

## Molecular phylogenetics, phylogenomics, and phylogeography

# First Phylogenomic Assessment of the Amphitropical New World Ant Genus *Dorymyrmex* (Hymenoptera: Formicidae), a Longstanding Taxonomic Puzzle

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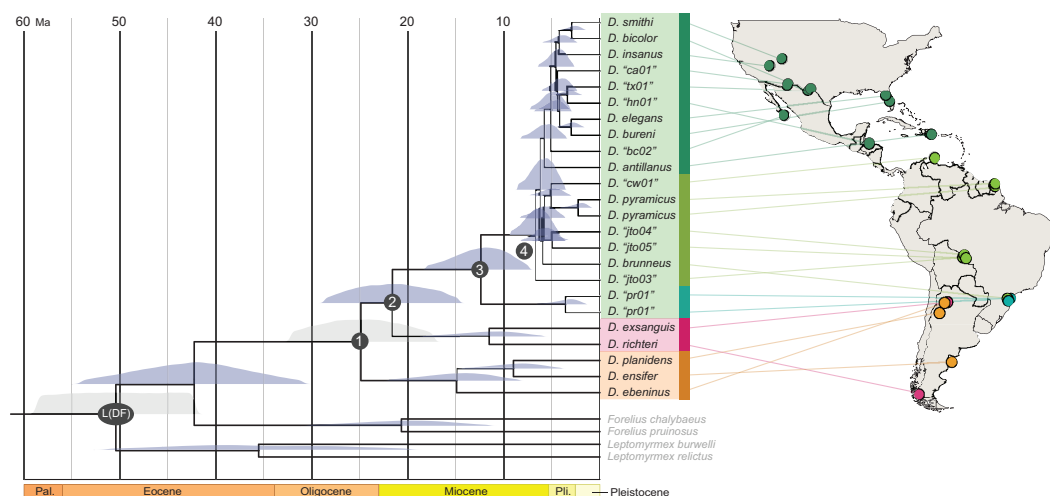
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### Abstract

*Dorymyrmex* Mayr 1866, the ‘pyramid ants’ or ‘cone ants’, are conspicuous inhabitants of arid landscapes across the Americas. Ranging from the Great Plains to Patagonia, they are concentrated north and south of the tropics in contrast to the latitudinal diversity gradient canon. Despite being frequently collected and ecologically important, *Dorymyrmex* ants exemplify the taxonomic neglect typical in the subfamily Dolichoderinae. The genus has never had the benefit of a global revision, and even the major lineages are still uncertain. This work characterizes the issues at hand and ushers 22 *Dorymyrmex* species into the world of modern-day phylogenomics: By targeting ultraconserved elements (UCEs) across the genome, I construct an alignment of 1,891 loci, infer phylogenies under maximum likelