	-	-	-	-	-	No	-	[493]
Leptogenys	sp._24	181	13	1	-	-	-	-	-	Yes	-	[232]

Leptogenys	spandax	181	-	-	0.98	1	-	-	-	-	-	[487]
Leptogenys	sterops	181	-	-	1.04	5	-	-	-	-	-	[487]
Leptogenys	strator	181	-	-	0.88	2	-	-	-	-	-	[487]
Leptogenys	striatidens	181	-	-	0.92	1	-	-	-	-	-	[487]
Leptogenys	stuhlmanni	181	-	-	1.39	6	-	-	-	-	-	[487]
Leptogenys	stygia	181	-	-	0.5	7	-	-	-	-	-	[487]
Leptogenys	sulcinoda	181	-	-	0.72	1	-	-	-	-	-	[487]
Leptogenys	tama	181	-	-	1.04	1	-	-	-	-	-	[488]
Leptogenys	terroni	181	-	-	1.18	1	-	-	-	-	-	[487]
Leptogenys	testacea	181	-	-	0.61	8	-	-	-	-	-	[487]
Leptogenys	tiobil	181	-	-	1.48	5	-	-	-	-	-	[488]
Leptogenys	titan	181	-	-	2.02	1	-	-	-	-	-	[487]
Leptogenys	toxeres	181	-	-	0.85	3	0.81	1	-	-	-	[488]
Leptogenys	trilobata	181	-	-	0.8	2	-	-	-	-	-	[487]
Leptogenys	truncatirostris	181	-	-	1.66	1	-	-	-	-	-	[487]
Leptogenys	unistimulosa	181	-	-	1.5	10	-	-	-	-	-	[488]
Leptogenys	vindicis	181	-	-	1.14	1	-	-	-	-	-	[487]
Leptogenys	vogeli	181	-	-	0.8	2	-	-	-	-	-	[488]
Leptogenys	volcanica	181	-	-	0.69	5	-	-	-	-	-	[488]
Leptogenys	wheeleri	181	-	-	1.37	5	1.11	1	-	-	-	[488]
Leptogenys	yocota	181	-	-	0.86	4	0.94	2	-	-	-	[488]
Leptogenys	zapyxis	181	-	-	1.11	7	-	-	-	-	-	[487]
Leptothorax	acervorum	1052	78.04	264	-	-	-	-	-	Yes	-	[158, 273, 494-496]
Leptothorax	gredleri	1052	-	-	0.32	12	0.32	1	-	-	-	[497]

Leptothorax	muscorum	1052	300	1	-	-	-	-	-	-	-	[19]
Leptothorax	paraxenus	1052	-	-	-	-	0.35	3	-	-	-	[498]
Leptothorax	scamni	1052	-	-	0.53	2	0.37	1	-	-	-	[499]
Leptothorax	sp.	1052	-	-	-	-	-	-	-	Yes	-	[138]
Leptothorax	wilsoni	1052	-	-	-	-	0.48	4	-	Yes	-	[500]
Linepithema	humile	830	15000	1	-	-	-	-	-	Yes	-	[19, 70]
Liometopum	apiculatum	87	-	-	-	-	-	-	-	No	-	[70]
Liomyrmex	gestroi	7	-	-	0.74	60	1.31	5	-	-	-	[501, 502]
Lophomyrmex	bedoti	22	50	1	-	-	-	-	-	-	-	[283]
Lophomyrmex	terraceensis	22	-	-	0.7	2	-	-	-	-	-	[503]
Manica	rubida	235	-	-	-	-	-	-	-	Yes	-	[504]
Mayriella	occidua	15	-	-	0.22	1	-	-	-	-	-	[335]
Megalomyrmex	acauna	46	-	-	1.52	38	-	-	No	-	-	[505]
Megalomyrmex	adamsae	46	-	-	0.79	7	0.98	3	-	-	-	[506]
Megalomyrmex	ayri	46	-	-	0.76	72	-	-	No	-	-	[505]
Megalomyrmex	balzani	46	-	-	1.87	102	-	-	No	-	-	[505]
Megalomyrmex	caete	46	-	-	0.82	12	-	-	No	-	-	[505]
Megalomyrmex	cuatiara	46	-	-	0.52	38	-	-	No	-	-	[505]
Megalomyrmex	cupecuara	46	-	-	1.1	10	-	-	No	-	-	[505]
Megalomyrmex	cyendyra	46	-	-	1.18	26	-	-	No	-	-	[505]
Megalomyrmex	drifti	46	-	-	0.46	43	-	-	No	-	-	[505, 506]
Megalomyrmex	emeryi	46	-	-	1.3	2	-	-	No	-	-	[505]
Megalomyrmex	foreli	46	-	-	1.76	90	-	-	No	-	-	[505]
Megalomyrmex	glaesarius	46	-	-	1.41	70	-	-	No	-	-	[505]

Megalomyrmex	gnomus	46	-	-	0.5	6	-	-	No	-	-	[505]
Megalomyrmex	goeldii	46	350	5	0.81	62	-	-	No	Yes	-	[505]
Megalomyrmex	iheringi	46	260	2	1.06	62	-	-	No	No	-	[505]
Megalomyrmex	incisus	46	-	-	0.75	42	-	-	No	-	-	[505]
Megalomyrmex	leoninus	46	-	-	1.68	82	-	-	No	-	-	[505]
Megalomyrmex	miri	46	-	-	0.36	6	-	-	No	-	-	[505]
Megalomyrmex	modestus	46	-	-	0.86	28	-	-	No	-	-	[505]
Megalomyrmex	mondabora	46	-	-	0.73	21	0.96	3	No	-	-	[505, 506]
Megalomyrmex	mondaboroides	46	-	-	0.62	7	0.41	1	-	-	-	[506]
Megalomyrmex	myops	46	-	-	0.68	52	-	-	No	-	-	[505]
Megalomyrmex	nocarina	46	-	-	0.68	9	-	-	-	-	-	[506]
Megalomyrmex	pacova	46	-	-	1.35	16	-	-	No	-	-	[505]
Megalomyrmex	piriana	46	-	-	0.47	6	-	-	No	-	-	[505]
Megalomyrmex	poatan	46	-	-	0.53	2	-	-	No	-	-	[505]
Megalomyrmex	pusillus	46	-	-	0.73	62	-	-	No	-	-	[505]
Megalomyrmex	reina	46	-	-	-	-	0.42	2	-	-	-	[506]
Megalomyrmex	silvestrii	46	39.5	3	0.66	62	-	-	No	Yes	-	[411, 505, 506]
Megalomyrmex	staudingeri	46	-	-	2.06	18	-	-	No	-	-	[505]
Megalomyrmex	symmetochus	46	-	-	0.69	97	-	-	No	-	-	[505, 506]
Megalomyrmex	tasyba	46	-	-	0.68	6	-	-	No	-	-	[505]
Megalomyrmex	timbira	46	-	-	1.51	6	-	-	No	-	-	[505]
Megalomyrmex	wallacei	46	-	-	1.01	66	-	-	No	-	-	[505]
Megalomyrmex	wettereri	46	-	-	0.26	1	-	-	-	-	-	[506]

Megalomyrmex	weyrauchi	46	-	-	1.06	56	-	-	No	-	-	[505]
Melissotarsus	beccarii	15	-	-	0.62	1	0.66	1	-	-	-	[507]
Melophorus	anderseni	157	-	-	0.98	8	1.04	1	-	-	-	[508]
Melophorus	bagoti	157	1400	1	2.6	18	-	-	-	-	-	[509, 510]
Melophorus	majeri	157	-	-	0.51	10	-	-	-	-	-	[508]
Melophorus	turneri	157	230.4	5	-	-	-	-	-	No	-	[511]
Meranoplus	bellii	73	-	-	1.19	14	-	-	-	-	-	[512]
Meranoplus	bicolor	73	-	-	0.95	16	-	-	-	-	-	[512]
Meranoplus	biliran	73	-	-	0.82	8	-	-	-	-	-	[512]
Meranoplus	boltoni	73	-	-	0.39	3	-	-	-	-	-	[512]
Meranoplus	borneensis	73	-	-	0.69	14	-	-	-	-	-	[512]
Meranoplus	castaneus	73	-	-	1.12	10	-	-	-	-	-	[512]
Meranoplus	curvispina	73	-	-	0.8	41	0.94	3	-	-	-	[513]
Meranoplus	laeviventris	73	-	-	1	15	-	-	-	-	-	[512]
Meranoplus	levis	73	-	-	0.99	2	-	-	-	-	-	[512]
Meranoplus	loebli	73	-	-	0.73	15	-	-	-	-	-	[512]
Meranoplus	malaysianus	73	-	-	0.66	16	0.35	3	-	-	-	[512]
Meranoplus	montanus	73	-	-	0.4	2	0.42	1	-	-	-	[512]
Meranoplus	mucronatus	73	-	-	1.58	20	-	-	-	-	-	[512]
Meranoplus	nepalensis	73	-	-	0.75	21	0.63	1	-	-	-	[512]
Meranoplus	puryi	73	-	-	0.79	14	0.95	4	-	-	-	[513]
Meranoplus	rothneyi	73	-	-	0.7	10	-	-	-	-	-	[512]
Mesostruma	spinosa	13	-	-	0.28	1	-	-	-	-	-	[335]
Messor	barbarus	753	850	12	-	-	-	-	-	Yes	-	[70, 514]
Messor	bouvieri	753	-	-	-	-	-	-	Yes	-	-	[515]

Messor	buettikeri	753	-	-	0.65	1	0.95	1	-	-	-	[74]
Messor	minor	753	-	-	-	-	-	-	-	No	-	[516]
Messor	pergandei	753	-	-	1.39	1	1.8	130	Yes	Yes	Yes	[33, 517-521]
Messor	sancta	753	3500	1	-	-	-	-	-	-	-	[19]
Messor	structor	753	20	1	-	-	-	-	-	Yes	-	[522]
Messor	wasmanni	753	-	-	-	-	-	-	-	No	-	[516]
Metapone	emersoni	14	-	-	0.63	1	-	-	-	-	-	[523]
Metapone	madagascarica	14	27.77	13	0.54	1	0.56	1	-	Yes	-	[523, 524]
Metapone	nicobarensis	14	-	-	0.53	1	0.46	2	-	-	-	[502]
Metapone	truki	14	-	-	0.35	1	-	-	-	-	-	[525]
Metapone	vincimus	14	-	-	0.95	16	0.49	1	-	-	-	[526]
Monomorium	destructor	1062	-	-	-	-	-	-	-	Yes	-	[70]
Monomorium	floricola	1062	-	-	-	-	-	-	-	Yes	-	[70]
Monomorium	intrudens	1062	4291.5	3	-	-	-	-	-	Yes	-	[6]
Monomorium	pharaonis	1062	2071.95	41	-	-	-	-	-	Yes	-	[70, 527]
Monomorium	triviale	1062	132	74	-	-	-	-	-	Yes	-	[6]
Monomorium	viride	1062	10000	1	-	-	-	-	-	-	-	[61]
Mycetagroicus	inflatus	6	-	-	0.36	2	-	-	-	-	-	[528]
Mycetarotes	acutus	25	25	6	0.87	4	-	-	No	No	-	[529, 530]
Mycetarotes	carinatus	25	50	9	0.77	9	0.44	2	No	-	-	[529, 531]
Mycetarotes	parallelus	25	105.82	17	0.79	8	0.52	1	No	No	-	[529, 530]

Mycetarotes	senticosus	25	-	-	0.9	4	-	-	No	-	-	[529]
Mycetophylax	conformis	16	173	7	-	-	-	-	No	No	-	[449, 450]
Mycetophylax	morschi	16	-	-	-	-	-	-	No	-	-	[449]
Mycetophylax	simplex	16	251.19	25	-	-	-	-	No	Yes	-	[449, 450, 532]
Mycetosoritis	vinsoni	8	-	-	0.32	1	-	-	-	-	-	[533]
Mycocepurus	curvispinosus	57	-	-	0.73	5	-	-	-	-	-	[533]
Mycocepurus	goeldii	57	612.8	4	-	-	-	-	-	Yes	-	[534]
Mycocepurus	smithii	57	45.39	192	0.35	1	0.45	1	-	Yes	No	[534-537]
Myopias	emeryi	109	35	1	-	-	-	-	-	No	-	[410]
Myopias	maligna	109	60	1	-	-	-	-	-	Yes	-	[410]
Myrmecia	brevinoda	415	1682.5	2	-	-	-	-	-	Yes	Yes	[538-540]
Myrmecia	desertorum	415	302.5	2	-	-	-	-	-	Yes	-	[538]
Myrmecia	dispar	415	36	1	-	-	-	-	-	No	-	[538]
Myrmecia	dixoni	415	14	1	-	-	-	-	-	No	-	[538]
Myrmecia	forceps	415	112	1	-	-	-	-	-	No	-	[538]
Myrmecia	forficata	415	210	1	-	-	-	-	-	No	-	[538]
Myrmecia	froggatti	415	17	1	2.49	16	-	-	-	No	-	[538, 541]
Myrmecia	fulvipes	415	122	1	-	-	-	-	-	No	-	[538]
Myrmecia	gulosa	415	918.95	19	-	-	-	-	-	Yes	No	[163, 431, 538, 542]
Myrmecia	gulose	415	900	1	-	-	-	-	-	-	-	[19]
Myrmecia	inquilina	415	-	-	-	-	3.2	1	-	-	-	[541]

Myrmecia	michaelseni	415	17	1	-	-	-	-	-	No	-	[538]
Myrmecia	nigriceps	415	158.5	2	-	-	-	-	-	No	-	[538]
Myrmecia	nigrocincta	415	455	1	-	-	-	-	-	No	-	[538]
Myrmecia	pavida	415	-	-	-	-	-	-	-	Yes	Yes	[543]
Myrmecia	picta	415	32	1	-	-	-	-	-	No	-	[538]
Myrmecia	piliventris	415	113	1	-	-	-	-	-	No	-	[538]
Myrmecia	pilosula	415	359.2	5	-	-	-	-	-	Yes	Yes	[538, 544, 545]
Myrmecia	pyriformis	415	796	2	-	-	-	-	-	-	Yes	[538, 546]
Myrmecia	simillima	415	137	3	2.5	780	-	-	-	No	-	[538, 541]
Myrmecia	tarsata	415	1125	1	-	-	-	-	-	No	-	[538]
Myrmecia	tepperi	415	12	1	-	-	-	-	-	No	-	[538]
Myrmecia	varians	415	84.53	15	2.27	584	-	-	-	Yes	-	[538, 541]
Myrmecina	alpina	124	-	-	0.75	5	-	-	-	-	-	[547]
Myrmecina	americana	124	50	1	-	-	-	-	-	-	-	[61]
Myrmecina	atlantis	124	-	-	0.71	13	-	-	-	-	-	[548]
Myrmecina	australis	124	-	-	0.76	8	-	-	-	-	-	[547]
Myrmecina	difficulta	124	-	-	0.73	24	-	-	-	-	-	[547]
Myrmecina	eruga	124	-	-	0.75	10	-	-	-	-	-	[547]
Myrmecina	graminicola	124	36.68	235	0.85	263	0.93	52	Yes	Yes	-	[548-553]
Myrmecina	inaequala	124	-	-	0.7	8	-	-	-	-	-	[547]
Myrmecina	mellonii	124	-	-	0.69	34	-	-	-	-	-	[548]

Myrmecina	nipponica	124	34.38	40	0.89	348	0.9	325	Yes	Yes	No	[62, 554-557]
Myrmecina	pauca	124	-	-	0.6	6	1.09	3	-	-	-	[477]
Myrmecina	pumila	124	-	-	0.53	8	-	-	-	-	-	[547]
Myrmecina	rugosa	124	-	-	0.33	1	-	-	-	-	-	[547]
Myrmecina	sauteri	124	-	-	0.6	7	-	-	No	-	-	[3]
Myrmecina	sicula	124	-	-	0.66	2	-	-	-	-	-	[548]
Myrmecina	silvalaeva	124	-	-	0.58	3	-	-	-	-	-	[547]
Myrmecina	silvampla	124	-	-	0.41	1	-	-	-	-	-	[547]
Myrmecina	silvangula	124	-	-	0.58	6	-	-	-	-	-	[547]
Myrmecina	silvarugosa	124	-	-	0.63	4	-	-	-	-	-	[547]
Myrmecina	silvatransversa	124	-	-	0.3	1	-	-	-	-	-	[547]
Myrmecina	strigis	124	-	-	0.87	7	-	-	No	-	-	[3]
Myrmecina	taiwana	124	-	-	0.6	17	-	-	No	-	-	[3]
Myrmecina	wesselensis	124	-	-	0.34	1	-	-	-	-	-	[547]
Myrmecocystus	christineae	116	-	-	1.02	725	1.72	16	-	-	-	[558]
Myrmecocystus	depilis	116	-	-	-	-	-	-	-	No	No	[559]
Myrmecocystus	mendax	116	1991	1	-	-	-	-	-	-	-	[560]
Myrmecocystus	mexicanus	116	2506.33	3	-	-	-	-	-	Yes	-	[561, 562]
Myrmecocystus	mimicus	116	-	-	-	-	-	-	-	Yes	Yes	[559]
Myrmecocystus	snellingi	116	-	-	0.89	213	1.39	8	-	-	-	[558]
Myrmecocystus	sp.	116	-	-	-	-	-	-	-	No	-	[562]
Myrmelachista	catharinae	61	263.08	25	-	-	-	-	-	No	-	[563]
Myrmelachista	cooperi	61	-	-	0.8	6	0.56	2	-	-	-	[564, 565]

Myrmelachista	flavocetea	61	-	-	0.64	10	0.97	26	-	No	-	[564, 565]
Myrmelachista	flavoguarea	61	-	-	0.7	10	1.21	10	-	No	-	[564, 565]
Myrmelachista	haberi	61	-	-	0.58	8	0.92	14	-	No	-	[564, 565]
Myrmelachista	joycei	61	-	-	0.61	10	0.92	24	-	Yes	-	[564, 565]
Myrmelachista	kraatzii	61	-	-	-	-	-	-	-	No	-	[564, 565]
Myrmelachista	lauroatlantica	61	-	-	0.5	10	0.85	22	-	Yes	-	[564, 565]
Myrmelachista	lauropacifica	61	-	-	0.48	8	0.76	8	-	-	-	[564, 565]
Myrmelachista	longiceps	61	-	-	0.64	10	0.93	22	-	Yes	-	[564, 565]
Myrmelachista	meganaranja	61	-	-	0.91	10	1.32	4	-	-	-	[564, 565]
Myrmelachista	mexicana	61	-	-	0.41	10	0.48	4	-	Yes	-	[564, 565]
Myrmelachista	nigrocotea	61	-	-	0.59	10	1.18	18	-	Yes	-	[564, 565]
Myrmelachista	nodigera	61	45.25	4	-	-	-	-	-	No	-	[563]
Myrmelachista	osa	61	-	-	0.5	6	0.98	6	-	-	-	[564, 565]
Myrmelachista	plebecula	61	-	-	0.47	10	0.65	18	-	-	-	[564, 565]

Myrmelachista	ruszkii	61	111.53	58	-	-	-	-	-	No	-	[563]
Myrmelachista	schumanni	61	1500000	1	-	-	-	-	-	Yes	-	[566]
Myrmelachista	zeledoni	61	-	-	0.61	10	0.89	10	-	-	-	[564, 565]
Myrmica	adrijae	1727	-	-	0.99	6	-	-	-	-	-	[567]
Myrmica	alperti	1727	-	-	1.26	24	-	-	-	-	-	[568]
Myrmica	anatolica	1727	-	-	0.93	32	1.06	8	-	-	-	[569]
Myrmica	angulata	1727	-	-	-	-	0.72	1	-	-	-	[570]
Myrmica	arisana	1727	-	-	1.03	5	-	-	-	-	-	[571]
Myrmica	bibikoffi	1727	-	-	1.05	5	1.28	2	-	-	-	[572]
Myrmica	curiosa	1727	-	-	0.97	3	1.19	2	-	-	-	[573]
Myrmica	elmesi	1727	-	-	0.84	13	-	-	-	-	-	[574]
Myrmica	ereptrix	1727	-	-	-	-	0.54	2	-	-	-	[572, 575]
Myrmica	formosae	1727	-	-	1.11	8	-	-	-	-	-	[571]
Myrmica	hirsuta	1727	15.25	4	0.68	6	0.96	431	-	Yes	-	[572, 576, 577]
Myrmica	hyungokae	1727	-	-	0.89	14	-	-	-	-	-	[578]
Myrmica	indica	1727	-	-	1.17	59	-	-	-	-	-	[568]
Myrmica	jennyae	1727	-	-	0.82	30	0.95	19	-	-	-	[569]
Myrmica	jessensis	1727	-	-	1.01	15	-	-	-	-	-	[578]
Myrmica	kabylica	1727	-	-	-	-	0.38	1	-	-	-	[572]
Myrmica	karavajevi	1727	-	-	-	-	0.79	31	-	-	-	[572]
Myrmica	koreana	1727	-	-	0.99	29	-	-	-	-	-	[578]
Myrmica	kotokui	1727	362.12	297	1.12	4	1.24	4	No	Yes	-	[579-581]
Myrmica	laurae	1727	-	-	-	-	0.96	14	-	-	-	[572]

Myrmica	lemasnei	1727	-	-	-	-	0.84	3	-	-	-	[572]
Myrmica	limanica	1727	836	200	-	-	-	-	-	Yes	-	[582]
Myrmica	lobicornis	1727	275	48	-	-	-	-	-	Yes	-	[583]
Myrmica	longisculpta	1727	-	-	0.74	7	-	-	-	-	-	[584]
Myrmica	mirabilis	1727	-	-	1.64	11	-	-	-	-	-	[571]
Myrmica	mixta	1727	-	-	-	-	0.51	1	-	-	-	[573]
Myrmica	myrmicoxena	1727	-	-	-	-	0.96	6	-	-	-	[572]
Myrmica	nefaria	1727	-	-	0.83	5	1	64	-	-	-	[567]
Myrmica	pararitae	1727	-	-	1.18	21	1.32	10	-	-	-	[573]
Myrmica	poldii	1727	-	-	0.54	1	-	-	-	-	-	[573]
Myrmica	polyglypta	1727	-	-	1.02	21	-	-	-	-	-	[573]
Myrmica	pseudorugosa	1727	-	-	0.72	4	-	-	-	-	-	[567]
Myrmica	radchenkoi	1727	-	-	0.75	4	0.49	1	-	-	-	[585]
Myrmica	rubra	1727	1133.66	510	-	-	0.9	15	-	Yes	-	[60, 572, 582, 586-591]
Myrmica	ruginodis	1727	497.28	230	-	-	-	-	-	Yes	Yes	[70, 583, 588, 592, 593]
Myrmica	sabuleti	1727	419.72	214	0.98	214	1.19	216	-	Yes	-	[576, 577, 587, 588, 594, 595]
Myrmica	salina	1727	-	-	1	33	1.1	2	-	-	-	[596]
Myrmica	scabrinodis	1727	317.45	75	0.89	49	1.09	183	-	Yes	-	[576, 587, 588, 595]

Myrmica	schencki	1727	-	-	1.08	26	-	-	-	Yes	-	[578, 588]
Myrmica	schoedli	1727	-	-	0.86	6	0.57	1	-	-	-	[570]
Myrmica	serica	1727	500	1	1.16	9	-	-	-	-	-	[570, 571]
Myrmica	sinoschencki	1727	-	-	0.84	3	-	-	-	-	-	[573]
Myrmica	sulcinodis	1727	467.39	195	-	-	0.62	22	-	Yes	Yes	[70, 243, 588, 597, 598]
Myrmica	symbiotica	1727	-	-	0.48	1	-	-	-	-	-	[572]
Myrmica	tahoensis	1727	447	58	-	-	-	-	-	Yes	-	[599]
Myrmica	tamarae	1727	-	-	0.89	16	0.54	1	-	-	-	[569]
Myrmica	tulinae	1727	-	-	0.96	30	1.15	8	-	-	-	[569]
Myrmica	weberi	1727	-	-	0.92	30	0.49	1	-	-	-	[568]
Myrmica	weii	1727	-	-	0.73	1	-	-	-	-	-	[573]
Myrmicaria	brunnea	110	7500	2	-	-	-	-	-	-	-	[600]
Myrmicaria	eumenoides	110	20000	1	-	-	-	-	-	-	-	[19]
Myrmicaria	natalensis	110	-	-	-	-	-	-	-	Yes	-	[70]
Myrmicaria	opaciventris	110	1531.58	98	1.54	5821	2.65	30	Yes	Yes	-	[70, 601, 602]
Myrmicocrypta	bucki	34	-	-	0.62	15	-	-	-	-	-	[603]
Myrmicocrypta	camargoi	34	-	-	0.72	11	1.09	2	-	-	-	[603]
Myrmicocrypta	ednaella	34	60.34	35	-	-	-	-	-	No	Yes	[18, 22, 227]
Myrmicocrypta	erectapilosa	34	-	-	0.54	5	0.36	1	-	-	-	[603]
Myrmotera	barbouri	14	8	1	0.64	1	-	-	No	-	-	[604, 605]

Myrmoteras	arcoelinae	14	-	-	0.52	1	-	-	-	-	-	[605]
Myrmoteras	bakeri	14	-	-	0.88	3	-	-	-	-	-	[605]
Myrmoteras	baslerorum	14	-	-	0.56	1	-	-	-	-	-	[605]
Myrmoteras	brigitteae	14	-	-	0.51	1	-	-	-	-	-	[605]
Myrmoteras	chondrogastrum	14	-	-	0.51	1	-	-	-	-	-	[605]
Myrmoteras	cuneonodum	14	-	-	0.52	1	-	-	-	-	-	[606]
Myrmoteras	danieli	14	-	-	0.54	1	-	-	-	-	-	[605]
Myrmoteras	diastematum	14	-	-	0.54	1	-	-	-	-	-	[605]
Myrmoteras	donisthorpei	14	-	-	0.87	1	-	-	-	-	-	[605]
Myrmoteras	elfeorum	14	-	-	0.47	1	-	-	-	-	-	[605]
Myrmoteras	estrudae	14	-	-	0.5	1	-	-	-	-	-	[605]
Myrmoteras	glabrum	14	-	-	0.84	20	0.46	1	-	-	-	[44]
Myrmoteras	iriodum	14	-	-	1.17	6	-	-	-	-	-	[605]
Myrmoteras	ivani	14	-	-	0.41	1	-	-	-	-	-	[605]
Myrmoteras	karnyi	14	-	-	-	-	-	-	No	-	-	[604]
Myrmoteras	marianneae	14	-	-	0.52	1	-	-	-	-	-	[605]
Myrmoteras	maudeae	14	-	-	0.64	1	-	-	-	-	-	[605]
Myrmoteras	mcarthuri	14	-	-	0.92	11	-	-	-	-	-	[44]
Myrmoteras	mjoebergi	14	-	-	1.05	3	-	-	No	-	-	[604, 605]
Myrmoteras	morowali	14	-	-	0.81	5	-	-	-	-	-	[605]
Myrmoteras	nicolettae	14	-	-	0.53	1	-	-	-	-	-	[605]
Myrmoteras	toro	14	22	1	-	-	-	-	-	-	-	[19]
Myrmoteras	williamsi	14	-	-	-	-	-	-	No	-	-	[604]
Mystrium	sp.	31	14.5	1	-	-	-	-	-	-	-	[163]

Neivamyrmex	carolinensis	153	30000	1	-	-	-	-	-	Yes	Yes	[61, 189, 452, 607]
Neivamyrmex	chamelensis	153	-	-	1.1	1	1.6	1	-	-	-	[608]
Neivamyrmex	crassiscapus	153	-	-	1.75	1	-	-	-	-	-	[609]
Neivamyrmex	cristatus	153	-	-	0.86	1	-	-	-	No	-	[197, 452]
Neivamyrmex	graciellae	153	-	-	-	-	2.3	1	-	-	-	[610]
Neivamyrmex	harrisii	153	100000	1	-	-	-	-	-	-	Yes	[47]
Neivamyrmex	hetschkoi	153	-	-	-	-	-	-	-	Yes	-	[452]
Neivamyrmex	moseri	153	-	-	0.57	25	-	-	-	No	-	[452, 533]
Neivamyrmex	nigrescens	153	48050.88	17	-	-	-	-	Yes	No	Yes	[47, 57, 452, 611, 612]
Neivamyrmex	opacithorax	153	-	-	-	-	-	-	-	No	-	[452]
Neivamyrmex	opcaithorax	153	30000	1	-	-	-	-	-	-	-	[61]
Neivamyrmex	pauxillus	153	-	-	-	-	-	-	-	No	-	[452]
Neivamyrmex	pilosus	153	-	-	-	-	-	-	-	No	-	[452]
Neivamyrmex	rugulosus	153	-	-	-	-	-	-	-	No	-	[452]
Neivamyrmex	texanus	153	30000	1	-	-	-	-	-	-	-	[61]
Nesomyrmex	angulatus	15	-	-	0.65	81	-	-	-	-	-	[613]
Nesomyrmex	antoinetteae	15	-	-	0.84	18	-	-	-	-	-	[613]
Nesomyrmex	braunsi	15	-	-	1.09	30	-	-	-	-	-	[613, 614]
Nesomyrmex	cederbergensis	15	-	-	0.66	1	-	-	-	-	-	[613]
Nesomyrmex	denticulatus	15	-	-	0.71	61	-	-	-	-	-	[613]

Nesomyrmex	entabeni	15	-	-	0.55	10	-	-	-	-	-	[613]
Nesomyrmex	ezantsi	15	-	-	0.65	3	-	-	-	-	-	[613]
Nesomyrmex	inye	15	-	-	0.6	1	-	-	-	-	-	[613]
Nesomyrmex	karooensis	15	-	-	0.64	19	-	-	-	-	-	[613]
Nesomyrmex	koebergensis	15	-	-	0.7	7	-	-	-	-	-	[613]
Nesomyrmex	larsenae	15	-	-	0.56	3	-	-	-	-	-	[613]
Nesomyrmex	mcgregori	15	-	-	0.93	4	-	-	-	-	-	[613]
Nesomyrmex	nanniae	15	-	-	0.56	7	-	-	-	-	-	[613]
Nesomyrmex	njengelanga	15	-	-	0.56	5	-	-	-	-	-	[613]
Nesomyrmex	ruani	15	-	-	0.68	4	-	-	-	-	-	[613]
Nesomyrmex	saasveldensis	15	-	-	0.85	15	-	-	-	-	-	[613]
Nesomyrmex	simoni	15	-	-	0.85	3	-	-	-	-	-	[613]
Nesomyrmex	stramineus	15	-	-	0.52	1	-	-	-	-	-	[613]
Nesomyrmex	tshiguvhoae	15	-	-	0.69	31	-	-	-	-	-	[613]
Nesomyrmex	vannoorti	15	-	-	0.54	46	-	-	-	-	-	[613]
Nesomyrmex	vargasi	15	32	1	0.36	1	-	-	-	No	-	[40]
Nomamyrmex	esenbeckii	32	1000000	1	4.4	55	-	-	Yes	-	-	[197, 615, 616]
Nothomyrmecia	macrops	50	36.64	66	-	-	-	-	-	No	Yes	[168, 431, 617-619]
Nylanderia	arenivaga	79	-	-	0.56	62	-	-	-	-	-	[620]
Nylanderia	austrococcidus	79	-	-	0.52	65	-	-	-	-	-	[620]
Nylanderia	bourbonica	79	-	-	0.66	40	-	-	-	Yes	-	[70, 620]
Nylanderia	bruesii	79	-	-	0.62	32	-	-	-	-	-	[620]
Nylanderia	burgesi	79	-	-	0.65	11	-	-	-	-	-	[621]

Nylanderia	caeciliae	79	242	9	-	-	-	-	No	-	-	[96]
Nylanderia	concinna	79	-	-	0.58	42	-	-	-	-	-	[620]
Nylanderia	dodo	79	-	-	0.66	9	-	-	-	-	-	[622]
Nylanderia	faisonensis	79	-	-	0.52	41	-	-	-	-	-	[620]
Nylanderia	flavipes	79	497	5	0.5	46	-	-	-	No	-	[62, 70, 620, 623, 624]
Nylanderia	fulva	79	-	-	-	-	-	-	-	Yes	-	[625, 626]
Nylanderia	guatemalensis	79	-	-	0.48	37	-	-	-	-	-	[620]
Nylanderia	hystrix	79	-	-	0.57	19	-	-	-	-	-	[620]
Nylanderia	laevigata	79	-	-	0.7	3	-	-	-	-	-	[627]
Nylanderia	nr_sp_fulva	79	-	-	-	-	-	-	-	Yes	-	[628]
Nylanderia	opisopthalmia	79	-	-	0.63	15	-	-	-	-	-	[629]
Nylanderia	parvula	79	-	-	0.51	53	-	-	-	-	-	[620]
Nylanderia	phantasma	79	-	-	0.5	38	-	-	-	-	-	[620]
Nylanderia	pubens	79	-	-	0.71	35	-	-	-	-	-	[620]
Nylanderia	terricola	79	125	7	0.53	43	-	-	-	-	-	[86, 620]
Nylanderia	vividula	79	-	-	0.52	59	-	-	-	-	-	[620]
Nylanderia	wojciki	79	-	-	0.44	45	-	-	-	-	-	[620]
Octostruma	impressa	16	-	-	0.65	5	-	-	-	-	-	[630]
Octostruma	stenoscapa	16	-	-	0.45	4	-	-	-	-	-	[630]
Ocymyrmex	afradu	49	-	-	1.09	3	-	-	No	-	-	[631]
Ocymyrmex	alacer	49	-	-	2.02	9	-	-	No	-	-	[631]
Ocymyrmex	ankhu	49	-	-	2.14	8	-	-	No	-	-	[64]
Ocymyrmex	barbiger	49	200	1	1.59	21	1.54	2	No	-	-	[19, 64]

Ocymyrmex	cavatodorsatus	49	-	-	1.12	10	-	-	No	-	-	[64, 631]
Ocymyrmex	celer	49	-	-	1.85	4	-	-	No	-	-	[64]
Ocymyrmex	cursor	49	-	-	1.02	2	-	-	No	-	-	[64, 631]
Ocymyrmex	dekerus	49	-	-	1.3	6	-	-	No	-	-	[631]
Ocymyrmex	engytachys	49	-	-	1.18	2	-	-	No	-	-	[631]
Ocymyrmex	flavescens	49	-	-	0.62	1	-	-	No	-	-	[631]
Ocymyrmex	flaviventris	49	-	-	1.62	19	1.57	3	No	-	-	[64, 631]
Ocymyrmex	foreli	49	801	12	1.7	15	1.7	2	No	Yes	-	[64, 632]
Ocymyrmex	fortior	49	-	-	1.78	21	1.74	5	No	-	-	[64]
Ocymyrmex	gordoni	49	-	-	0.48	1	-	-	-	-	-	[631]
Ocymyrmex	hirsutus	49	-	-	1.61	7	-	-	No	-	-	[64]
Ocymyrmex	ignotus	49	-	-	1.79	11	-	-	No	-	-	[631]
Ocymyrmex	kahas	49	-	-	1.42	9	-	-	No	-	-	[631]
Ocymyrmex	laticeps	49	-	-	1.72	3	-	-	No	-	-	[64, 631]
Ocymyrmex	micans	49	-	-	1.48	2	-	-	No	-	-	[64]
Ocymyrmex	monardi	49	-	-	1.77	3	-	-	No	-	-	[64]
Ocymyrmex	nitidulus	49	-	-	1.73	21	1.72	8	No	-	-	[64]
Ocymyrmex	okys	49	-	-	1.58	5	-	-	No	-	-	[631]
Ocymyrmex	phraxus	49	-	-	1.69	7	-	-	No	-	-	[64]
Ocymyrmex	picardi	49	-	-	2.49	22	2.49	2	No	-	-	[64, 631]
Ocymyrmex	resekhes	49	-	-	1.76	21	-	-	No	-	-	[631]
Ocymyrmex	robecchii	49	-	-	2.03	2	-	-	No	-	-	[64]
Ocymyrmex	shushan	49	-	-	0.79	1	-	-	No	-	-	[64]
Ocymyrmex	sobek	49	-	-	1.77	28	1.82	4	No	-	-	[64]
Ocymyrmex	sphinx	49	-	-	2.03	13	-	-	No	-	-	[64]
Ocymyrmex	tachys	49	-	-	1.13	5	-	-	No	-	-	[631]

Ocymyrmex	turneri	49	-	-	1.2	11	-	-	No	-	-	[64, 631]
Ocymyrmex	velox	49	-	-	2.19	9	2.13	3	No	-	-	[64]
Ocymyrmex	weitzeckeri	49	-	-	1.57	9	0.82	1	No	-	-	[64]
Ocymyrmex	zekhem	49	-	-	1.88	11	-	-	No	-	-	[64, 631]
Odontomachus	affinis	282	-	-	1.98	1	-	-	-	No	-	[65, 633]
Odontomachus	alius	282	-	-	2.21	101	2.57	2	-	-	-	[634]
Odontomachus	allolabis	282	-	-	1.05	1	-	-	-	-	-	[633]
Odontomachus	assiniensis	282	-	-	-	-	-	-	-	Yes	-	[65]
Odontomachus	banksi	282	-	-	2.34	59	-	-	-	-	-	[634]
Odontomachus	bauri	282	300	1	1.83	1	-	-	-	-	-	[19, 633]
Odontomachus	biolleyi	282	-	-	1.72	1	-	-	-	-	-	[633]
Odontomachus	biumbonatus	282	-	-	2.15	5	2.43	4	-	-	-	[633]
Odontomachus	bradleyi	282	-	-	2.13	4	-	-	-	-	-	[633]
Odontomachus	brunneus	282	497.78	9	1.69	5	-	-	-	Yes	-	[61, 79, 633, 635-638]
Odontomachus	caelatus	282	-	-	2.55	44	-	-	-	-	-	[633]
Odontomachus	cephalotes	282	1000	1	2.28	2	-	-	-	Yes	-	[60, 65, 636, 638]
Odontomachus	chelifer	282	-	-	2.39	2	-	-	-	Yes	-	[65, 158, 633, 636, 639]
Odontomachus	clarus	282	-	-	1.82	2	-	-	-	-	-	[633, 636]
Odontomachus	coquereli	282	18.9	29	1.72	120	1.72	22	-	No	-	[66, 640]
Odontomachus	erythrocephalus	282	-	-	2.07	3	-	-	-	-	-	[633, 636, 638]

Odontomachus	floresensis	282	-	-	1.78	4	-	-	-	-	-	[633]
Odontomachus	haematodus	282	125	2	1.65	3	-	-	-	Yes	-	[226, 633, 636, 638, 641]
Odontomachus	hastatus	282	276.8	20	1.59	1	-	-	-	Yes	-	[633, 642]
Odontomachus	infandus	282	-	-	2.18	159	2.52	3	-	-	-	[634]
Odontomachus	insularis	282	-	-	1.58	1	-	-	-	-	-	[633]
Odontomachus	laticeps	282	-	-	1.96	2	-	-	-	-	-	[633, 643]
Odontomachus	latidens	282	-	-	2.59	1	-	-	-	-	-	[633]
Odontomachus	latissimus	282	-	-	1.87	1	-	-	-	-	-	[633]
Odontomachus	malignus	282	-	-	2.32	17	-	-	-	-	-	[634]
Odontomachus	mayi	282	-	-	1.57	1	-	-	-	No	-	[70, 633]
Odontomachus	monticola	282	-	-	1.8	1	-	-	-	-	-	[633]
Odontomachus	mormo	282	-	-	2.27	3	-	-	-	-	-	[633]
Odontomachus	opaciventris	282	3484	2	1.84	151	-	-	No	No	-	[633, 644]
Odontomachus	panamensis	282	-	-	1.38	1	-	-	-	-	-	[633]
Odontomachus	papuanus	282	-	-	1.54	1	-	-	-	-	-	[633]
Odontomachus	philippinus	282	-	-	2.34	44	-	-	-	-	-	[634]
Odontomachus	relictus	282	200	1	1.8	1	1.77	1	-	-	-	[61, 645]
Odontomachus	rixosus	282	136.54	13	1.81	35	1.91	106	-	Yes	-	[65, 410, 633, 634, 641]
Odontomachus	ruginodis	282	-	-	1.62	1	-	-	-	-	-	[636]
Odontomachus	ruginodus	282	200	1	-	-	-	-	-	-	-	[61]

Odontomachus	scalptus	282	-	-	1.92	2	-	-	-	-	-	[643]
Odontomachus	schoedli	282	-	-	2.38	24	-	-	-	-	-	[634]
Odontomachus	scifictus	282	-	-	2.2	70	-	-	-	-	-	[634]
Odontomachus	simillimus	282	43.33	6	2.03	93	1.97	6	-	Yes	-	[66, 410, 634, 641]
Odontomachus	sp._1	282	-	-	2.27	16	2.51	2	-	-	-	[634]
Odontomachus	sp._2	282	-	-	2.22	1	-	-	-	-	-	[634]
Odontomachus	spissus	282	-	-	1.6	1	-	-	-	-	-	[633]
Odontomachus	sumbensis	282	-	-	1.66	8	-	-	-	-	-	[633]
Odontomachus	troglodytes	282	650	4	1.84	20	2.08	7	-	Yes	-	[60, 65, 66, 633, 640]
Odontomachus	yucatecus	282	-	-	1.83	10	-	-	-	-	-	[633]
Odontoponera	denticulata	26	50	1	-	-	-	-	-	-	-	[283]
Odontoponera	transversa	26	50	1	-	-	-	-	-	-	-	[283]
Oecophylla	longinoda	540	2657.62	65	1.33	2	-	-	Yes	No	-	[70, 331, 646, 647]
Oecophylla	smaragdina	540	3540.17	18	1.38	4	3.33	1	-	Yes	Yes	[70, 648-656]
Onychomyrmex	hedleyi	13	848.27	121	0.71	401	0.73	60	No	No	-	[60, 163]
Ophthalmopone	berthoudi	20	400	1	-	-	-	-	-	-	-	[19]
Opisthopsis	haddoni	16	150	1	-	-	-	-	-	Yes	-	[657]
Orectognathus	clarki	21	25	1	-	-	-	-	Yes	Yes	-	[658]
Orectognathus	mjobergi	21	-	-	-	-	-	-	No	-	-	[658]
Orectognathus	phyllobates	21	-	-	0.49	1	-	-	-	-	-	[659]
Orectognathus	sarasini	21	30	1	0.91	1	0.52	1	-	No	-	[659]

Orectognathus	szentivanyi	21	-	-	1.05	9	0.64	1	-	-	-	[659]
Orectognathus	versicolor	21	-	-	0.83	51	-	-	Yes	No	-	[660, 661]
Pachycondla	foetens	584	1300	1	-	-	2.64	3	Yes	No	-	[60, 258]
Pachycondyla	apicalis	584	48.53	187	2.34	19	-	-	No	Yes	No	[410, 431, 662-666]
Pachycondyla	astuta	584	19	1	-	-	-	-	-	No	-	[410]
Pachycondyla	australis	584	50	1	-	-	-	-	-	No	-	[60]
Pachycondyla	berthoudi	584	176.74	72	-	-	1.77	1	No	Yes	-	[60, 65, 232, 266, 418, 667-671]
Pachycondyla	caffraria	584	76.61	18	-	-	1.61	2	No	Yes	-	[19, 60, 672, 673]
Pachycondyla	chinensis	584	27.85	240	0.75	77	0.86	81	-	Yes	-	[674]
Pachycondyla	commutata	584	350	2	-	-	-	-	-	-	-	[19, 163]
Pachycondyla	goeldii	584	191.8	132	-	-	-	-	-	Yes	-	[70, 439, 675-677]
Pachycondyla	havilandi	584	25	1	-	-	-	-	-	No	-	[232]
Pachycondyla	inversa	584	34.18	40	-	-	-	-	-	Yes	Yes	[168, 211, 678, 679]
Pachycondyla	kruegeri	584	43.59	17	-	-	2.02	6	-	No	-	[60, 232, 233, 667, 671]
Pachycondyla	lutea	584	1500	1	-	-	-	-	-	-	-	[11]

Pachycondyla	luteola	584	-	-	-	-	-	-	-	Yes	-	[322, 439]
Pachycondyla	marginata	584	-	-	-	-	-	-	-	Yes	-	[33, 642]
Pachycondyla	nakasujii	584	-	-	0.82	15	0.87	1	-	-	-	[680]
Pachycondyla	obscuricornis	584	71	4	1.98	9	-	-	-	Yes	-	[19, 60, 322, 410, 665, 681-683]
Pachycondyla	sennaarensis	584	1000	1	-	-	-	-	-	Yes	-	[33, 674]
Pachycondyla	sp._2	584	50	1	-	-	-	-	-	-	-	[283]
Pachycondyla	striata	584	76.21	37	-	-	-	-	-	Yes	-	[322, 684]
Pachycondyla	sublaevis	584	9.5	4	-	-	-	-	-	No	-	[138, 232, 272, 418, 671, 685]
Pachycondyla	tarsata	584	481.25	2	-	-	3.89	5	-	Yes	-	[60, 410]
Pachycondyla	tesseronoda	584	101.68	18	1.63	80	1.62	31	-	Yes	-	[671]
Pachycondyla	tridentata	584	56.25	12	-	-	-	-	-	Yes	-	[232, 639, 686-688]
Pachycondyla	tristis	584	-	-	-	-	0.4	1	-	-	-	[414]
Pachycondyla	verenae	584	39.39	28	1.74	23	-	-	-	Yes	-	[665]
Pachycondyla	villosa	584	112.5	2	-	-	-	-	-	Yes	Yes	[33, 168, 226, 269, 689, 690]
Pachycondyla	wroughtonii	584	500	1	-	-	-	-	-	No	-	[60]

Paramycetophylax	bruchi	2	-	-	-	-	-	-	No	-	-	[449]
Paraparatrechina	albipes	16	-	-	0.39	20	0.37	1	-	-	-	[691]
Paraparatrechina	brunnella	16	-	-	0.35	10	-	-	-	-	-	[691]
Paraparatrechina	concinnata	16	-	-	0.41	12	-	-	-	-	-	[691]
Paraparatrechina	glabra	16	-	-	0.42	39	0.5	1	-	-	-	[691]
Paraparatrechina	gnoma	16	-	-	0.33	12	-	-	-	-	-	[691]
Paraparatrechina	myops	16	-	-	0.47	27	-	-	-	-	-	[691]
Paraparatrechina	ocellatula	16	-	-	0.44	56	-	-	-	-	-	[691]
Paraparatrechina	oreias	16	-	-	0.38	10	-	-	-	-	-	[691]
Paraparatrechina	splendida	16	-	-	0.49	8	-	-	-	-	-	[691]
Paraparatrechina	subtilis	16	-	-	0.4	10	-	-	-	-	-	[691]
Paraparatrechina	umbranatis	16	-	-	0.35	12	-	-	-	-	-	[691]
Paraponera	clavata	151	-	-	-	-	-	-	-	No	-	[70]
Paratopula	ankistra	7	-	-	0.5	1	-	-	-	-	-	[575]
Paratopula	catocha	7	-	-	1.02	3	-	-	-	-	-	[575]
Paratopula	ceylonica	7	-	-	1.18	1	-	-	-	-	-	[575]
Paratopula	demeta	7	-	-	0.6	1	-	-	-	-	-	[575]
Paratopula	longispina	7	-	-	-	-	1.05	1	-	-	-	[575]
Paratopula	macta	7	-	-	0.57	2	-	-	-	-	-	[575]
Paratrechina	concinna	500	100	1	-	-	-	-	-	-	-	[61]
Paratrechina	faisonensis	500	100	1	-	-	-	-	-	-	-	[61]
Paratrechina	longicornis	500	-	-	0.54	15	-	-	-	Yes	-	[70, 620, 692]
Paratrechina	parvula	500	100	1	-	-	-	-	-	-	-	[61]
Paratrechina	phantasma	500	100	1	-	-	-	-	-	-	-	[61]
Paratrechina	wojciki	500	100	1	-	-	-	-	-	-	-	[61]

Perissomyrmex	bidentatus	11	-	-	1.05	15	1.28	4	Yes	No	-	[693, 694]
Perissomyrmex	fissus	11	-	-	0.4	1	-	-	-	-	-	[695]
Perissomyrmex	guizhouensis	11	-	-	0.82	9	-	-	Yes	-	-	[694]
Perissomyrmex	medogensis	11	70	1	1.03	13	0.59	1	Yes	No	-	[693]
Perissomyrmex	monticola	11	-	-	0.54	3	0.6	1	-	-	-	[696, 697]
Perissomyrmex	nepalensis	11	-	-	0.93	5	-	-	-	-	-	[697]
Perissomyrmex	snyderi	11	-	-	1.3	215	0.68	1	Yes	-	-	[697, 698]
Peronomyrmex	bartoni	4	-	-	0.42	2	-	-	-	-	-	[699]
Peronomyrmex	greavesi	4	-	-	0.37	1	-	-	-	-	-	[700]
Peronomyrmex	overbecki	4	-	-	0.37	1	-	-	-	-	-	[339]
Petalomyrmex	phylax	37	900.12	386	0.35	199	-	-	-	Yes	-	[95, 181, 182, 701]
Pheidole	adrianoi	1798	350	1	-	-	-	-	-	-	-	[61]
Pheidole	batrachorum	1798	-	-	0.95	22	-	-	-	-	-	[702]
Pheidole	bergi	1798	-	-	0.35	1	-	-	-	-	-	[703]
Pheidole	bigote	1798	-	-	0.98	10	-	-	-	No	-	[704]
Pheidole	branstetteri	1798	-	-	0.74	23	-	-	-	-	-	[704]
Pheidole	bula	1798	-	-	1.26	13	1.29	3	-	-	-	[705]
Pheidole	capellinii	1798	-	-	1.21	8	-	-	-	-	-	[706]
Pheidole	carinote	1798	-	-	0.58	25	-	-	-	-	-	[704]
Pheidole	christinae	1798	-	-	0.78	22	-	-	-	-	-	[702]
Pheidole	colaensis	1798	-	-	1.35	17	1.32	2	-	-	-	[705]
Pheidole	colpigaleata	1798	-	-	0.86	2	-	-	-	-	-	[706]

Pheidole	darwini	1798	-	-	1.2	27	-	-	-	-	-	[702]
Pheidole	dea	1798	-	-	0.95	40	-	-	-	-	-	[702]
Pheidole	debilis	1798	-	-	0.65	27	-	-	-	-	-	[704]
Pheidole	defecta	1798	-	-	0.55	1	-	-	-	-	-	[707]
Pheidole	dentata	1798	311.63	43	-	-	-	-	Yes	No	-	[61, 381, 708]
Pheidole	dentigula	1798	300	1	-	-	-	-	-	-	-	[61]
Pheidole	desertorum	1798	-	-	-	-	-	-	Yes	Yes	-	[70, 445]
Pheidole	dugasi	1798	-	-	2.11	10	-	-	-	-	-	[706]
Pheidole	elongicephala	1798	-	-	1.08	10	-	-	-	-	-	[706]
Pheidole	emblyox	1798	300	1	-	-	-	-	-	-	-	[19]
Pheidole	eowilsoni	1798	-	-	0.85	12	-	-	-	No	-	[704]
Pheidole	epiphyta	1798	-	-	0.43	2	-	-	-	-	-	[704]
Pheidole	fallax	1798	10000	1	-	-	-	-	-	-	-	[19]
Pheidole	fervens	1798	-	-	0.95	10	-	-	-	-	-	[706]
Pheidole	fervida	1798	-	-	0.42	2	1.5	1	Yes	-	-	[709, 710]
Pheidole	fiorii	1798	992.5	10	-	-	-	-	Yes	-	-	[96]
Pheidole	floridana	1798	1000	1	-	-	-	-	-	-	-	[61]
Pheidole	fortis	1798	-	-	1.3	2	-	-	-	-	-	[706]
Pheidole	fossimandibula	1798	-	-	0.67	12	-	-	-	No	-	[704]
Pheidole	foveolata	1798	-	-	0.69	2	-	-	-	-	-	[706]
Pheidole	funki	1798	-	-	0.39	1	-	-	-	-	-	[711]
Pheidole	furcata	1798	-	-	1.28	15	1.15	3	-	-	-	[705]
Pheidole	gatesi	1798	-	-	1.93	10	-	-	-	-	-	[706]
Pheidole	glabrella	1798	-	-	0.98	32	-	-	-	-	-	[702]

Pheidole	guilelmimuelleri	1798	-	-	-	-	-	-	Yes	-	-	[712]
Pheidole	gymnoceras	1798	-	-	0.63	11	-	-	-	No	-	[704]
Pheidole	heliosa	1798	-	-	0.84	9	-	-	-	-	-	[702]
Pheidole	hongkongensis	1798	-	-	0.65	16	-	-	-	-	-	[706]
Pheidole	indica	1798	-	-	-	-	1.5	3	-	-	-	[713]
Pheidole	indosinensis	1798	-	-	1.16	10	-	-	-	-	-	[706]
Pheidole	inquilina	1798	-	-	-	-	-	-	Yes	-	-	[713]
Pheidole	janzeni	1798	-	-	0.46	12	-	-	-	-	-	[704]
Pheidole	karolmorae	1798	-	-	0.53	22	-	-	-	-	-	[704]
Pheidole	karolsetosa	1798	-	-	0.59	18	-	-	-	-	-	[704]
Pheidole	laevicolor	1798	-	-	0.75	2	-	-	-	-	-	[706]
Pheidole	laevithorax	1798	-	-	0.94	9	-	-	-	-	-	[706]
Pheidole	lagunculinoda	1798	-	-	0.75	12	-	-	-	-	-	[704]
Pheidole	lamia	1798	3000	1	-	-	-	-	-	-	-	[714]
Pheidole	lanuginosa	1798	-	-	-	-	0.76	2	-	-	-	[713]
Pheidole	leoncortesi	1798	-	-	0.89	19	-	-	-	-	-	[704]
Pheidole	mackayi	1798	-	-	0.34	2	-	-	-	-	-	[704]
Pheidole	magna	1798	-	-	1.54	2	-	-	-	-	-	[706]
Pheidole	megacephala	1798	-	-	0.92	12	-	-	Yes	Yes	-	[70, 706, 712, 715]
Pheidole	mesomontana	1798	-	-	0.75	11	-	-	-	-	-	[704]
Pheidole	metallescens	1798	1000	1	-	-	-	-	-	-	-	[61]
Pheidole	microgyna	1798	-	-	-	-	0.44	7	-	-	-	[713]
Pheidole	militicida	1798	-	-	-	-	-	-	Yes	-	-	[716]
Pheidole	minuscula	1798	-	-	0.42	1	-	-	-	-	-	[74]
Pheidole	moerens	1798	600	1	-	-	-	-	-	-	-	[61]

Pheidole	morrisi	1798	2500	1	-	-	-	-	-	-	-	[61]
Pheidole	morrisii	1798	285	1	-	-	-	-	Yes	No	-	[717]
Pheidole	nasutoides	1798	-	-	0.32	2	-	-	-	-	-	[707]
Pheidole	nimba	1798	-	-	0.38	1	-	-	-	-	-	[702]
Pheidole	noda	1798	-	-	1.16	10	-	-	-	-	-	[706]
Pheidole	obscurifrons	1798	-	-	0.85	1	-	-	-	-	-	[718]
Pheidole	obtusospinosa	1798	1783	6	0.7	134	-	-	Yes	-	-	[719, 720]
Pheidole	ochracea	1798	-	-	1.12	10	-	-	-	-	-	[706]
Pheidole	pallidula	1798	9000	26	0.66	2	-	-	Yes	Yes	Yes	[70, 243, 721-724]
Pheidole	pararugiceps	1798	-	-	0.65	9	-	-	-	-	-	[704]
Pheidole	parasitica	1798	-	-	-	-	0.58	25	-	-	-	[713]
Pheidole	parva	1798	-	-	0.67	2	-	-	-	-	-	[706]
Pheidole	pegasus	1798	-	-	1.48	16	0.98	1	-	-	-	[705]
Pheidole	phanigaster	1798	-	-	0.66	16	-	-	-	-	-	[704]
Pheidole	picobarva	1798	-	-	0.74	11	-	-	-	No	-	[704]
Pheidole	pieli	1798	-	-	0.49	4	0.5	1	-	-	-	[706, 710]
Pheidole	plagiaria	1798	-	-	1.2	10	-	-	-	-	-	[706]
Pheidole	planifrons	1798	-	-	1.18	10	-	-	-	-	-	[706]
Pheidole	pubiventris	1798	-	-	-	-	-	-	Yes	-	-	[712]
Pheidole	pulchella	1798	-	-	1.41	28	-	-	-	-	-	[702]
Pheidole	purpurea	1798	-	-	0.8	26	-	-	-	-	-	[704]
Pheidole	quinata	1798	-	-	1.49	2	-	-	-	-	-	[725]
Pheidole	rabo	1798	-	-	0.86	2	-	-	-	-	-	[706]

Pheidole	rebeccae	1798	-	-	1	15	-	-	-	-	-	[702]
Pheidole	rhea	1798	33574	5	1.21	5	-	-	Yes	-	-	[720]
Pheidole	rhinomontana	1798	-	-	0.9	21	-	-	-	No	-	[704]
Pheidole	roosevelti	1798	-	-	1.34	18	1.63	6	-	-	-	[705]
Pheidole	rugithorax	1798	-	-	0.81	10	-	-	-	-	-	[706]
Pheidole	ryukyuensis	1798	-	-	0.87	10	0.63	1	Yes	-	-	[710]
Pheidole	sabahna	1798	-	-	1.58	2	-	-	-	-	-	[725]
Pheidole	schoedli	1798	-	-	1.18	11	-	-	Yes	-	-	[726]
Pheidole	schultzei	1798	-	-	0.25	2	-	-	Yes	-	-	[711]
Pheidole	sculpturata	1798	-	-	2.6	1	-	-	-	-	-	[74]
Pheidole	sebofila	1798	-	-	0.82	13	-	-	-	-	-	[704]
Pheidole	semidea	1798	-	-	1.06	9	-	-	-	-	-	[702]
Pheidole	setosa	1798	-	-	0.76	2	-	-	-	-	-	[702]
Pheidole	simplispinosa	1798	-	-	1.13	17	0.69	1	-	-	-	[705]
Pheidole	smythiesii	1798	-	-	1.89	10	-	-	-	-	-	[706]
Pheidole	sp.21	1798	420.16	31	-	-	-	-	-	No	-	[252]
Pheidole	spadonia	1798	1221	5	1.16	32	-	-	Yes	-	-	[720]
Pheidole	sparsisculpta	1798	-	-	0.52	14	-	-	-	-	-	[704]
Pheidole	spininodis	1798	-	-	0.45	1	-	-	-	-	-	[703]
Pheidole	synanthropica	1798	-	-	0.65	14	-	-	-	-	-	[704]
Pheidole	taipoana	1798	-	-	0.66	12	-	-	-	-	-	[706]
Pheidole	teneriffana	1798	-	-	1.45	1	-	-	-	-	-	[727]
Pheidole	tenuicephala	1798	-	-	0.76	18	-	-	-	-	-	[704]
Pheidole	tepicana	1798	22337	1	1.2	1	-	-	Yes	-	-	[720]
Pheidole	tjibodana	1798	-	-	0.76	10	-	-	-	-	-	[706]
Pheidole	tumida	1798	-	-	1.21	10	-	-	-	-	-	[706]

Pheidole	uncagena	1798	-	-	1.26	13	-	-	-	-	-	[705]
Pheidole	vieti	1798	-	-	0.81	5	-	-	-	-	-	[706]
Pheidole	vulgaris	1798	-	-	0.82	2	-	-	-	-	-	[706]
Pheidole	yeensis	1798	-	-	1.24	10	-	-	-	-	-	[706]
Pheidole	zoceana	1798	-	-	0.72	8	-	-	-	-	-	[706]
Pheidologeton	affinis	69	5000	1	-	-	-	-	-	-	-	[283]
Pheidologeton	diversus	69	250000	1	-	-	-	-	-	-	-	[19]
Pheidologeton	silenus	69	100000	1	-	-	-	-	-	-	-	[19]
Phrynoponera	bequaerti	2	-	-	1.18	20	-	-	-	-	-	[183]
Phrynoponera	gabonensis	2	-	-	1.94	25	-	-	-	-	-	[183]
Phrynoponera	pulchella	2	-	-	2.51	3	-	-	-	-	-	[183]
Phrynoponera	sveni	2	-	-	2.21	7	-	-	-	-	-	[183]
Phrynoponera	transversa	2	-	-	2.04	8	-	-	-	-	-	[183]
Pilotrochus	besmerus	2	-	-	0.3	1	-	-	-	-	-	[643]
Plagiolepis	abyssinica	235	-	-	0.14	4	-	-	-	-	-	[74, 728]
Plagiolepis	boltoni	235	-	-	0.35	6	-	-	-	-	-	[728]
Plagiolepis	breviscapa	235	-	-	0.21	2	-	-	-	-	-	[134, 728]
Plagiolepis	exigua	235	-	-	0.16	1	-	-	-	-	-	[728]
Plagiolepis	juddi	235	-	-	0.14	1	-	-	-	-	-	[728]
Plagiolepis	pallescens	235	-	-	0.2	3	0.28	1	-	-	-	[74, 728]
Plagiolepis	pygmaea	235	25050	1	0.39	3	-	-	-	Yes	-	[477, 728-730]
Plagiolepis	pygmea	235	-	-	-	-	-	-	-	Yes	-	[70, 154]
Plagiolepis	schmitzii	235	-	-	0.23	3	-	-	-	-	-	[74, 728]
Plagiolepis	tumidula	235	-	-	0.18	2	-	-	-	-	-	[74]

Plagiolepis	vindobonensis	235	25050	1	-	-	-	-	-	-	-	[477]
Plagiolepis	xene	235	-	-	-	-	-	-	-	Yes	-	[730]
Platythyrea	angusta	98	125	1	-	-	-	-	-	-	-	[226]
Platythyrea	arnoldi	98	120	2	1.97	5	1.87	5	-	Yes	-	[60]
Platythyrea	conradti	98	112	29	-	-	-	-	-	No	-	[731, 732]
Platythyrea	lamellosa	98	120	2	-	-	2.37	4	-	No	-	[60, 232]
Platythyrea	modesta	98	50	1	-	-	-	-	-	Yes	-	[733]
Platythyrea	prizo	98	-	-	1.19	10	-	-	-	-	-	[734]
Platythyrea	punctata	98	41.2	407	-	-	-	-	-	Yes	-	[61, 735-741]
Platythyrea	quadridenta	98	24.5	2	-	-	-	-	-	Yes	-	[232]
Platythyrea	schultzei	98	23	2	-	-	1.65	4	-	No	-	[60, 232]
Platythyrea	sp._A	98	45	1	-	-	2.62	3	-	No	-	[60]
Platythyrea	sp.1	98	18	2	-	-	-	-	-	Yes	-	[232]
Plectroctena	anops	23	-	-	1.32	1	-	-	-	-	-	[742]
Plectroctena	cristata	23	-	-	4.22	5	4.52	1	-	-	-	[742]
Plectroctena	cryptica	23	-	-	1	3	1.32	1	-	-	-	[742]
Plectroctena	dentata	23	-	-	3.12	5	4.1	2	-	-	-	[742]
Plectroctena	gestroi	23	-	-	2.84	2	3.12	1	-	-	-	[742]
Plectroctena	hastifera	23	-	-	1.84	1	-	-	-	-	-	[742]
Plectroctena	laevior	23	-	-	3.44	1	-	-	-	-	-	[742]
Plectroctena	latinodis	23	-	-	2.92	1	3.08	2	-	-	-	[742]
Plectroctena	macgeei	23	-	-	2	1	-	-	-	-	-	[742]
Plectroctena	mandibularis	23	82.5	3	3.3	35	3.64	14	-	Yes	-	[60, 742, 743]

Plectroctena	minor	23	79.69	16	2.9	18	3.45	4	-	-	-	[742, 744-746]
Plectroctena	strigosa	23	-	-	3.32	10	-	-	-	-	-	[742]
Plectroctena	subterranea	23	-	-	1.68	6	2.24	1	-	-	-	[742]
Plectroctena	ugandensis	23	-	-	-	-	1.64	2	-	-	-	[742]
Pogonomyrmex	anzensis	1138	-	-	-	-	0.94	1	-	-	-	[747]
Pogonomyrmex	badius	1138	3286.36	37	-	-	-	-	-	-	-	[61, 79, 748-750]
Pogonomyrmex	barbatus	1138	11000	1	-	-	-	-	-	No	Yes	[751, 752]
Pogonomyrmex	bigbendensis	1138	-	-	1.71	25	-	-	-	-	-	[753]
Pogonomyrmex	californicus	1138	4500	1	-	-	-	-	-	-	-	[19]
Pogonomyrmex	colei	1138	-	-	-	-	1.72	73	-	-	-	[754]
Pogonomyrmex	cunicularius	1138	-	-	1.77	12	2.16	12	-	No	-	[755]
Pogonomyrmex	huachucanus	1138	-	-	-	-	-	-	-	No	-	[755]
Pogonomyrmex	imberbiculus	1138	20.7	10	1.03	10	1.1	10	-	Yes	-	[756]
Pogonomyrmex	inermis	1138	700	1	-	-	-	-	-	-	-	[749]
Pogonomyrmex	laevinodis	1138	-	-	0.98	35	-	-	-	-	-	[754]
Pogonomyrmex	mayri	1138	603	8	-	-	-	-	-	Yes	-	[757]
Pogonomyrmex	mohavensis	1138	650	3	1.44	13	-	-	-	-	-	[758]
Pogonomyrmex	montanus	1138	-	-	1.44	21	1.66	16	-	-	-	[759]
Pogonomyrmex	occidentalis	1138	6550	2	-	-	-	-	-	No	Yes	[16, 749, 760]
Pogonomyrmex	pima	1138	171.82	49	1.05	20	1.11	40	-	Yes	-	[749, 761]
Pogonomyrmex	rugosus	1138	11750	2	-	-	-	-	-	-	-	[749]

Pogonomyrmex	salinus	1138	-	-	1	63	-	-	-	Yes	-	[762]
Pogonomyrmex	stefani	1138	-	-	1.16	5	-	-	-	-	-	[763]
Pogonomyrmex	texanus	1138	50	21	1.79	2	2.68	10	-	Yes	-	[753, 764]
Pogonomyrmex	wheeleri	1138	-	-	-	-	3.23	4	-	-	-	[754]
Polyergus	breviceps	299	51	1	-	-	-	-	-	No	No	[379, 765]
Polyergus	lucidus	299	1789.75	4	-	-	-	-	-	No	Yes	[131, 766-768]
Polyrhachis	abbreviata	421	-	-	1.18	20	-	-	-	-	-	[769]
Polyrhachis	achterbergi	421	-	-	2.14	14	-	-	-	-	-	[769]
Polyrhachis	aporema	421	-	-	1.45	11	0.77	1	-	-	-	[769]
Polyrhachis	arachne	421	1971.14	5	-	-	-	-	-	No	-	[70, 770-772]
Polyrhachis	aureovestita	421	-	-	2.54	20	-	-	-	-	-	[773]
Polyrhachis	australis	421	-	-	-	-	-	-	-	Yes	-	[70, 772]
Polyrhachis	barryi	421	-	-	1.34	6	0.84	1	-	-	-	[769]
Polyrhachis	bellicosa	421	14425	7	-	-	-	-	-	No	-	[70, 771, 772]
Polyrhachis	bicolor	421	625.5	41	-	-	-	-	-	No	-	[70, 771]
Polyrhachis	bicolour	421	-	-	-	-	-	-	-	No	-	[772]
Polyrhachis	bismarckensis	421	-	-	-	-	-	-	-	Yes	-	[772]
Polyrhachis	boltoni	421	-	-	1.18	18	1.26	12	-	-	-	[774]
Polyrhachis	brevinoda	421	-	-	1.28	31	0.7	1	-	No	-	[769, 772]
Polyrhachis	bruehli	421	-	-	0.91	1	-	-	-	-	-	[769]

Polyrhachis	bubastes	421	-	-	1.8	20	-	-	-	-	-	[773]
Polyrhachis	bugnioni	421	27	1	1.1	12	1.28	2	-	No	-	[772, 774]
Polyrhachis	calypso	421	-	-	1.62	13	-	-	-	-	-	[773]
Polyrhachis	conspicua	421	-	-	1.38	6	-	-	-	-	-	[769]
Polyrhachis	cryptoceroides	421	-	-	0.68	3	0.86	1	-	-	-	[769]
Polyrhachis	cyaniventris	421	-	-	1.91	11	2.13	10	-	-	-	[634]
Polyrhachis	danum	421	-	-	1.47	31	0.8	2	-	-	-	[769]
Polyrhachis	decumbens	421	-	-	1.26	23	-	-	-	-	-	[769]
Polyrhachis	delecta	421	-	-	1.47	25	1.67	6	-	-	-	[769]
Polyrhachis	dives	421	5483.2	1316	-	-	-	-	-	Yes	-	[70, 771, 772, 775]
Polyrhachis	dorsena	421	-	-	1.39	6	0.84	1	-	-	-	[769]
Polyrhachis	equina	421	-	-	1.32	13	-	-	-	-	-	[776]
Polyrhachis	erosispina	421	-	-	-	-	-	-	-	No	-	[772]
Polyrhachis	etheli	421	-	-	0.65	1	0.71	1	-	-	-	[777]
Polyrhachis	expressa	421	-	-	1.44	16	-	-	-	-	-	[769]
Polyrhachis	furcata	421	3821	25	-	-	-	-	-	No	-	[70, 771, 772]
Polyrhachis	glabrinotum	421	-	-	1.69	2	-	-	-	No	-	[772, 773]
Polyrhachis	gribodoi	421	-	-	1.7	19	-	-	-	-	-	[776]
Polyrhachis	hashimotoi	421	-	-	0.74	1	-	-	-	-	-	[776]
Polyrhachis	hoelldobleri	421	-	-	1.45	9	0.89	1	-	-	-	[769]
Polyrhachis	hybosa	421	-	-	1.44	3	-	-	-	-	-	[769]

Polyrhachis	illaudata	421	411.5	31	-	-	-	-	-	Yes	-	[70, 771, 772]
Polyrhachis	inducta	421	-	-	1.29	13	-	-	-	-	-	[769]
Polyrhachis	inflata	421	-	-	1.54	5	0.86	1	-	-	-	[769]
Polyrhachis	integra	421	-	-	0.74	1	-	-	-	-	-	[769]
Polyrhachis	jerdonii	421	-	-	1.32	3	-	-	-	-	-	[769]
Polyrhachis	kyawthani	421	-	-	1.46	12	0.94	1	-	-	-	[769]
Polyrhachis	laboriosa	421	-	-	-	-	-	-	-	No	-	[70]
Polyrhachis	lama	421	4.48	60	1.36	5	0.77	1	-	No	-	[251, 778-780]
Polyrhachis	lepida	421	-	-	1.27	12	1.48	7	-	-	-	[769]
Polyrhachis	lombokensis	421	-	-	-	-	-	-	-	No	-	[772]
Polyrhachis	loweryi	421	40.05	10	-	-	-	-	No	No	-	[772, 781]
Polyrhachis	magnifica	421	-	-	2.12	3	-	-	-	-	-	[773]
Polyrhachis	moesta	421	250.5	300	1.72	413	-	-	-	Yes	-	[782, 783]
Polyrhachis	monteithi	421	-	-	1.5	19	1.66	5	-	-	-	[769]
Polyrhachis	muara	421	-	-	0.65	2	-	-	-	-	-	[784]
Polyrhachis	mucronata	421	-	-	-	-	-	-	-	No	-	[772]
Polyrhachis	muelleri	421	45.94	50	-	-	-	-	-	No	-	[70, 771, 772]
Polyrhachis	nigropilosa	421	671	27	-	-	-	-	-	No	-	[70, 771, 772]
Polyrhachis	nofra	421	-	-	0.56	3	-	-	-	-	-	[773]
Polyrhachis	olybria	421	-	-	-	-	-	-	-	No	-	[772]

Polyrhachis	osiris	421	-	-	1.12	1	-	-	-	-	-	[773]
Polyrhachis	pacifica	421	-	-	0.65	2	-	-	-	-	-	[769]
Polyrhachis	parabiotica	421	-	-	0.68	1	0.74	1	-	-	-	[777]
Polyrhachis	pirata	421	-	-	2.24	11	-	-	-	-	-	[634]
Polyrhachis	proxima	421	821.5	15	-	-	-	-	-	Yes	-	[70, 771, 772]
Polyrhachis	punjabi	421	-	-	1.32	16	-	-	-	-	-	[785]
Polyrhachis	redi	421	-	-	0.88	1	-	-	-	-	-	[776]
Polyrhachis	rhea	421	-	-	2.08	6	-	-	-	-	-	[773]
Polyrhachis	robsoni	421	-	-	1.47	32	1.72	5	-	Yes	-	[769, 772]
Polyrhachis	rufofemorata	421	-	-	-	-	-	-	-	No	-	[772]
Polyrhachis	rugifrons	421	-	-	1.82	5	-	-	-	-	-	[773]
Polyrhachis	rutila	421	-	-	1.25	9	-	-	-	-	-	[769]
Polyrhachis	schellerichae	421	4948	29	1.34	20	1.48	20	-	No	-	[70, 771, 772, 786]
Polyrhachis	scissa	421	-	-	1.37	14	1.46	2	-	-	-	[774]
Polyrhachis	sedlaceki	421	-	-	0.69	2	-	-	-	-	-	[769]
Polyrhachis	setosa	421	-	-	1.12	4	0.64	1	-	-	-	[769]
Polyrhachis	sexspinosa	421	-	-	1.95	26	-	-	-	No	-	[772, 773]
Polyrhachis	strumosa	421	-	-	1.49	8	-	-	-	-	-	[769]
Polyrhachis	sukarmani	421	-	-	1.39	7	0.84	1	-	-	-	[776]
Polyrhachis	sulang	421	-	-	0.72	2	-	-	-	-	-	[769]
Polyrhachis	taylori	421	-	-	-	-	-	-	-	Yes	-	[772]
Polyrhachis	thailandica	421	-	-	0.64	2	-	-	-	-	-	[769]

Polyrhachis	tschu	421	-	-	0.86	1	-	-	-	-	-	[773]
Polyrhachis	tuberosa	421	-	-	1.52	9	-	-	-	-	-	[769]
Polyrhachis	turneri	421	-	-	-	-	-	-	-	No	-	[772]
Polyrhachis	undulata	421	-	-	1.23	3	-	-	-	-	-	[769]
Polyrhachis	vicina	421	8433.48	12	-	-	-	-	-	Yes	-	[787]
Polyrhachis	widodoi	421	-	-	1.04	2	-	-	-	-	-	[769]
Polyrhachis	wroughtonii	421	-	-	1.08	4	-	-	-	-	-	[769]
Polyrhachis	yorkana	421	-	-	-	-	-	-	-	No	-	[772]
Ponera	alisana	205	-	-	0.6	12	0.66	5	-	-	-	[788, 789]
Ponera	chiponensis	205	-	-	0.41	5	0.44	2	-	-	-	[788]
Ponera	coarctata	205	-	-	-	-	0.64	11	-	Yes	-	[790, 791]
Ponera	eduardi	205	1500	1	-	-	-	-	-	-	-	[19]
Ponera	exotica	205	50	1	-	-	-	-	-	-	-	[61]
Ponera	pennsylvanica	205	19.6	6	-	-	-	-	-	Yes	-	[792]
Ponera	testacea	205	-	-	-	-	0.59	16	-	-	-	[791]
Prenolepis	fisheri	143	-	-	0.64	8	0.49	1	-	-	-	[793]
Prenolepis	imparis	143	1980.11	56	0.68	2	-	-	-	Yes	Yes	[86, 131, 794, 795]
Prenolepis	naoroji	143	-	-	0.58	20	0.54	1	-	-	-	[793]
Prenolepis	sphingthoraxa	143	-	-	0.67	12	-	-	-	-	-	[629]
Prenolepis	umbra	143	-	-	0.59	4	-	-	-	-	-	[629]
Prionopelta	amabilis	30	350	1	-	-	-	-	-	No	-	[70, 163]
Prionopelta	modesta	30	-	-	-	-	-	-	-	No	-	[70]
Pristomyrmex	africanus	126	-	-	0.8	20	-	-	No	-	-	[64]

Pristomyrmex	brevispinosus	126	-	-	1.01	99	-	-	Yes	-	-	[3]
Pristomyrmex	cebuensis	126	-	-	1.2	10	-	-	-	-	-	[796]
Pristomyrmex	cribrarius	126	-	-	0.89	3	-	-	No	-	-	[64]
Pristomyrmex	fossulatus	126	-	-	0.66	3	-	-	No	-	-	[64]
Pristomyrmex	orbiceps	126	-	-	0.85	25	-	-	No	-	-	[64]
Pristomyrmex	punctatus	126	7665.22	23	0.86	681	-	-	Yes	Yes	-	[3, 6, 797-804]
Pristomyrmex	trogor	126	-	-	0.85	5	-	-	No	-	-	[64]
Proatta	butteli	6	10000	1	0.59	10	-	-	-	-	-	[19, 228]
Probolomyrmex	dammermani	34	12.5	1	-	-	-	-	-	No	-	[410]
Procerapachys	sulcatus	1	-	-	0.58	1	-	-	-	-	-	[414]
Proceratium	goliath	73	-	-	0.69	6	-	-	-	-	-	[411]
Proceratium	itoi	73	225	1	-	-	-	-	-	No	-	[410]
Proceratium	pergandei	73	25	1	-	-	-	-	-	-	-	[61]
Procryptocerus	carbonarius	27	-	-	-	-	-	-	-	No	-	[70]
Procryptocerus	mayri	27	-	-	-	-	-	-	-	No	-	[70]
Procryptocerus	paleatus	27	-	-	0.77	1	-	-	-	-	-	[805]
Procryptocerus	scabriusculus	27	47.75	4	1.25	136	-	-	No	Yes	-	[187]
Procryptocerus	tortuguero	27	108	1	-	-	-	-	-	Yes	-	[805]
Proformica	korbi	92	133	2	-	-	-	-	-	No	-	[806]
Proformica	longiseta	92	653.61	157	-	-	-	-	Yes	Yes	Yes	[70, 477, 806-812]
Proformica	nasuta	92	25050	1	-	-	-	-	-	-	-	[477]
Proformica	sp.	92	288.5	2	-	-	-	-	-	No	-	[806]
Promyopias	silvestrii	1	-	-	1.06	10	1.17	2	-	-	-	[102, 183]

Protomognathus	americanus	39	-	-	-	-	-	-	-	No	-	[70]
Psalidomyrmex	feae	5	-	-	2.1	4	-	-	-	-	-	[813]
Psalidomyrmex	foveolatus	5	-	-	1.76	10	1.84	3	-	-	-	[813]
Psalidomyrmex	procerus	5	-	-	2.58	20	-	-	-	-	-	[813]
Psalidomyrmex	reichenspergeri	5	-	-	2.98	5	-	-	-	-	-	[813]
Psalidomyrmex	sallyae	5	-	-	1.84	4	-	-	-	-	-	[813]
Psalidomyrmex	wheeleri	5	-	-	2.4	8	-	-	-	-	-	[813]
Pseudolasius	machhediensis	42	-	-	0.87	33	-	-	-	-	-	[814]
Pseudolasius	sp.	42	-	-	-	-	-	-	-	Yes	-	[70]
Pseudolasius	typhlops	42	-	-	-	-	-	-	Yes	-	-	[815]
Pseudomyrmex	ejectus	288	80	1	-	-	-	-	-	Yes	-	[61, 70]
Pseudomyrmex	elongatus	288	80	1	-	-	-	-	-	-	-	[61]
Pseudomyrmex	gracilis	288	80	1	-	-	-	-	-	-	-	[61]
Pseudomyrmex	pallidus	288	30	1	-	-	-	-	-	Yes	-	[61, 70]
Pseudomyrmex	seminole	288	-	-	-	-	-	-	-	No	-	[70]
Pseudomyrmex	termitarius	288	75	1	-	-	-	-	-	-	-	[19]
Pseudomyrmex	triplarinus	288	10000	1	-	-	-	-	-	-	-	[19]
Pseudomyrmex	veneficus	288	-	-	-	-	-	-	-	Yes	-	[70]
Pyramica	bunki	184	40	1	-	-	-	-	-	-	-	[61]
Pyramica	clypeata	184	50	1	-	-	-	-	-	-	-	[61]
Pyramica	creightoni	184	50	1	-	-	-	-	-	-	-	[61]
Pyramica	deyrupi	184	50	1	-	-	-	-	-	-	-	[61]
Pyramica	dietrichi	184	50	1	-	-	-	-	-	-	-	[61]
Pyramica	eggersi	184	50	1	-	-	-	-	-	-	-	[61]
Recurvidris	browni	10	-	-	0.47	12	-	-	No	-	-	[816]
Recurvidris	hebe	10	-	-	0.35	11	-	-	No	-	-	[816]

Recurvidris	kemneri	10	-	-	0.5	20	-	-	No	-	-	[816]
Recurvidris	nuwa	10	-	-	0.36	3	-	-	-	-	-	[451]
Recurvidris	pickburni	10	-	-	0.4	5	-	-	No	-	-	[816]
Recurvidris	proles	10	-	-	0.56	3	-	-	No	-	-	[816]
Recurvidris	recurvispinosa	10	-	-	0.38	20	-	-	No	-	-	[816]
Recurvidris	williami	10	-	-	0.2	1	-	-	No	-	-	[816]
Rhopalothrix	orbis	19	-	-	-	-	0.38	1	-	-	-	[339]
Rhoptromyrmex	rawlinsoni	7	-	-	-	-	0.56	1	-	-	-	[817]
Rhytidoponera	aurata	205	135.26	49	2.14	332	2.14	249	-	Yes	-	[232, 818]
Rhytidoponera	chalybaea	205	237.13	182	1.36	80	-	-	-	Yes	Yes	[60, 232, 667, 819-823]
Rhytidoponera	confusa	205	169.56	358	-	-	-	-	-	Yes	Yes	[60, 81, 232, 264, 266, 436, 667, 820, 822]
Rhytidoponera	croesus	205	-	-	1.25	8	-	-	-	-	-	[819]
Rhytidoponera	enigmatica	205	-	-	-	-	-	-	-	Yes	-	[820]
Rhytidoponera	fulgens	205	4	1	-	-	-	-	-	No	-	[820]
Rhytidoponera	impressa	205	-	-	-	-	-	-	-	No	-	[823]
Rhytidoponera	inornata	205	197.6	5	-	-	-	-	-	Yes	-	[823]
Rhytidoponera	mayri	205	398.58	19	-	-	-	-	No	Yes	Yes	[232, 824-829]

Rhytidoponera	metallica	205	82.55	97	-	-	-	-	-	Yes	-	[232, 244, 821, 823, 830-832]
Rhytidoponera	purpurea	205	375	2	-	-	-	-	-	No	-	[60, 819, 823]
Rhytidoponera	sp.	205	122.75	10	-	-	-	-	-	-	-	[781]
Rhytidoponera	sp._12	205	500	1	-	-	-	-	-	Yes	-	[60]
Rhytidoponera	tasmaniensis	205	6	1	-	-	-	-	-	No	-	[820, 823]
Rhytidoponera	victoriae	205	-	-	-	-	-	-	-	Yes	-	[823]
Rhytidoponera	violacea	205	186.89	27	-	-	-	-	-	No	-	[511, 823, 833]
Romblonella	heatwolei	9	-	-	0.7	4	-	-	-	-	-	[834]
Rossomyrmex	anatolicus	32	-	-	1.14	1	-	-	-	No	-	[806, 835]
Rossomyrmex	minuchae	32	122.5	9	-	-	-	-	-	Yes	Yes	[806, 810, 836, 837]
Rossomyrmex	proformicarum	32	469	1	-	-	-	-	-	No	-	[838]
Rossomyrmex	quandratinodum	32	-	-	-	-	-	-	-	No	-	[806]
Secostruma	lethifera	3	-	-	0.47	1	-	-	-	-	-	[839]
Sericomyrmex	amabilis	52	200	12	-	-	-	-	-	No	Yes	[22, 98]
Simopelta	laticeps	17	-	-	0.98	1	-	-	-	-	-	[840]
Simopelta	oculata	17	361	1	0.59	10	0.67	1	-	No	-	[840]
Simopelta	oculata_	17	1500	1	-	-	-	-	-	No	-	[840]
Simopelta	pentadentata	17	-	-	-	-	-	-	-	No	No	[841]

Simopelta	pergandei	17	-	-	-	-	-	-	-	No	No	[841]
Solenopsis	geminata	9439	28000	1	-	-	-	-	-	Yes	-	[61, 70]
Solenopsis	globularia	9439	50	1	-	-	-	-	-	-	-	[61]
Solenopsis	invicta	9439	150000	1	-	-	-	-	-	Yes	-	[60, 61, 70, 158, 244]
Solenopsis	nickersoni	9439	200	1	-	-	-	-	-	-	-	[61]
Solenopsis	pergandei	9439	10000	1	-	-	-	-	-	-	-	[61]
Solenopsis	picta	9439	200	1	-	-	-	-	-	-	-	[61]
Solenopsis	tennesseensis	9439	200	1	-	-	-	-	-	-	-	[61]
Solenopsis	tonta	9439	200	1	-	-	-	-	-	-	-	[61]
Solenopsis	virulens	9439	-	-	0.43	1	-	-	-	-	-	[411]
Sphinctomyrmex	steinheili	15	-	-	-	-	-	-	-	Yes	-	[189]
Stegomyrmex	connectens	8	-	-	-	-	0.68	1	-	-	-	[842]
Stegomyrmex	manni	8	-	-	0.57	1	-	-	-	-	-	[842]
Stegomyrmex	vizottoi	8	188	2	0.93	4	0.96	3	-	Yes	-	[842, 843]
Stereomyrmex	anderseni	3	-	-	0.23	1	-	-	-	-	-	[834]
Stereomyrmex	dispar	3	-	-	0.36	1	-	-	-	-	-	[834]
Stigmatomma	pallipes	14	16.07	15	-	-	-	-	-	Yes	-	[11, 60, 62, 70, 163]
Stigmatomma	reclinatum	14	102	1	-	-	-	-	-	Yes	-	[232, 671]
Stigmatomma	silvestrii	14	27.5	2	-	-	-	-	-	Yes	-	[33, 431]

Streblognathus	aethiopicus	15	30	14	4.31	297	4.39	15	-	No	No	[60, 232, 671, 844, 845]
Streblognathus	peetersi	15	106.6	86	-	-	-	-	-	No	-	[232, 271, 846-848]
Strongylognathus	kabakovi	59	-	-	-	-	0.35	1	-	-	-	[849]
Strumigenys	beebei	184	32.5	2	-	-	-	-	-	No	-	[6]
Strumigenys	boltoni	184	-	-	0.17	1	0.19	1	-	-	-	[850]
Strumigenys	cascanteae	184	-	-	0.27	1	-	-	-	-	-	[40]
Strumigenys	choii	184	-	-	0.48	30	-	-	-	-	-	[851]
Strumigenys	chuchihensis	184	-	-	0.49	8	0.57	3	-	-	-	[852]
Strumigenys	cincinnata	184	-	-	0.17	2	-	-	-	-	-	[853]
Strumigenys	elegantula	184	-	-	0.48	23	0.27	1	-	-	-	[54]
Strumigenys	emarginata	184	199	1	-	-	-	-	-	-	-	[19]
Strumigenys	emmae	184	100	1	-	-	-	-	-	-	-	[61]
Strumigenys	epinotalis	184	192.5	2	-	-	-	-	-	Yes	-	[658]
Strumigenys	erikae	184	-	-	0.27	1	-	-	-	-	-	[40]
Strumigenys	formosensis	184	-	-	-	-	0.3	1	-	-	-	[54]
Strumigenys	hexamera	184	50	1	-	-	-	-	-	No	-	[854]
Strumigenys	hispida	184	-	-	0.64	11	0.58	5	-	-	-	[855]
Strumigenys	konteiensis	184	-	-	0.26	1	-	-	-	-	-	[852]
Strumigenys	lacunosa	184	-	-	0.58	44	0.71	2	-	-	-	[855]
Strumigenys	leptothrix	184	-	-	-	-	0.53	2	-	-	-	[54]
Strumigenys	lewisi	184	127	15	-	-	-	-	-	Yes	-	[6]
Strumigenys	lichiaensis	184	-	-	0.25	2	0.27	1	-	-	-	[855]

Strumigenys	liukueiensis	184	-	-	0.44	26	0.24	1	-	-	-	[54]
Strumigenys	louisianae	184	90	1	-	-	-	-	-	-	-	[61]
Strumigenys	lujae	184	57	1	-	-	-	-	-	-	-	[19]
Strumigenys	margaritae	184	250	1	-	-	-	-	-	-	-	[658]
Strumigenys	maynei	184	236.2	5	-	-	-	-	-	No	-	[856]
Strumigenys	medialis	184	30	1	-	-	-	-	-	Yes	-	[857]
Strumigenys	membranifera	184	154	5	-	-	-	-	-	Yes	-	[6]
Strumigenys	minutula	184	-	-	0.37	14	0.22	1	-	-	-	[54]
Strumigenys	nanzanensis	184	-	-	0.43	7	0.28	3	-	-	-	[855]
Strumigenys	oconitrilloae	184	-	-	0.21	1	0.22	1	-	-	-	[40]
Strumigenys	orchidensis	184	-	-	0.55	8	0.28	1	-	-	-	[852]
Strumigenys	ornato	184	20	1	-	-	-	-	-	-	-	[857]
Strumigenys	panamensis	184	-	-	0.18	1	-	-	-	-	-	[853]
Strumigenys	paniaguae	184	-	-	0.31	1	-	-	-	-	-	[40]
Strumigenys	princeps	184	-	-	0.96	26	1.06	6	-	-	-	[858]
Strumigenys	rogeri	184	100	1	-	-	-	-	-	-	-	[61]
Strumigenys	rohweri	184	87.5	1	-	-	-	-	-	Yes	-	[658]
Strumigenys	rotogenys	184	36	7	-	-	-	-	-	Yes	-	[859]
Strumigenys	serrula	184	78	1	-	-	-	-	-	-	-	[19]
Strumigenys	sp.1	184	193	40	-	-	-	-	-	Yes	-	[252]
Strumigenys	talpa	184	60	1	-	-	-	-	-	-	-	[857]
Strumigenys	trada	184	-	-	0.23	1	-	-	-	-	-	[855]
Strumigenys	trudifera	184	-	-	0.41	5	0.25	2	-	-	-	[858]
Strumigenys	truncatidens	184	113.5	2	-	-	-	-	No	No	-	[19, 860]
Strumigenys	augustandrewi	184	-	-	0.3	1	-	-	-	-	-	[40]
Tapinolepis	longitarsis	1	-	-	0.28	2	-	-	-	-	-	[137]

Tapinoma	erraticum	637	1000	1	-	-	-	-	-	-	-	[19]
Tapinoma	melanocephalum	637	-	-	-	-	-	-	-	Yes	-	[70]
Tapinoma	ramulorum	637	150	11	-	-	-	-	No	-	-	[96]
Technomyrmex	albipes	168	444139.53	43	0.62	400	0.75	100	-	Yes	-	[70, 435, 436, 861, 862]
Technomyrmex	setosus	168	-	-	0.33	1	-	-	-	-	-	[74]
Temnothorax	albipennis	384	-	-	-	-	-	-	-	No	-	[683]
Temnothorax	alienus	384	-	-	0.56	16	0.69	4	-	-	-	[863]
Temnothorax	ambiguus	384	50	1	-	-	-	-	-	-	-	[19]
Temnothorax	angulohumerus	384	-	-	0.47	3	-	-	-	-	-	[864]
Temnothorax	bradleyi	384	50	1	-	-	-	-	-	-	-	[61]
Temnothorax	caesari	384	18	1	0.46	42	0.49	15	-	No	-	[865]
Temnothorax	crassispinus	384	280	1	-	-	-	-	-	-	-	[19]
Temnothorax	curvispinosus	384	50	1	-	-	-	-	-	Yes	-	[19, 70]
Temnothorax	duoloticus	384	12	1	-	-	-	-	-	-	-	[19]
Temnothorax	hengshanensis	384	-	-	0.24	1	-	-	-	-	-	[614]
Temnothorax	leyeensis	384	-	-	0.46	1	-	-	-	-	-	[864]
Temnothorax	longispinosus	384	65	1	-	-	-	-	-	-	-	[19]
Temnothorax	maoerensis	384	-	-	0.6	6	-	-	-	-	-	[864]
Temnothorax	nigriceps	384	-	-	0.28	7	0.35	1	-	No	-	[497]
Temnothorax	nylanderi	384	-	-	-	-	-	-	-	No	-	[70]
Temnothorax	orchidus	384	-	-	0.54	5	-	-	-	-	-	[864]
Temnothorax	palustris	384	50	1	0.25	1	0.39	1	-	-	-	[61, 866]
Temnothorax	pergandei	384	50	1	-	-	-	-	-	-	-	[61]
Temnothorax	ruginosus	384	-	-	0.5	6	-	-	-	-	-	[864]

Temnothorax	saxatilis	384	-	-	0.49	11	0.34	1	-	-	-	[863]
Temnothorax	shannxiensis	384	-	-	0.56	2	-	-	-	-	-	[864]
Temnothorax	sordidulus	384	-	-	-	-	0.35	1	-	-	-	[497]
Temnothorax	striatus	384	-	-	0.48	6	-	-	-	-	-	[864]
Temnothorax	texanus	384	50	1	-	-	-	-	-	-	-	[61]
Temnothorax	unifasciatus	384	325	1	-	-	-	-	-	-	-	[19]
Temnothorax	zhejiangensis	384	-	-	0.46	2	-	-	-	-	-	[864]
Terataner	alluaudi	1	43.5	7	-	-	-	-	No	Yes	-	[64, 867]
Terataner	bottegoi	1	-	-	1.23	5	-	-	No	-	-	[64]
Terataner	elegans	1	-	-	1.21	20	-	-	No	-	-	[64]
Terataner	foreli	1	14.5	9	-	-	-	-	No	No	-	[64, 867]
Terataner	luteus	1	-	-	1.24	15	-	-	No	-	-	[64]
Terataner	piceus	1	-	-	1.13	9	-	-	No	-	-	[64]
Terataner	rufipes	1	-	-	-	-	-	-	No	-	-	[64]
Terataner	scotti	1	-	-	-	-	-	-	No	-	-	[64]
Terataner	steinheili	1	-	-	-	-	-	-	No	-	-	[64]
Terataner	transvaalensis	1	-	-	0.79	1	-	-	No	-	-	[64]
Terataner	velatus	1	-	-	0.94	6	-	-	No	-	-	[64]
Terataner	xaltus	1	-	-	0.89	1	-	-	No	-	-	[64]
Tetramorium	aculeatum	876	-	-	-	-	-	-	-	No	-	[70]
Tetramorium	adamsi	876	-	-	0.93	18	-	-	-	-	-	[868]
Tetramorium	africanum	876	-	-	-	-	-	-	-	No	-	[70]
Tetramorium	aherni	876	-	-	0.82	12	-	-	-	-	-	[868]
Tetramorium	akermani	876	-	-	0.85	1	-	-	-	-	-	[869]
Tetramorium	ala	876	-	-	0.86	12	-	-	-	-	-	[868]
Tetramorium	amalae	876	-	-	0.31	1	-	-	-	-	-	[869]

Tetramorium	ambanizana	876	-	-	0.79	5	-	-	-	-	-	[868]
Tetramorium	andohahela	876	-	-	1.01	14	-	-	-	-	-	[868]
Tetramorium	andrei	876	-	-	0.89	65	-	-	-	-	-	[868]
Tetramorium	ankarana	876	-	-	0.76	4	-	-	-	-	-	[868]
Tetramorium	avaratra	876	-	-	0.83	15	-	-	-	-	-	[868]
Tetramorium	azcatltontlium	876	-	-	0.61	16	-	-	-	-	-	[870]
Tetramorium	belgaense	876	-	-	0.68	1	-	-	-	-	-	[871]
Tetramorium	bicarinatum	876	600	10	0.74	23	-	-	-	Yes	-	[872, 873]
Tetramorium	bicolorum	876	-	-	0.89	1	-	-	-	-	-	[874]
Tetramorium	boehmei	876	-	-	0.67	2	-	-	-	-	-	[875]
Tetramorium	brevicorne	876	-	-	-	-	1.06	10	-	No	-	[63]
Tetramorium	caespitum	876	1900	5	-	-	1.24	4	Yes	No	-	[63, 70, 876, 877]
Tetramorium	caldarium	876	-	-	0.55	9	-	-	-	-	-	[871]
Tetramorium	cordatum	876	-	-	0.3	1	-	-	-	-	-	[878]
Tetramorium	dysderke	876	-	-	0.25	1	-	-	-	-	-	[869]
Tetramorium	electrum	876	-	-	1.03	20	-	-	-	-	-	[868]
Tetramorium	elf	876	-	-	0.94	10	-	-	-	-	-	[868]
Tetramorium	forte	876	-	-	0.77	35	1.13	23	-	Yes	-	[879]
Tetramorium	guineense	876	-	-	0.77	1	-	-	-	-	-	[875]

Tetramorium	hasinae	876	-	-	0.26	1	0.3	1	No	-	-	[880]
Tetramorium	hispidum	876	-	-	0.89	1	-	-	-	-	-	[874]
Tetramorium	impurum	876	1762.5	4	-	-	-	-	-	No	-	[876, 881]
Tetramorium	insolens	876	-	-	0.7	12	-	-	-	-	-	[873]
Tetramorium	isectum	876	-	-	1.12	12	-	-	-	-	-	[868]
Tetramorium	isoelectrum	876	-	-	1	7	-	-	-	-	-	[868]
Tetramorium	jedi	876	-	-	0.88	12	-	-	-	-	-	[868]
Tetramorium	jizane	876	-	-	0.28	1	0.42	1	-	-	-	[74]
Tetramorium	juba	876	-	-	0.35	1	0.58	1	-	-	-	[74]
Tetramorium	kelleri	876	-	-	0.89	25	-	-	-	-	-	[868]
Tetramorium	keralense	876	-	-	0.37	2	-	-	-	-	-	[878]
Tetramorium	lanuginosum	876	-	-	0.59	21	-	-	-	-	-	[871, 873]

Tetramorium	latinode	876	-	-	0.66	15	0.36	1	-	No	-	[869]
Tetramorium	latreillei	876	-	-	0.89	3	-	-	-	-	-	[868]
Tetramorium	mahafaly	876	-	-	0.58	20	-	-	-	-	-	[873]
Tetramorium	malabarense	876	-	-	0.37	1	-	-	-	-	-	[878]
Tetramorium	marojejy	876	-	-	0.99	12	-	-	-	-	-	[868]
Tetramorium	meridionale	876	-	-	-	-	-	-	-	Yes	-	[63]
Tetramorium	nazgul	876	-	-	0.88	12	-	-	-	-	-	[868]
Tetramorium	nify	876	-	-	0.79	5	-	-	-	-	-	[868]
Tetramorium	noeli	876	-	-	0.84	15	-	-	-	-	-	[868]
Tetramorium	notomelanum	876	-	-	0.78	5	-	-	-	-	-	[874]
Tetramorium	obesum	876	-	-	0.79	1	-	-	-	-	-	[871]
Tetramorium	pacificum	876	-	-	0.74	20	-	-	-	-	-	[873]

Tetramorium	petiolatum	876	-	-	0.33	1	-	-	-	-	-	[878]
Tetramorium	placidum	876	-	-	0.69	2	-	-	-	-	-	[870, 874]
Tetramorium	pleganon	876	-	-	0.9	14	-	-	-	-	-	[868]
Tetramorium	polymorphum	876	-	-	0.73	4	0.55	1	Yes	-	-	[880]
Tetramorium	punctatum	876	-	-	-	-	0.84	10	-	-	-	[63]
Tetramorium	sabatra	876	-	-	1.02	10	-	-	-	-	-	[868]
Tetramorium	semilaeve	876	-	-	-	-	1.13	10	-	No	-	[63]
Tetramorium	sentosum	876	-	-	0.27	1	-	-	-	-	-	[878]
Tetramorium	sericeiventre	876	-	-	0.75	38	-	-	-	-	-	[873]
Tetramorium	shivalikense	876	-	-	0.51	11	-	-	-	-	-	[871]
Tetramorium	simillimum	876	300	1	-	-	-	-	-	-	-	[61]
Tetramorium	singletonae	876	-	-	0.83	8	-	-	-	-	-	[868]

Tetramorium	smaug	876	-	-	0.94	6	-	-	-	-	-	[868]
Tetramorium	snellingi	876	-	-	0.59	21	0.71	2	-	-	-	[875]
Tetramorium	spinosum	876	-	-	0.89	1	-	-	-	-	-	[874]
Tetramorium	tantillum	876	-	-	0.94	5	-	-	-	-	-	[873]
Tetramorium	tonganum	876	-	-	0.58	7	0.65	3	-	-	-	[871]
Tetramorium	tortuosum	876	-	-	0.82	1	-	-	-	-	-	[871]
Tetramorium	tosii	876	-	-	0.88	20	-	-	-	-	-	[873]
Tetramorium	triangulatum	876	-	-	0.46	9	0.63	3	-	-	-	[871]
Tetramorium	tsushimae	876	-	-	-	-	-	-	-	Yes	-	[882]
Tetramorium	urbanii	876	-	-	0.75	2	-	-	-	-	-	[871]
Tetramorium	voasary	876	-	-	0.96	10	-	-	-	-	-	[868]
Tetramorium	weitzeckeri	876	-	-	0.78	1	-	-	-	-	-	[875]

Tetraponera	europaea	172	-	-	0.39	1	0.4	1	-	-	-	[414]
Tetraponera	ocellata	172	-	-	0.47	3	-	-	-	-	-	[414]
Tetraponera	simplex	172	-	-	0.33	3	0.4	1	-	-	-	[414]
Tetraponera	sp.	172	-	-	-	-	-	-	-	No	-	[70]
Thaumatomyrmex	atrox	28	4	1	0.54	1	-	-	-	No	-	[232, 883]
Thaumatomyrmex	bariay	28	-	-	0.88	1	-	-	-	-	-	[884]
Thaumatomyrmex	cochlearis	28	-	-	0.8	4	-	-	-	-	-	[884]
Thaumatomyrmex	contumax	28	2.5	1	-	-	-	-	-	No	-	[232]
Thaumatomyrmex	mandibularis	28	-	-	1.17	6	-	-	-	-	-	[884]
Thaumatomyrmex	nageli	28	-	-	0.84	2	-	-	-	-	-	[884]
Trachymyrmex	arizonensis	183	-	-	1.08	1	1.29	1	-	-	-	[885]
Trachymyrmex	atlanticus	183	-	-	1.39	9	-	-	-	-	-	[886]

Trachymyrmex	carinatus	183	50	1	0.92	1	1.28	1	-	-	-	[885]
Trachymyrmex	cornetzi	183	-	-	-	-	-	-	-	No	-	[98]
Trachymyrmex	desertorum	183	-	-	1.04	1	1.38	1	-	-	-	[885]
Trachymyrmex	haytianus	183	-	-	1.28	3	-	-	-	-	-	[886]
Trachymyrmex	isthmicus	183	60	43	1.28	4	1.28	1	-	No	No	[22, 886]
Trachymyrmex	ixyodus	183	-	-	1.32	8	-	-	-	-	-	[886]
Trachymyrmex	jamaicensis	183	-	-	1.38	12	1.65	1	-	-	-	[885, 886]
Trachymyrmex	kempfi	183	-	-	1	19	-	-	-	-	-	[887]
Trachymyrmex	nogalensis	183	-	-	0.53	1	1.43	1	-	-	-	[885]
Trachymyrmex	pomonae	183	183	1	0.86	112	0.55	10	-	Yes	-	[885]
Trachymyrmex	septentrionalis	183	588.83	67	1	3	1.18	1	Yes	Yes	-	[61, 885, 888-892]
Trachymyrmex	smithi	183	786	1	1.19	1	1.38	1	-	Yes	-	[885]

Trachymyrmex	turrifex	183	150	1	0.88	1	1.15	1	-	No	-	[885]
Trachymyrmex	urichi	183	100	1	-	-	-	-	-	-	-	[19]
Trachymyrmex	urichii	183	-	-	-	-	-	-	-	No	-	[893]
Trachymyrmex	zeteki	183	78.3	136	1.44	3	1.63	1	-	Yes	-	[98, 886, 894]
Typhlomyrmex	clavicornis	17	-	-	0.3	2	-	-	-	-	-	[895]
Typhlomyrmex	major	17	-	-	0.3	2	-	-	-	-	-	[895]
Typhlomyrmex	meire	17	-	-	0.48	11	0.55	10	-	-	-	[896]
Typhlomyrmex	prolatus	17	-	-	-	-	0.3	2	-	-	-	[895]
Typhlomyrmex	pusillus	17	21	1	0.28	1	0.29	1	-	No	-	[895]
Typhlomyrmex	rogenhoferi	17	-	-	-	-	0.43	1	-	-	-	[895]
Tyrannomyrmex	rex	3	-	-	0.3	1	-	-	-	-	-	[897]
Vollenhovia	emeryi	63	-	-	-	-	-	-	-	Yes	-	[692]

Vombisidris	humboldticola	8	25	1	0.28	1	0.3	1	-	-	-	[898]
Vombisidris	umbrabdomina	8	-	-	0.36	1	-	-	-	-	-	[899]
Wasmannia	auropunctata	329	1095.56	287	-	-	-	-	-	Yes	Yes	[61, 70, 226, 692, 900-902]
Xenomyrmex	floridanus	13	50	1	-	-	-	-	-	-	-	[61]
Zatania	albimaculata	5	-	-	0.67	2	-	-	-	-	-	[903]
Zatania	cisipa	5	-	-	0.62	6	-	-	-	-	-	[903]
Zatania	gibberosa	5	-	-	0.93	3	-	-	-	-	-	[903]
Zatania	gloriosa	5	-	-	0.61	5	-	-	-	-	-	[903]

(b)

Genus	**se**	**cs**	**cs ss**	**wk hw**	**wk hw ss**	**q hw**	**q hw ss**	**w pm**	**pg**	**pa**	**ref**
Acanthognathus	29	-	-	0.49	28	0.44	6	-	-	-	[1, 2]
Acanthomyrmex	15	24.78	91	1.18	261	1.05	27	Yes	No	-	[3-9]
Acanthostichus	26	-	-	0.95	139	1.38	5	-	-	-	[10-13]
Acromyrmex	923	5232.26	39	1.47	126	-	-	Yes	Yes	Yes	[14-34]

Acropyga	81	167	2	0.49	12	-	9	-	Yes	-	[35-38]
Adelomyrmex	12	28.75	3	0.5	56	-	-	Yes	No	-	[39, 40]
Aenictus	134	79293.37	57	0.64	412	1.39	7	Yes	-	Yes	[41-59]
Amblyopone	111	25.4	17	-	-	-	-	-	Yes	-	[11, 60-62]
Aneuretus	21	40	1	-	-	-	-	-	-	-	[19]
Ankylomyrma	2	-	-	1.4	4	-	-	No	-	-	[64]
Anochetus	88	-	-	1.43	96	1.38	20	-	No	-	[65-69]
Anoplolepis	309	3599.06	80	0.28	1	-	-	-	Yes	-	[70-74]
Aphaenogaster	590	848.1	343	0.85	301	1.09	36	Yes	No	No	[19, 38, 61, 75-94]
Aphomomyrmex	17	-	-	0.44	2087	-	-	-	-	-	[95]
Apterostigma	77	27.68	97	0.74	3	-	-	No	No	No	[18, 22, 96-99]
Aptinoma	2	-	-	-	22	0.59	1	-	-	-	[100]
Asphinctanilloides	6	-	-	0.36	17	-	-	-	-	-	[101]
Asphinctopone	5	-	-	0.72	22	-	-	-	-	-	[102, 103]
Atopomyrmex	11	-	-	1.59	85	-	-	Yes	-	-	[64]
Atta	1722	3389250	8	1.67	9	-	-	Yes	No	Yes	[18, 22, 104-118]
Axinidris	7	-	-	0.76	141	0.76	6	-	-	-	[119, 120]
Baracidris	2	-	-	0.28	6	0.2	1	No	-	-	[64]
Basiceros	22	31.67	3	0.83	15	0.72	6	Yes	No	Yes	[121-124]
Belonopelta	8	10	1	-	-	-	-	-	No	-	[41]
Blepharidatta	10	161.37	132	-	-	-	-	No	No	-	[125-127]
Bothriomyrmex	52	-	-	0.52	5	0.54	4	-	-	-	[128]
Brachymyrmex	171	200	1	0.49	166	0.53	24	-	No	Yes	[61, 129-131]
Camponotus	5444	4128.41	110	1.35	664	1.61	64	Yes	Yes	No	[19, 40, 61, 70, 74, 76, 79, 80, 132-167, 248]
Cardiocondyla	235	50	3	0.46	283	0.49	17	Yes	Yes	Yes	[61, 70, 168-170]
Carebara	41	290	2	0.29	8	-	-	Yes	-	-	[19, 171]

Cataglyphis	894	861.39	3525	1.18	2531	1.43	38	-	No	Yes	[19, 70, 74, 131, 137, 172-180]
Cataulacus	57	248	75	-	-	-	-	-	Yes	-	[70, 181, 182]
Centromyrmex	21	329.44	8	1.08	300	1.37	28	Yes	Yes	-	[11, 102, 183, 184]
Cephalotes	299	2768.14	13	1.46	802	-	-	Yes	Yes	-	[19, 70, 185-188]
Cerapachys	95	405.36	14	0.62	435	1.23	3	-	No	-	[8, 74, 189-193]
Chalepoxenus	45	-	-	0.5	16	0.46	9	-	No	-	[194-196]
Cheliomyrmex	22	-	-	1.8	1	-	-	Yes	-	-	[197-199]
Chimaeridris	1	-	-	0.41	3	-	-	-	-	-	[200]
Cladomyrma	28	15000	1	0.75	236	1.16	105	-	Yes	-	[201-203]
Crematogaster	1225	1601.19	125	0.83	518	1	62	Yes	Yes	-	[19, 61, 70, 204-220]
Cyphoidris	2	-	-	0.61	28	-	-	No	-	-	[64]
Cyphomyrmex	116	388.14	665	0.67	352	0.72	67	No	No	No	[18, 22, 61, 98, 221-227]
Dacatria	2	-	-	0.34	1	-	-	-	-	-	[228]
Daceton	28	168811.65	10	1.96	179	-	-	Yes	Yes	-	[229-231]
Diacamma	190	131.12	621	2.06	22	-	-	No	Yes	No	[81, 232-261]
Dilobocondyla	8	42.5	4	0.85	10	0.53	1	-	No	-	[262]
Dinoponera	139	53.78	240	5.18	240	-	-	No	Yes	No	[19, 81, 148, 232, 255, 263-277]
Dolichoderus	290	125	1	-	6730	1.56	510	-	No	-	[70, 226, 278]
Dorylus	223	9206250	10	1.51	1251	2.75	2	Yes	No	Yes	[16, 47, 118, 163, 189, 279-286]
Dorymyrmex	149	1666.67	6	-	-	-	-	-	Yes	-	[19, 61, 70]
Echinopla	14	-	-	0.95	1	-	-	-	-	-	[287]
Eciton	345	327360.96	25	2.02	2	-	-	Yes	No	Yes	[19, 47, 57, 163, 189, 197, 288-305]
Ectatomma	374	84.71	636	2.63	8	3.24	232	No	Yes	No	[269, 306-333]
Epopostruma	14	-	-	0.29	1	-	-	-	-	-	[335]
Euprenolepis	11	6375	2	0.78	28	0.57	3	-	-	-	[336, 337]

Eurhopalothrix	20	129.67	4	0.64	89	0.52	3	No	No	-	[61, 338-342]
Eutetramorium	6	41.11	18	-	-	-	-	-	-	-	[343]
Feroponera	1	-	-	0.61	8	-	-	-	-	-	[102, 183]
Forelius	114	10000	1	-	-	-	-	-	-	-	[61]
Forelophilus	2	-	-	0.74	12	0.69	1	-	-	-	[344]
Formica	6671	2921591.28	651	1.33	2359	1.52	190	Yes	Yes	Yes	[19, 61, 70, 118, 131, 243, 345-407]
Gesomyrmex	13	-	-	0.75	1	-	-	-	-	-	[408]
Gigantiops	26	57.35	42	-	-	-	-	-	No	-	[70, 175]
Gnamptogenys	129	156.77	204	0.84	130	1.11	25	No	No	No	[5, 81, 232, 264, 274, 409-429]
Harpegnathos	149	90.89	179	2.08	46	2.25	29	-	Yes	-	[81, 232, 266, 274, 410, 418, 431-438]
Heteroponera	35	80	1	-	-	-	-	-	No	-	[60]
Hypoponera	199	52.9	192	0.49	1062	0.58	83	-	Yes	No	[60, 61, 70, 322, 436, 439-447]
Ishakidris	2	-	-	0.53	1	-	-	-	-	-	[448]
Kalathomyrmex	2	145	10	-	-	-	-	No	No	-	[449, 450]
Kartidris	9	-	-	0.77	8	0.93	1	-	-	-	[451]
Labidus	121	1500000	3	1.54	1	-	-	-	No	-	[19, 197, 452-454]
Lasius	2018	15004.19	148	0.94	898	1.41	96	-	Yes	Yes	[70, 131, 153, 154, 455-478]
Lenomyrmex	5	-	-	0.46	69	0.33	4	No	-	-	[40, 479, 480]
Lepisiota	46	-	-	0.51	91	-	-	No	-	-	[74, 137, 481]
Leptanilla	56	68.58	12	0.24	127	0.31	1	-	No	-	[62, 482-485]
Leptanilloides	13	-	-	0.35	22	0.58	4	-	-	-	[101, 486]
Leptogenys	181	4204.49	25	1.01	554	0.94	28	No	-	-	[19, 60, 232, 410, 487-493]
Leptothorax	1052	189.02	265	0.42	14	0.38	9	-	Yes	-	[19, 138, 158, 273, 494-500]

Linepithema	830	15000	1	-	-	-	-	-	Yes	-	[19, 70]
Liomyrmex	7	-	-	0.74	60	1.31	5	-	-	-	[501, 502]
Lophomyrmex	22	50	1	0.7	2	-	-	-	-	-	[283, 503]
Martialis	3	-	-	0.65	1	-	-	-	-	-	[904]
Mayriella	15	-	-	0.22	1	-	-	-	-	-	[335]
Megalomyrmex	46	216.5	10	0.95	1285	0.69	9	No	-	-	[411, 505, 506]
Melissotarsus	15	-	-	0.62	1	0.66	1	-	-	-	[507]
Melophorus	157	815.2	6	1.36	36	-	1	-	No	-	[508-511]
Meranoplus	73	-	-	0.85	221	0.66	12	-	-	-	[512, 513]
Mesostruma	13	-	-	0.28	1	-	-	-	-	-	[335]
Messor	753	1456.67	14	1.02	2	1.37	131	Yes	Yes	Yes	[19, 33, 70, 74, 514-522]
Metapone	14	27.77	13	0.6	20	0.5	4	-	No	-	[502, 523-526]
Monomorium	1062	4123.86	119	-	-	-	-	-	Yes	-	[6, 61, 70, 527]
Mycetagroicus	6	-	-	0.36	2	-	-	No	-	-	[528]
Mycetarotes	25	60.27	32	0.83	25	0.48	3	No	No	-	[529-531]
Mycetophylax	16	212.1	32	-	-	-	-	No	No	-	[449, 450, 532]
Mycetosoritis	8	-	-	0.32	1	-	-	No	-	-	[533]
Mycocepurus	57	329.09	196	0.54	6	0.45	1	No	No	No	[533-537]
Myopias	109	47.5	2	-	-	-	-	-	No	-	[410]
Myrmecia	415	362.1	63	2.42	1413	3.2	1	No	Yes	Yes	[19, 163, 431, 538-546]
Myrmecina	124	40.35	276	0.63	777	0.97	380	Yes	Yes	No	[3, 61, 62, 477, 547-557]
Myrmecocystus	116	2248.67	4	0.96	938	1.55	24	-	No	No	[558-562]
Myrmelachista	61	375104.97	88	0.6	128	0.9	188	-	Yes	-	[563-566]
Myrmica	1727	479.17	1832	0.94	745	0.88	1049	No	Yes	Yes	[60, 70, 243, 567-599]
Myrmicaria	110	9677.19	101	1.54	5821	2.65	30	Yes	Yes	-	[19, 70, 600-602]
Myrmicocrypta	34	60.34	35	0.63	31	0.72	3	No	No	No	[18, 22, 227, 603]
Myrmoteras	14	15	2	0.66	63	0.46	1	No	-	-	[19, 44, 604-606]
Mystrium	31	14.5	1	-	-	-	-	-	-	-	[163]

Neivamyrmex	153	47610.18	21	1.07	28	-	2	Yes	Yes	Yes	[47, 57, 61, 189, 197, 452, 533, 607-612]
Nesomyrmex	15	32	1	0.68	351	-	-	-	No	-	[40, 613, 614]
Nomamyrmex	32	1000000	1	4.4	55	-	-	Yes	-	-	[197, 615, 616]
Nothomyrmecia	50	36.64	66	-	-	-	-	No	No	Yes	[168, 431, 617-619]
Nylanderia	79	288	21	0.57	695	-	-	No	Yes	-	[62, 70, 86, 96, 620-629]
Octostruma	16	-	-	0.55	9	-	-	-	-	-	[630]
Ocymyrmex	49	500.5	13	1.56	322	1.73	30	No	No	-	[19, 64, 631, 632]
Odontomachus	282	577.7	89	1.94	1024	2.16	153	No	Yes	-	[19, 60, 61, 65, 66, 70, 79, 158, 226, 410, 633-645]
Odontoponera	26	50	2	-	-	-	-	-	-	-	[283]
Oecophylla	540	3098.89	83	1.35	6	3.33	1	Yes	Yes	Yes	[70, 331, 646-656]
Onychomyrmex	13	848.27	121	0.71	401	0.73	60	No	No	-	[60, 163]
Ophthalmopone	20	400	1	-	-	-	-				[19]
Opisthopsis	16	150	1	-	-	-	-	-	No	-	[657]
Orectognathus	21	27.5	2	0.82	62	0.58	2	Yes	No	-	[658-661]
Pachycondyla	584	254.08	824	1.54	223	1.73	128	Yes	Yes	Yes	[11, 19, 33, 60, 65, 70, 138, 163, 168, 211, 226, 232, 233, 266, 269, 272, 283, 322, 410, 414, 418, 431, 439, 639, 642, 662-690]
Paraparatrechina	16	-	-	0.4	216	0.44	2	-	-	-	[691]
Paratopula	7	-	-	0.77	8	1.05	1	-	-	-	[575]
Paratrechina	500	100	5	0.54	15	-	-	-	Yes	-	[61, 70, 620, 692]
Perissomyrmex	11	70	1	0.87	261	0.79	7	Yes	No	-	[693-698]
Peronomyrmex	4	-	-	0.39	4	-	-	-	-	-	[339, 699, 700]
Petalomyrmex	37	900.12	386	0.35	199	-	-	-	Yes	-	[95, 181, 182, 701]

Pheidole	1798	4943.02	137	0.93	1119	-	56	Yes	Yes	No	[19, 61, 70, 74, 96, 243, 252, 381, 445, 702-727]
Pheidologeton	69	118333.33	3	-	-	-	-	Yes	-	-	[19, 283]
Phrynoponera	2	-	-	1.98	63	-	-	-	-	-	[183]
Pilotrochus	2	-	-	0.3	1	-	-	-	-	-	[643]
Plagiolepis	235	25050	2	0.22	25	-	1	-	Yes	-	[70, 74, 134, 154, 477, 728-730]
Platythyrea	98	67.87	449	1.58	15	2.13	16	-	No	-	[60, 61, 226, 232, 731-741]
Plectroctena	23	81.09	19	2.61	89	3.01	28	-	No	-	[60, 742-746]
Pogonomyrmex	1138	3571.08	135	1.34	206	1.82	166	Yes	Yes	Yes	[16, 19, 61, 79, 747-764]
Polyergus	299	920.38	5	-	-	-	-	-	No	No	[131, 379, 765-768]
Polyrhachis	421	2798.62	1929	1.32	1014	1.1	84	No	Yes	-	[70, 251, 634, 769-787]
Ponera	205	523.2	8	0.51	17	-	34	No	Yes	-	[19, 61, 788-792]
Prenolepis	143	1980.11	56	0.63	46	0.52	2	No	Yes	Yes	[86, 131, 629, 793-795]
Prionopelta	30	350	1	-	-	-	-	-	No	-	[70, 163]
Pristomyrmex	126	7665.22	23	0.89	846	-	-	Yes	No	-	[3, 6, 64, 796-804]
Proatta	6	10000	1	0.59	10	-	-	-	-	-	[19, 228]
Probolomyrmex	34	12.5	1	-	-	-	-	-	No	-	[410]
Proceratium	73	125	2	0.69	6	-	-	-	No	-	[61, 410, 411]
Procryptocerus	27	77.88	5	1.01	137	-	-	No	Yes	-	[70, 187, 805]
Proformica	92	6531.28	162	-	-	-	-	Yes	Yes	Yes	[70, 477, 806-812]
Promyopias	1	-	-	1.06	10	1.17	2	-	-	-	[102, 183]
Psalidomyrmex	5	-	-	2.28	51	1.84	3	-	-	-	[813]
Pseudolasius	42	-	-	0.87	33	-	-	Yes	Yes	-	[70, 814, 815]
Pseudomyrmex	288	1724.17	6	-	-	-	-	-	Yes	-	[19, 61, 70]
Recurvidris	10	-	-	0.4	75	-	-	No	-	-	[451, 816]
Rhopalothrix	19	-	-	-	-	0.38	1	-	-	-	[339]
Rhoptromyrmex	7	-	-	-	-	0.56	1	-	-	-	[817]

Rhytidoponera	205	201.28	752	1.58	420	2.14	249	No	Yes	No	[60, 81, 232, 244, 264, 266, 436, 511, 667, 781, 818-833]
Romblonella	9	-	-	0.7	4	-	-	-	-	-	[834]
Rossomyrmex	32	295.75	10	1.14	1	-	-	-	No	Yes	[806, 810, 835-838]
Secostruma	3	-	-	0.47	1	-	-	-	-	-	[839]
Sericomyrmex	52	200	12	0.93	-	-	-	No	No	No	[22, 98]
Simopelta	17	953.67	3	0.78	11	0.67	1	-	No	No	[840, 841]
Solenopsis	9439	23606.25	8	0.43	1	-	-	Yes	Yes	-	[60, 61, 70, 158, 244, 411]
Stegomyrmex	8	188	2	0.75	5	0.82	4	-	No	-	[842, 843]
Stereomyrmex	3	-	-	0.3	2	-	-	-	-	-	[834]
Stigmatomma	14	48.52	18	-	-	-	-	-	Yes	-	[11, 33, 60, 62, 70, 163, 232, 431, 671]
Streblognathus	15	68.3	100	4.31	297	4.39	15	-	No	No	[60, 232, 271, 671, 844-848]
Strongylognathus	59	-	-	-	-	0.35	1	-	-	-	[849]
Strumigenys	184	110.31	96	0.39	214	0.4	31	No	Yes	-	[6, 19, 40, 54, 61, 252, 658, 850-860]
Tapinolepis	1	-	-	0.28	2	-	-	-	-	-	[137]
Tapinoma	637	575	12	-	-	-	-	No	Yes	-	[19, 70, 96]
Technomyrmex	168	444139.53	43	0.47	401	0.75	100	-	Yes	-	[70, 74, 435, 436, 861, 862]
Temnothorax	384	90.91	11	0.45	109	0.43	23	-	Yes	-	[19, 61, 70, 497, 614, 683, 863-866]
Terataner	1	29	16	1.06	57	-	-	No	Yes	-	[64, 867]
Tetramorium	876	1140.63	20	0.73	643	-	70	Yes	Yes	-	[61, 63, 70, 74, 868-882]
Tetraponera	172	-	-	0.39	7	0.4	2	-	No	-	[70, 414]
Thaumatomyrmex	28	3.25	2	0.85	14	-	-	-	No	-	[232, 883, 884]
Trachymyrmex	183	249.52	251	1.11	179	1.29	20	No	No	No	[19, 22, 61, 98, 885-894]
Typhlomyrmex	17	21	1	0.34	16	0.39	14	-	No	-	[895, 896]

Tyrannomyrmex	3	-	-	0.3	1	-	-	-	-	-	[897]
Vombisidris	8	25	1	0.32	2	0.3	1	-	-	-	[898, 899]
Wasmannia	329	1095.56	287	-	-	-	-	-	Yes	No	[61, 70, 226, 692, 900-902]
Xenomyrmex	13	50	1	-	-	-	-	-	-	-	[61]
Zatania	5	-	-	0.71	16	-	-	-	-	-	[903]

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9.2 Appendix 2

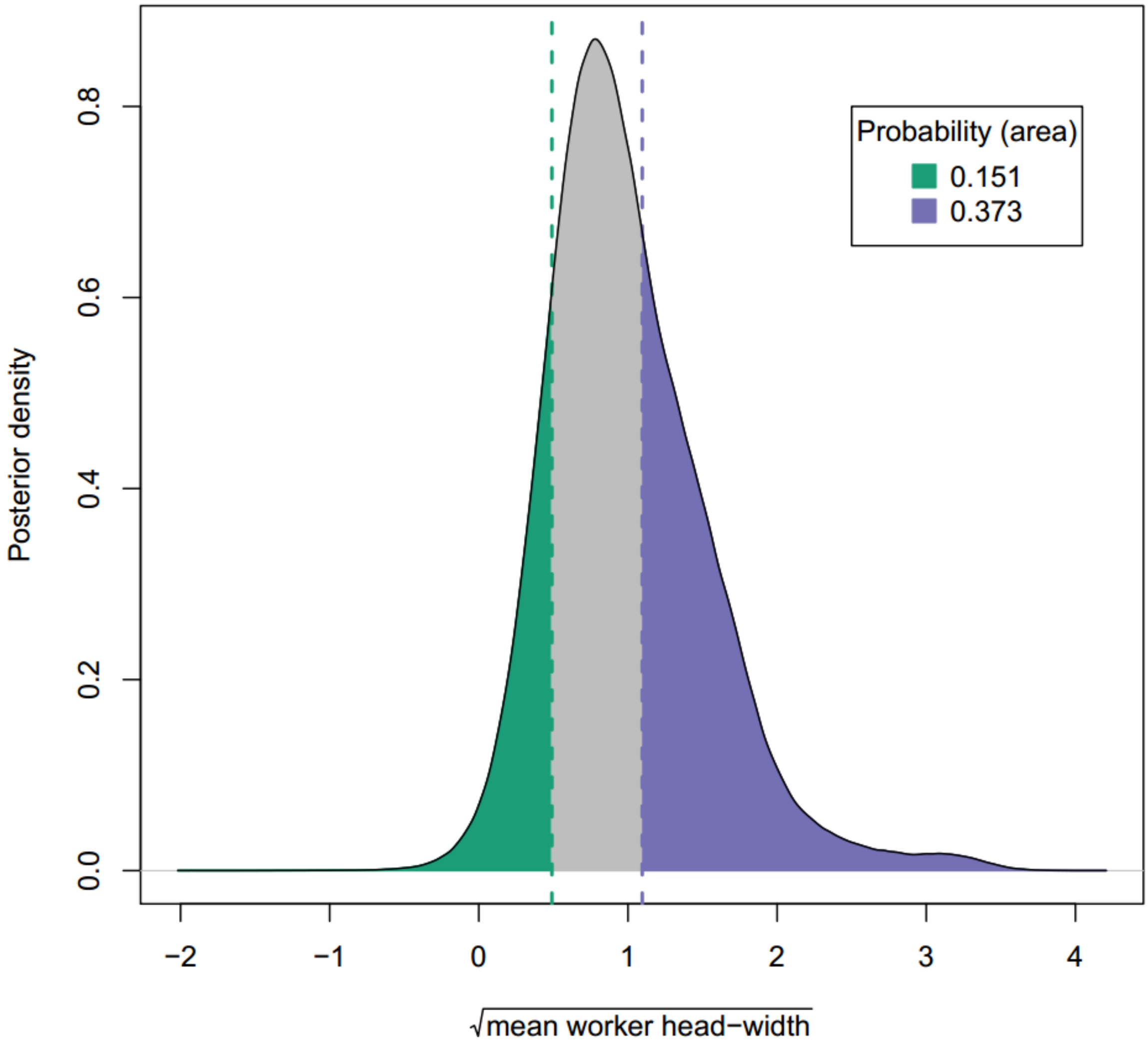

Figure A2.1 The posterior distribution of mean worker head-width at the root of a genus-level phylogeny of the ants excluding the genus *Martialis* (164 tips). Dotted lines indicate the expected head-widths under the *Leptanilla*-like ancestor hypothesis (green) and the *Sphecomyrma*-like ancestor hypothesis (purple). Coloured areas show the areas of unambiguous support for the two respective hypotheses (green, ancestral worker head width less than or equal to worker head width of *Leptanilla*; blue, ancestral worker head width equal to or greater than worker head width of *Sphecomyrma*).

9.3 Appendix 3

Table A3.1 Inferred colony sizes at the internal nodes of a genus-level phylogeny of the ants. Values are post-burnin means of a Bayesian estimation of colony size at each internal node of the phylogeny. Values were inferred from a Brownian motion-based model. Node numbers correspond to those on figure A4.1.

Node	Colony size	Node	Colony size	Node	Colony size
148	39.45	195	394.32	242	102.89
149	83.43	196	416.04	243	636.70
150	238.48	197	432.13	244	742.01
151	491.15	198	771.12	245	964.88
152	468.47	199	1300.16	246	1560.41
153	466.56	200	3854.28	247	2289.85
154	481.42	201	348.49	248	3606.11
155	436.15	202	357.06	249	6976.79
156	441.00	203	312.48	250	507.69
157	438.99	204	91.91	251	143.70
158	437.16	205	113.48	252	6460.23
159	211.57	206	653.29	253	24508.16
160	151.94	207	650.73	254	32671.54
161	143.50	208	1018.08	255	65989.67
162	130.54	209	675.15	256	128401.40
163	595.96	210	97.85	257	341593.84
164	618.69	211	78.59	258	212842.71
165	2785.60	212	868.05	259	100.12
166	106.15	213	836.92	260	103.02
167	64.59	214	849.98	261	118.00
168	49.27	215	1539.76	262	128.73
169	181.50	216	1792.86	263	128.95
170	295.43	217	1749.83	264	137.40
171	171.38	218	1726.60	265	152.17
172	106.35	219	1620.18	266	177.33
173	106.90	220	1887.97	267	123.73
174	108.19	221	998.64	268	181.02
175	140.84	222	4780.96	269	189.47
176	162.70	223	2740.74	270	239.27
177	1894.68	224	2507.41	271	390.05
178	3062.71	225	4575.65	272	111.43
179	2061.26	226	16818.23	273	126.47
180	1336.01	227	745.14	274	118.67
181	1233.22	228	623.74	275	119.12
182	1095.78	229	539.40	276	120.55
183	1098.82	230	724.60	277	120.98
184	1146.28	231	994.51	278	98.52
185	3673.43	232	2213.95	279	114.99
186	732.87	233	2526.34	280	60.10
187	728.89	234	756.19	281	92.44
188	867.90	235	1146.52	282	79.62

189	1197.73	236	3261.06	283	79.66
190	382.02	237	5529.82	284	59.61
191	393.78	238	6550.89	285	24.22
192	394.83	239	154.75	286	129.54
193	393.87	240	153.98	287	210.68
194	392.84	241	140.66	288	44.31

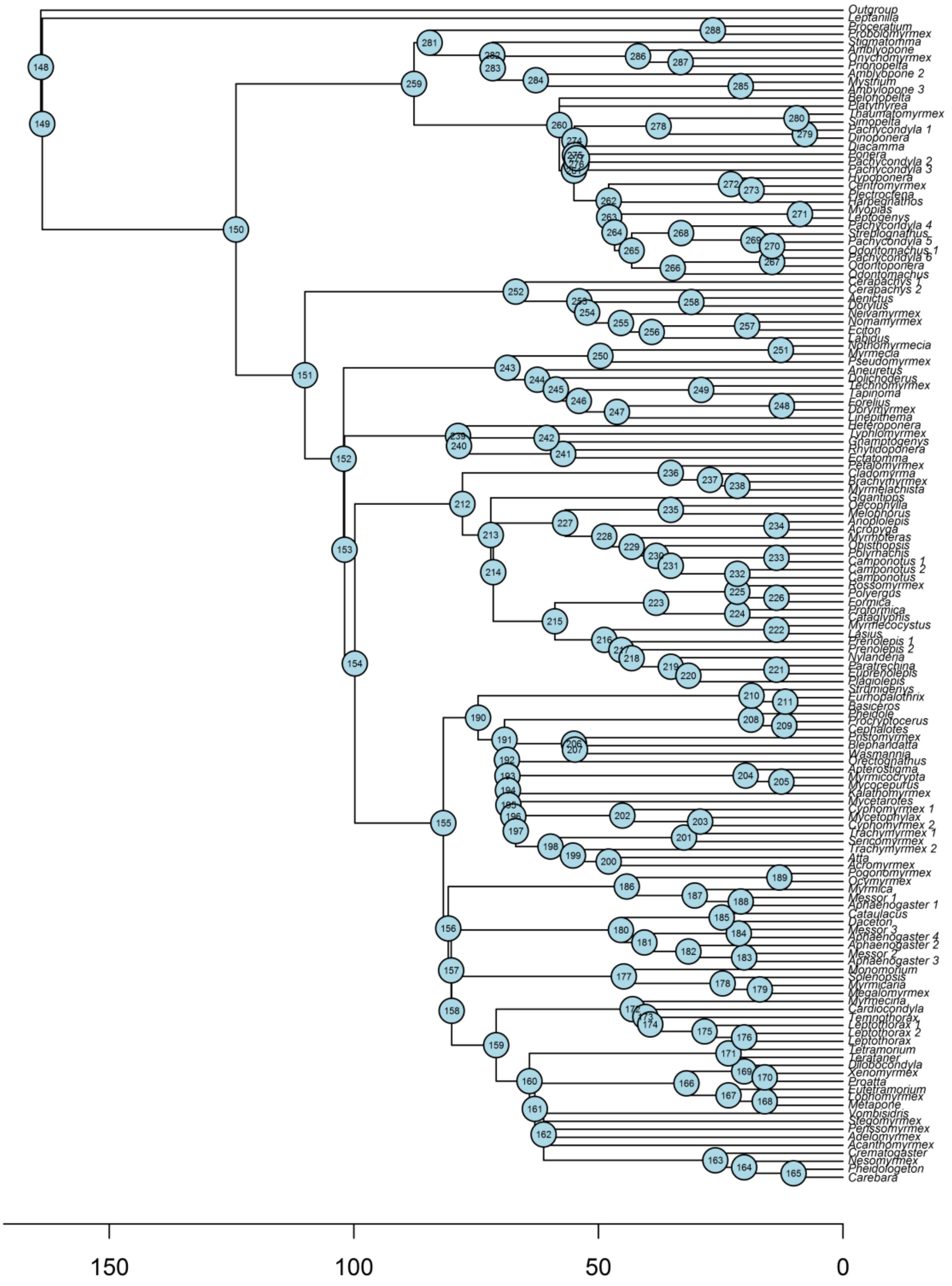

Figure A3.1 The pruned genus-level tree which was used to infer ancestral colony sizes. Node numbers correspond to table A3.1 The scale bar represents millions of years before present.

Table A3.2 The probabilities of the absence or presence of discrete worker castes at each internal node of a genus-level phylogeny, as inferred by the threshold model. Node numbers correspond to those on figure A3.2.

Node	**Absent**	**Present**	**Node**	**Absent**	**Present**
99	0.69	0.31	144	0.91	0.09
100	0.59	0.41	145	0.96	0.04
101	0.51	0.49	146	0.95	0.05
102	0.59	0.41	147	0.98	0.02
103	0.60	0.40	148	0.99	0.01
104	0.53	0.47	149	0.45	0.55
105	0.05	0.95	150	0.26	0.74
106	0.01	0.99	151	0.34	0.66
107	0.00	1.00	152	0.66	0.34
108	0.00	1.00	153	0.61	0.39
109	0.12	0.88	154	0.49	0.51
110	0.19	0.81	155	0.53	0.47
111	0.24	0.76	156	0.77	0.23
112	0.35	0.65	157	0.78	0.22
113	0.06	0.94	158	0.78	0.22
114	0.03	0.97	159	0.69	0.31
115	0.02	0.98	160	0.20	0.80
116	0.45	0.55	161	0.35	0.65
117	0.09	0.91	162	0.39	0.61
118	0.19	0.81	163	0.33	0.67
119	0.28	0.72	164	0.16	0.84
120	0.05	0.95	165	0.45	0.55
121	0.04	0.96	166	0.87	0.13
122	0.06	0.94	167	0.92	0.08
123	0.05	0.95	168	0.82	0.18
124	0.04	0.96	169	0.96	0.04
125	0.02	0.98	170	0.02	0.98
126	0.32	0.68	171	0.01	0.99
127	0.32	0.68	172	0.01	0.99
128	0.15	0.85	173	0.01	0.99
129	0.40	0.60	174	0.02	0.98
130	0.27	0.73	175	0.79	0.21
131	0.34	0.66	176	0.80	0.20
132	0.43	0.57	177	0.70	0.30
133	0.44	0.56	178	0.48	0.52
134	0.45	0.55	179	0.46	0.54
135	0.47	0.53	180	0.43	0.57
136	0.48	0.52	181	0.49	0.51
137	0.50	0.50	182	0.39	0.61
138	0.55	0.45	183	0.48	0.52
139	0.60	0.40	184	0.73	0.27
140	0.63	0.37	185	0.68	0.32
141	0.52	0.48	186	0.64	0.36
142	0.35	0.65	187	0.61	0.39
143	0.89	0.11	188	0.51	0.49

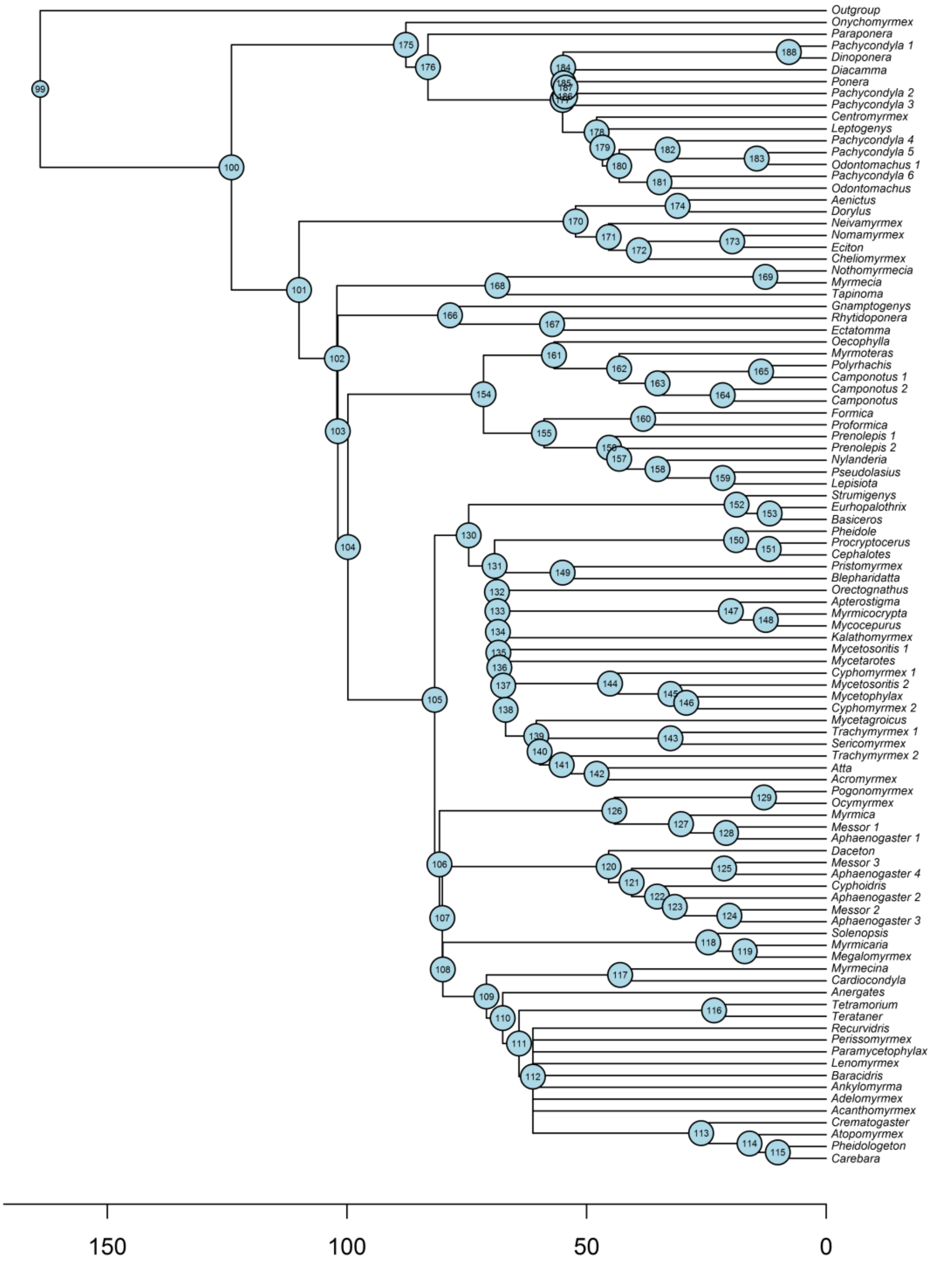

Figure A3.2 The pruned genus-level phylogeny used to infer the presence or absence of discrete worker castes. Node numbers correspond to those in table A3.2. The scale bar represents millions of years before present.

Table A3.3 The inferred probabilities of the absence and presence of polygyny at the internal nodes of a genus-level phylogeny of the ants. Probabilities were inferred under the threshold model. Node numbers correspond to those in figure A3.3.

Node	Absent	Present	Node	Absent	Present
146	0.89	0.11	216	0.01	0.99
147	0.89	0.11	217	0.01	0.99
148	0.56	0.44	218	0.01	0.99
149	0.36	0.64	219	0.28	0.72
150	0.04	0.96	220	0.35	0.65
151	0.02	0.98	221	0.35	0.65
152	0.08	0.92	222	0.57	0.43
153	0.26	0.74	223	0.57	0.43
154	0.26	0.74	224	0.13	0.87
155	0.21	0.79	225	0.10	0.90
156	0.17	0.83	226	0.06	0.94
157	0.55	0.45	227	0.04	0.96
158	0.76	0.24	228	0.03	0.97
159	0.86	0.14	229	0.02	0.98
160	0.87	0.13	230	0.05	0.95
161	0.89	0.11	231	0.30	0.70
162	0.61	0.39	232	0.12	0.88
163	0.92	0.08	233	0.12	0.88
164	0.26	0.74	234	0.20	0.80
165	0.20	0.80	235	0.02	0.98
166	0.25	0.75	236	0.02	0.98
167	0.22	0.78	237	0.10	0.90
168	0.20	0.80	238	0.53	0.47
169	0.20	0.80	239	0.20	0.80
170	0.17	0.83	240	0.11	0.89
171	0.10	0.90	241	0.05	0.95
172	0.53	0.47	242	0.03	0.97
173	0.50	0.50	243	0.03	0.97
174	0.09	0.91	244	0.03	0.97
175	0.05	0.95	245	0.04	0.96
176	0.30	0.70	246	0.14	0.86
177	0.37	0.63	247	0.23	0.77
178	0.50	0.50	248	0.37	0.63
179	0.52	0.48	249	0.44	0.56
180	0.43	0.57	250	0.52	0.48
181	0.11	0.89	251	0.88	0.12
182	0.31	0.69	252	0.95	0.05
183	0.16	0.84	253	0.95	0.05
184	0.30	0.70	254	0.90	0.10
185	0.05	0.95	255	0.92	0.08
186	0.46	0.54	256	0.94	0.06
187	0.44	0.56	257	0.54	0.46
188	0.53	0.47	258	0.60	0.40
189	0.60	0.40	259	0.70	0.30

190	0.59	0.41	260	0.63	0.37
191	0.56	0.44	261	0.78	0.22
192	0.55	0.45	262	0.84	0.16
193	0.60	0.40	263	0.71	0.29
194	0.69	0.31	264	0.49	0.51
195	0.75	0.25	265	0.35	0.65
196	0.76	0.24	266	0.32	0.68
197	0.69	0.31	267	0.32	0.68
198	0.90	0.10	268	0.24	0.76
199	0.88	0.12	269	0.14	0.86
200	0.92	0.08	270	0.31	0.69
201	0.96	0.04	271	0.32	0.68
202	0.99	0.01	272	0.61	0.39
203	0.23	0.77	273	0.59	0.41
204	0.24	0.76	274	0.61	0.39
205	0.05	0.95	275	0.65	0.35
206	0.04	0.96	276	0.53	0.47
207	0.64	0.36	277	0.05	0.95
208	0.82	0.18	278	0.94	0.06
209	0.15	0.85	279	0.52	0.48
210	0.13	0.87	280	0.15	0.85
211	0.15	0.85	281	0.14	0.86
212	0.13	0.87	282	0.16	0.84
213	0.04	0.96	283	0.62	0.38
214	0.01	0.99	284	0.78	0.22
215	0.01	0.99	285	0.94	0.06

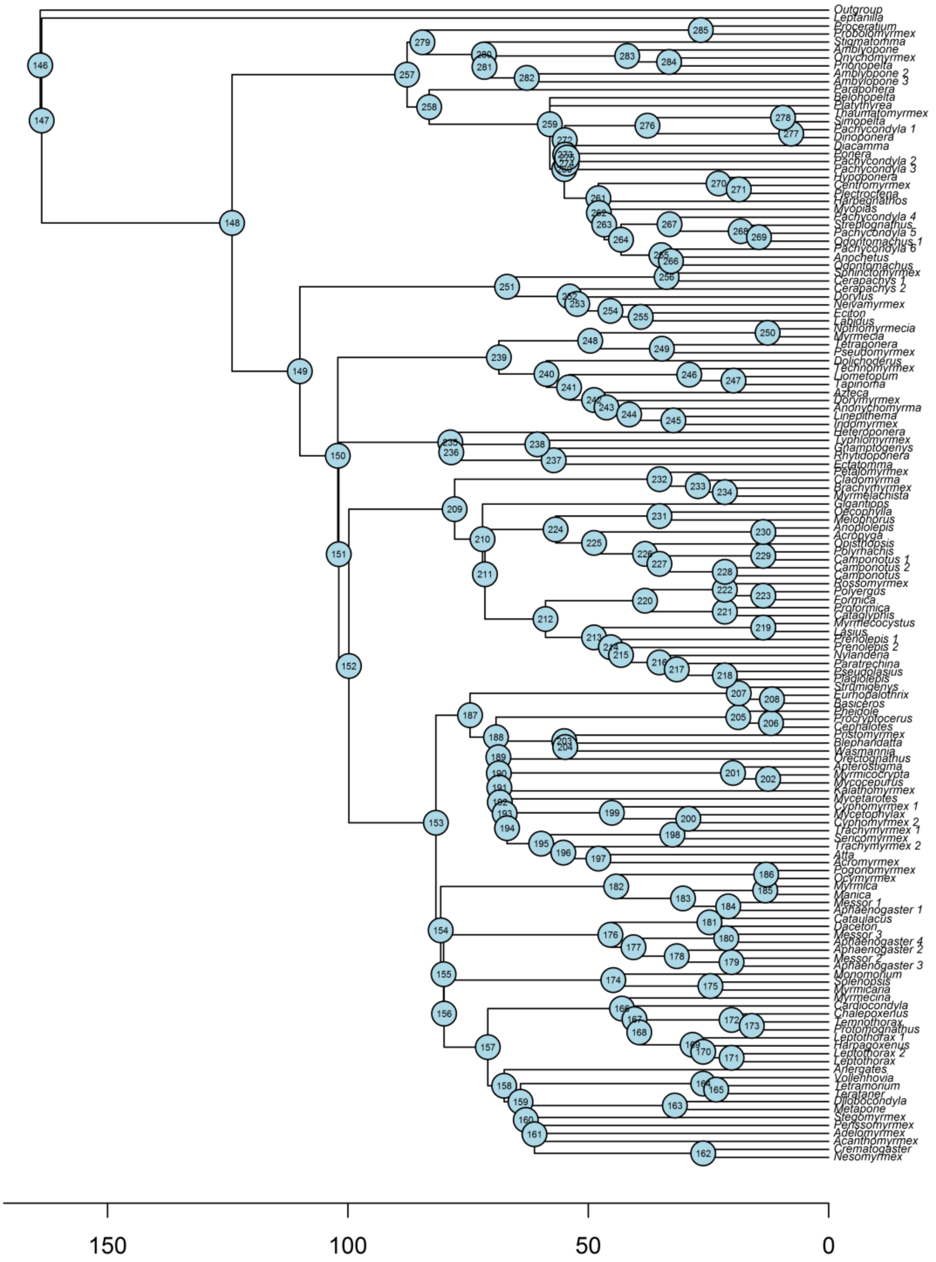

Figure A3.3 The pruned genus-level phylogeny of the ants that was used to infer the probability of the presence or absence of polygyny under a threshold model. Node numbers correspond to those in table A3.3. The scale bar represents millions of years before present.

Table A4.4 The inferred probabilities of the absence and presence of polyandry at each internal node of a genus-level phylogeny of the ants. Probabilites were inferred under a threshold model. Node numbers correspond to those on figure A4.4.

Node	Absent	Present	Node	Absent	Present
60	0.62	0.38	89	0.36	0.64
61	0.50	0.50	90	0.37	0.63
62	0.45	0.55	91	0.14	0.86
63	0.55	0.45	92	0.13	0.87
64	0.55	0.45	93	0.11	0.89
65	0.54	0.46	94	0.36	0.64
66	0.61	0.39	95	0.03	0.97
67	0.61	0.39	96	0.03	0.97
68	0.61	0.39	97	0.02	0.98
69	0.53	0.47	98	0.01	0.99
70	0.65	0.35	99	0.73	0.27
71	0.70	0.30	100	0.91	0.09
72	0.63	0.37	101	0.95	0.05
73	0.58	0.42	102	0.78	0.22
74	0.47	0.53	103	0.87	0.13
75	0.62	0.38	104	0.50	0.50
76	0.58	0.42	105	0.04	0.96
77	0.69	0.31	106	0.04	0.96
78	0.83	0.17	107	0.02	0.98
79	0.84	0.16	108	0.37	0.63
80	0.85	0.15	109	0.39	0.61
81	0.84	0.16	110	0.32	0.68
82	0.78	0.22	111	0.28	0.72
83	0.69	0.31	112	0.39	0.61
84	0.50	0.50	113	0.37	0.63
85	0.90	0.10	114	0.38	0.62
86	0.88	0.12	115	0.39	0.61
87	0.96	0.04	116	0.61	0.39
88	0.98	0.02	117	0.53	0.47

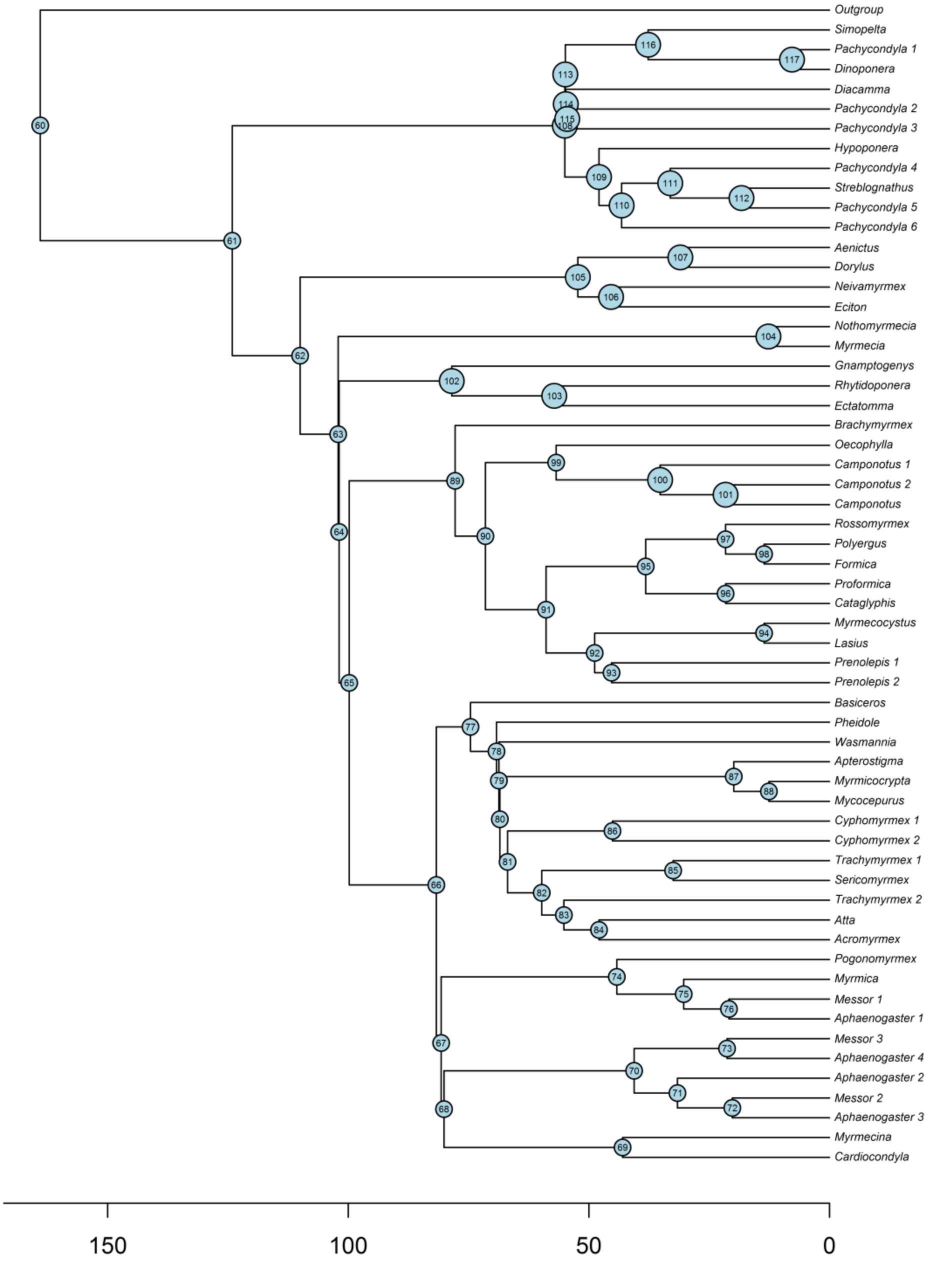

Figure A4.4 The pruned genus-level phylogeny of the ants that was used to infer the presence or absence of polyandry at each internal node. Node numbers correspond to those in table A4.4. The scale bar represents millions of years before present.

9.4 Appendix 4

Table A4.1 Life history and environmental traits and data sources for 57 species of Attini. All means are weighted by the sample sizes of the sources contributing to them. All sample sizes are the sum of the sample sizes of the observations contributing to the mean. cs represents mean colony size; cs ss represents colony size sample size; w hw representes mean worker head width (mm); w hw ss represents worker head width sample size; q hw represents mean queen head width (mm); q hw ss represents queen head width sample size; w sz vr represent worker size variation calculated as the coefficient of variation in worker head widths; qw dim represents queen worker dimorphism, calculated as the percentage difference between mean queen head width and mean worker head width; py represents polyandry; temp range represents mean diurnal temperature range; isotherm. represents isothermality; temp. seas. represents temperature seasonality; precip. seas. represents precipitation seasonality and N geo is the number of georeferenced points. Mean diurnal temperature range, isothermality, temperature seasonality and precipiration seasonality are taken from BioClim (www.worldclim.org/bioclim). taxonomy follows the Bolton World Catalogue (www.antweb.org). – denotes missing data.

Species	cs	cs ss	w hw	w hw ss	q hw	q hw ss	w sz vr	qw dim	py	temp. range	isotherm.	temp. seas.	precip. seas.	N geo	Ref
Acromyrmex ameliae	-	-		30	1.4	21	27.27	24	-	130	69	1681	85	6	[1]
Acromyrmex echinatior	137500	5	1.88	826	2.58	11	32.05	31.61	Yes	100.02	74.32	745.85	80.9	42	[2-7]
Acromyrmex insinuator	100	1	-	-	2.325	27	-	-	Yes	72	72	724	60	13	[3, 4, 7, 9, 10]
Acromyrmex octospinosus	13375	5	1.81	581	2.9	5	43.33	46.41	Yes	84	75.6	717.48	39.54	71	[2-4, 6, 11-14]
Acromyrmex subterraneus	4766.2	5	1.59	16	2.15	17	27.71	30.09	-	130	69	1681	85	4	[1, 15, 16]
Acromyrmex versicolor	-	-	2.07	5	-	-	33.36	-	Yes	162.56	46.22	6971.11	53.67	18	[1, 2, 15, 17]
Apterostigma collare	23.98	128	0.87	3	0.91	2	7.56	4.55	No	90.13	77.19	688.05	32.93	165	[3, 15, 19-21]
Apterostigma dentigerum	25	1	1.07	3	1.14	1	9.53	6.43	-	89.3	76.99	715.96	30.42	93	[3, 15]
Apterostigma mayri	20	25	-	-	-	-	-	-	-	70	72.5	706	58.5	10	[12]
Apterostigma sp. 2	25	1	-	-	1.09	1	-	-	-	72	72	724	60	2	[3]

Apterostigma urichii	23	1	-	-	-	-	-	-	-	95	83.33	470.67	46.33	3	[22]
Atta cephalotes	3000000	1	1.99	949	4.88	5	64.37	84.25	Yes	90.11	77.19	649.9	30.43	214	[3, 6, 15, 23, 24]
Atta colombica	2266666.67	5	-	-	4.31	5	-	-	-	76.58	74.21	680.68	56.68	30	[3, 12, 25, 26]
Atta laevigata	3500000	1	2.88	7	-	-	33.5	-	Yes	108.2	74.6	1095.2	62	5	[15, 25, 27, 28]
Atta sexdens	6000000	1	2.46	1016	3.62	4	50.93	38.16	Yes	84.67	78	667.33	79	6	[2, 3, 15, 25]
Atta texana	-	-	2.30	3	-	-	48.98	-	Yes	132	39	7287	16	7	[15, 29]
Atta vollenweideri	5500000	1	2.99	3	4.91	2	53.96	48.61	-	122.33	54.67	3465	46.33	5	[15, 25, 26]
Cyphomyrmex cornutus	2021.75	4	-	-	-	-	-	-	-	90.18	77.01	671.58	29.58	73	[15, 30]
Cyphomyrmex costatus	96.5	53	-	-	0.58	5	-	-	-	85.96	76.29	645.87	45.09	48	[3, 12, 15, 31]
Cyphomyrmex faunulus	16	1	-	-	-	-	-	-	-	92	86	338	20	2	[15, 22]
Cyphomyrmex longiscapus	54.13	203	0.66	93	0.75	25	10.53	12.66	No	85.24	75.36	637.48	49.14	42	[15, 21, 32, 33]
Cyphomyrmex muelleri	-	-	0.64	78	0.7	23	6.68	9.22	-	-	-	-	-	-	[33]
Cyphomyrmex rimosus	136.75	69	0.63	4	0.65	3	15.58	2.24	-	93.68	74.44	1005.29	45.61	259	[3, 12, 15, 34]
Kalathomyrmex emeryi	100	1	0.82	10	0.84	2	10.69	1.54	-	97.75	65.75	1826	61.75	5	[3, 15]
Mycetagroicus cerradensis	373	2	0.87	3	-	-	3.98	-	-	126	69	671.73	44.92	5	[15, 3]
Mycetagroicus inflatus	-	-	0.72	2	-	-	0.99	-	-	-	-	-	-	-	[36]
Mycetarotes carinatus	-	-	-	-	0.88	1	-	-	-	-	-	-	-	-	[58]

Mycetarotes parallelus	110.57	13	0.92	4	0.95	3	0.23	3.48	-	126.91	56.91	3284.68	20.41	21	[3, 15, 37]
Mycetophylax conformis	72.25	3	-	-	-	-	-	-	-	-	-	-	-	-	[15, 38]
Mycetophylax morschi	72.25	4	-	-	-	-	-	-	-	-	-	-	-	-	[15, 38]
Mycetophylax simplex	191.94	7	-	-	-	-	-	-	-	-	-	-	-	-	[15, 38, 39]
Mycetosoritis clorindae	70.5	2	-	-	-	-	-	-	-	92	48	3306	9	3	[40]
Mycetosoritis explicate	-	-	0.8	2	0.93	1	14.52	15.03	-	-	-	-	-	-	[41, 15]
Mycetosoritis hartmanni	50	2	0.64	4	0.77	3	4.53	18.83	-	110.4	45.5	5210.9	36.8	10	[3, 15]
Mycocepurus castrator	1	2	-	-	0.6	16	-	-	-	116	63	2405	71	6	[42]
Mycocepurus goeldii	678.86	7	-	-	0.78	2	-	-	-	91.63	76.88	945.63	50.44	16	[15, 42-44, 47]
Mycocepurus obsoletus	-	-	-	-	-	-	-	87	76	594	71	2	[15,	43]	
Mycocepurus smithii	62.63	162	0.63	4	0.614	1	6.65	2.17	-	89.83	78.07	779.41	27	46	[15, 39, 44-47]
Myrmicocrypta bucki	-	-	0.64	4	-	-	3.91	-	-	105	73	1014	45	3	[48]
Myrmicocrypta camargoi	-	-	0.75	4	1.09	2	5.53	36.53	-	117	63	2333	60	5	[48]
Myrmicocrypta ednaella	86.78	35	-	-	-	-	-	-	No	88.3	78.06	642.76	46.81	67	[12, 21, 34]
Myrmicocrypta erectapilosa	-	-	0.59	4	0.71	1	5.42	17.9	-	83	81	446	47	5	[48]
Sericomyrmex amabilis	972.67	12	0.93	10	1.26	6	6.74	29.38	No	88.26	76.74	708.61	32.36	334	[2, 3, 12, 15, 20, 49]
Trachymyrmex arizonensis	1000	1	1.15	6	1.29	2	14.11	10.8	-	172.5	49.44	6419.72	68.72	17	[15, 50, 52]

Trachymyrmex carinatus	100	1	0.95	5	1.25	2	13.63	27.2	-	166	51	5626	113	3	[15, 52]
Trachymyrmex cornetzi	161.83	62	0.98	5	1.06	2	12.46	8.35	No	87.96	76.58	721.07	33.04	147	[2, 3, 15, 49, 57]
Trachymyrmex desertorum	-	-	1.06	5	1.375	2	16.71	26.02	-	-	-	-	-	-	[15, 52]
Trachymyrmex isthmicus	100.67	43	-	-	-	-	-	-	-	81.5	75.29	722.14	39.86	28	[52]
Trachymyrmex jamaicensis	525	2	1.37	3	1.65	2	5.23	18.52	-	91.5	54.75	2696.25	48.25	7	[15, 52]
Trachymyrmex nogalensis	-	-	1.34	4	1.425	2	16.57	5.98	-	-	-	-	-	-	[52]
Trachymyrmex pomonae	183	1	0.87	2	1.07	3	13.9	20.88	-	178	50	6516	70	3	[52]
Trachymyrmex septentrionalis	474.7	93	0.97	552	1.16	2	7.87	18.2	-	122.93	48	4974.6	44.27	17	[15, 52-55]
Trachymyrmex smithi	652.5	4	1.37	6	1	2	10.76	31.46	-	167.5	55.5	4822	88.5	5	[15, 52]
Trachymyrmex sp.	1000	1	1.22	5	-	-	-	-	-	72	72	724	60	3	[3]
Trachymyrmex turrifex	300	1	0.95	4	1.15	2	11.72	18.68	-	173	51	5626	113	4	[15, 52]
Trachymyrmex urichii	-	-	-	-	-	-	-	-	-	109.5	78	586.5	57	3	[15, 56]
Trachymyrmex zeteki	146.78	136	-	-	1.29	5	-	-	No	80.55	74.62	708.28	46.76	30	[2, 3, 15, 20, 49, 51]

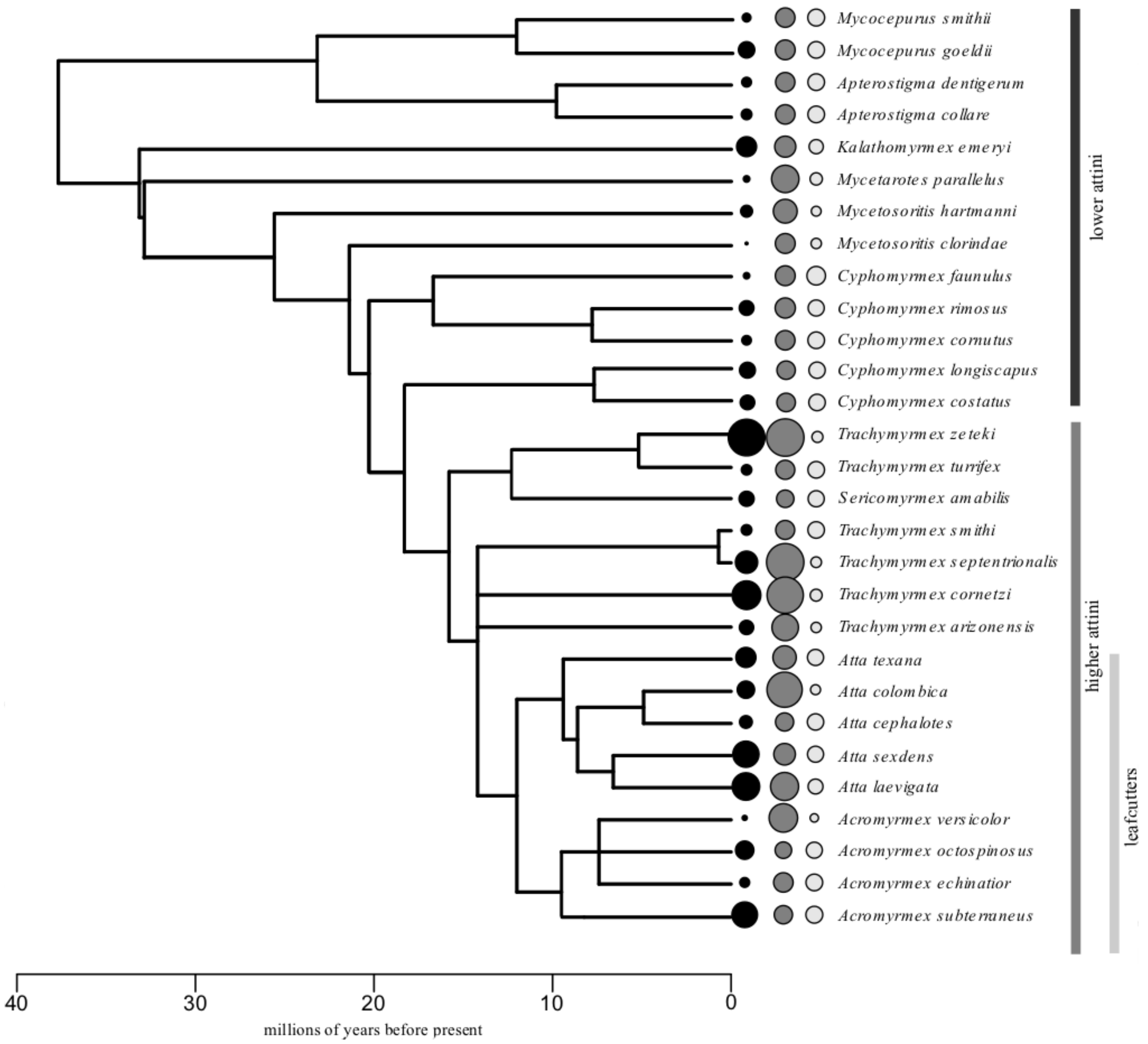

Figure A4.1 Distribution of precipitation seasonality, mean temperature fluctuation and isothermality on a phylogenetic supertree of the Attini (29 species). The full tree (Appendix, figure A5.22) was pruned to include only the species for which there were data on at least one trait and appeared in the phylogeny. Black, grey and white circles are proportional to precipitation seasonality, mean temperature fluctuation and isothermality, respectively. * denotes species used in the final analysis. Branch lengths are proportional to time (millions of years).

Table A4.2. Phylogenetic sources for the Attini supertree.

Reference	Figure number	Data type	No. Attini species
Bacci Jr et al 2009	1	mtDNA + tRNA	13
	2	nDNA	13
	3	mtDNA + nDNA	13
Brandao and Mayhé-Nunes 2007	2	Morphology	32
Moreau et al 2006	1	nDNA + mtDNA	4
Schultz and Brady 2008	1	nDNA + mtDNA	65
Shultz and Meier 1995	3	Larval morphology	51
Sumner et al 2004	1	mtDNA	19
Villesen et al 2004	6	mtDNA	12
Wetterer et al 1998	1	mtDNA + tRNA	14
	2	Amino acid sequence + morphology	14

Table A4.2 references.

Bacci Jr M, Solomon SE, Mueller UG, Martins VG, Carvalho AO, Vieira LG, Silva-Pinhati, ACO. 2009 Phylogeny of leafcutter ants in the genus *Atta* Fabricius (Formicidae: Attini) based on mitochondrial and nuclear DNA sequences. *Mol. Phylogenet. Evol.* **51**, 427-437.

Brandao CRF, Mayhé-Nunes AJ. 2007 A phylogenetic hypothesis for the Trachymyrmex species groups, and the transition from fungus-growing to leaf-cutting in the Attini. *Mem. Am. Entomol. Inst.* **80**, 72-88.

Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. 2006 Phylogeny of the ants: diversification in the age of angiosperms. *Science* **312**, 101-104.

Schultz TR, Brady SG. 2008 Major evolutionary transitions in ant agriculture. *Proc. Natl. Acad. Sci. USA* **105**, 5435-5440.

Schultz TR, Meier R. 1995 A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae. *Syst. Entomol.* **20**, 337-370.

Sumner S, Aanen DK, Delabie J, Boomsma JJ. 2004 The evolution of social parasitism in Acromyrmex leaf-cutting ants: a test of Emery's rule. *Insectes Soc.* **51**, 37-42.

Villesen P, Mueller UG, Schultz TR, Adams RM, Bouck AC. 2004 Evolution of ant-cultivar specialization and cultivar switching in Apterostigma fungus-growing ants. *Evolution* **58**, 2252-2265.

Wetterer JK, Schultz TR, Meier R. 1998 Phylogeny of fungus-growing ants (Tribe Attini) based on mtDNA sequence and morphology. *Mol. Phylogenet. Evol.* **9**, 42-47.

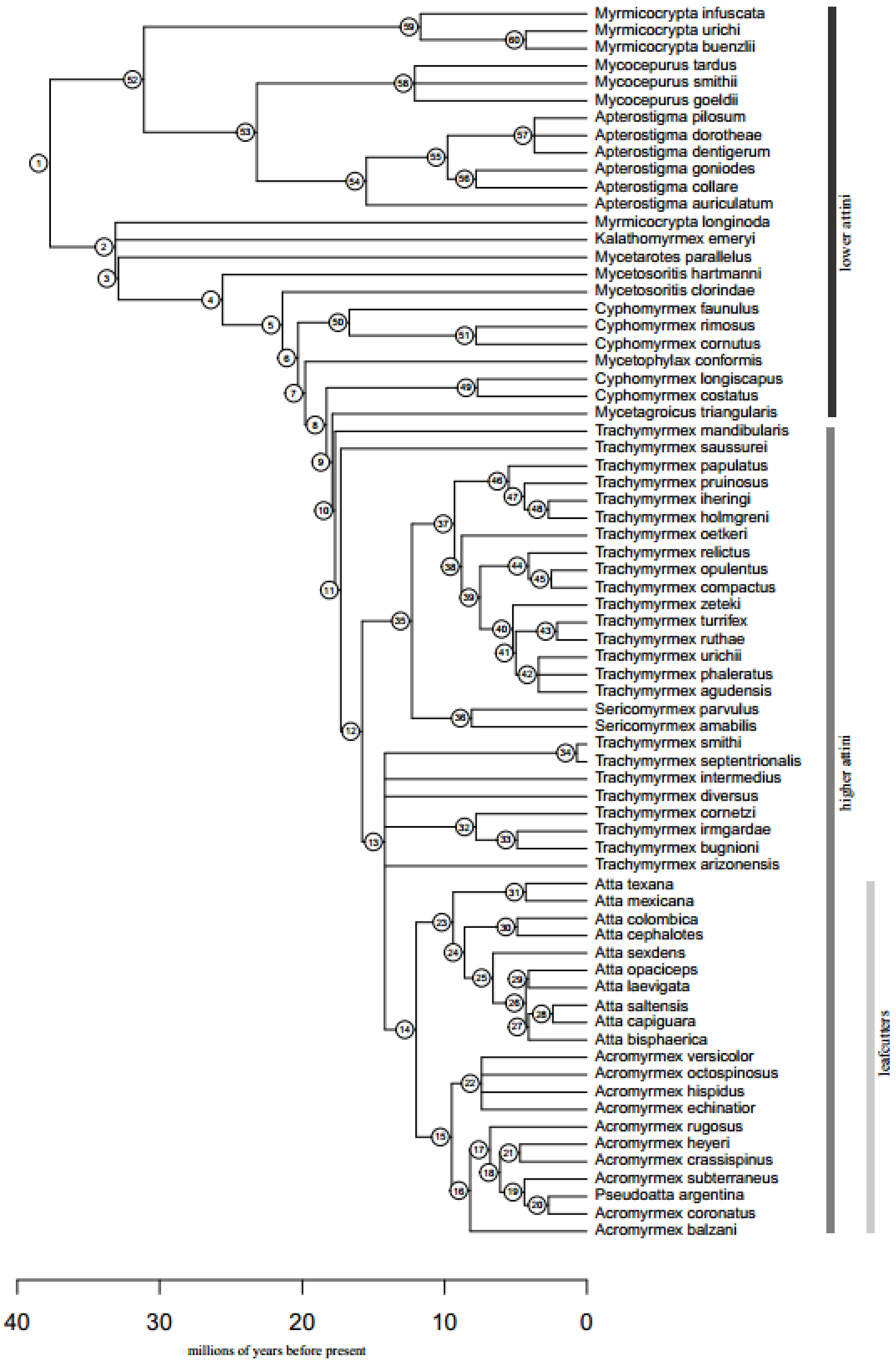

Figure A4.2 A phylogenetic supertree for 71 species of the Attini. Numbers on nodes are arbitrary numbers. Branch lengths are proportional to time (millions of years). See table S3 for nodal support values.

Table A4.3 Reduced qualitative support (rQS) scores for the Attini supertree (figure S1). rQS values range between 1 and -1 where 1 indicates full agreement for a node in the source trees, and -1 full disagreement.

Node #	rQS value	Node #	rQS value	Node #	rQS value
1	0.83	21	0.08	41	0.00
2	0.75	22	0.42	42	0.00
3	0.75	23	0.50	43	0.00
4	0.67	24	0.50	44	0.00
5	0.67	25	0.00	45	0.00
6	0.67	26	0.00	46	0.00
7	0.67	27	0.08	47	0.00
8	0.58	28	0.08	48	0.00
9	0.58	29	0.00	49	0.00
10	0.58	30	0.33	50	0.33
11	0.58	31	0.08	51	0.33
12	0.58	32	0.17	52	-0.83
13	0.33	33	0.00	53	0.25
14	0.50	34	0.08	54	0.42
15	0.33	35	0.17	55	0.25
16	0.83	36	0.33	56	0.25
17	0.42	37	0.00	57	0.01
18	0.17	38	0.00	58	0.25
19	0.17	39	0.00	59	-0.17
20	0.17	40	0.00	60	-0.17

Table A4.4 All models with ΔAICc < 7 describing the predictors of a) worker size variation, b) queen-worker dimorphism and c) colony size in the Attini. Regression slope estimates from phylogenetic least squares (PGLS) models are reported.

Table A4.4a.

Intercept	**Precipitation seasonality**	**Mean diurnal temperature fluctuation**	**log Colony size**	**Queen-worker dimorphism**	**Degrees of freedom**	**Log likelihood**	**AICc**	**ΔAICc**	**AICc weight**
2.342		-0.011	0.394		3	-23.97	55.7	0.68	0.19
1.027			0.401		2	-25.83	56.4	1.43	0.13
2.563	0.020	-0.020	0.347		4	-22.73	56.5	1.57	0.12
2.253	0.018	-0.020	0.353	0.152	5	-20.70	56.9	1.88	0.12
0.627	0.003		0.430	0.028	4	-22.79	56.9	1.93	0.10
0.832	0.005		0.391		3	-24.85	57.4	2.43	0.08

Table A4.4b.

Intercept	**Precipitation seasonality**	**Isothermality**	**log Colony size**	**Degrees of freedom**	**Log likelihood**	**AICc**	**ΔAICc**	**AICc weight**
0.912			0.154	2	-20.45	45.7	0	0.44
1.358		-0.007	0.168	3	-19.79	47.3	1.64	0.20
0.911	-0.001		0.159	3	-19.87	47.5	1.8	0.18
1.637				1	-23.84	49.9	4.26	0.05
1.291	0.008			2	-22.75	50.3	4.64	0.04
1.536	-0.002	-0.009	0.174	4	-19.76	50.6	4.93	0.04
0.681		0.014		2	-22.94	50.7	5.02	0.04
0.253	0.007	0.016		3	-22.34	52.4	6.74	0.02

Table A4.4c.

Intercept	Precipitation seasonality	Mean diurnal temperature fluctuation	Isothermality	Lattitude	Precipitation seasonality * isothermality	Degrees of freedom	Log Likelihood	AICc	ΔAICc	AICc weight
1.040			0.056			2	-61.93	128.4	0	0.17
6.658	0.044	-0.035				3	-60.73	128.6	0.18	0.16
4.245	0.015					2	-62.04	128.6	0.23	0.15
7.291	-0.173		-0.055		0.003	4	-59.81	129.5	1.14	0.10
4.976		-0.002				2	-62.57	129.7	1.29	0.09
1.437	0.011		0.044			3	-61.67	130.4	2.05	0.06
1.249		-0.002	0.056			3	-61.91	130.9	2.54	0.05
0.926			0.057	0.006		3	-61.92	130.9	2.55	0.05
4.240	0.015			0.002		3	-62.04	131.2	2.8	0.04
5.520	0.040	-0.032	0.015			4	-60.69	131.3	2.91	0.04
6.663	0.045	-0.035		0.007		4	-60.71	131.3	2.96	0.04
7.581	-0.202		-0.062	0.037	0.003	5	-59.36	131.7	3.34	0.03
4.992		-0.002		-0.005		3	-62.56	132.2	3.84	0.03

9.4.1 Multinomial Model Analysis

We categorised species by their agricultural system as follows: lower Attines (lower agriculture), higher Attines, excluding leafcutters (higher agriculture), and leafcutter ants (leafcutting agriculture). These classifications can be seen on figure 1, supplementary material figures S1 and S2. Using the fungal-agricultural system as the dependent variable and ln mean colony size as the independent variable, we fitted a univariate, multinomial logistic regression model using the R package MCMCglmm [1]. We used non-informative priors with a low degree of belief across all parameters, and ran the model for 6,000,000 generations, sampling every 1000th generation and discarding the first 25% of samples as burnin. We visually inspected the trace output to ensure model convergence and proper mixing, and made sure effective sample sizes were large enough to ensure robust parameter estimates.

We found strong evidence that the degree of fungal-agricultural system is predicted by colony size. Specifically, larger colony sizes are associated with a higher probability of higher agriculture versus lower agriculture (expected log-odds change per unit increase in ln colony size=1.21, CI95=2.34, pMCMC=0.02), and leafcutter agriculture versus lower agriculture (expected log-odds change per unit increase in ln colony size=4.71, CI95=7.19, pMCMC<<0.001).

1. Hadfield J.D. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33(2), 1-22.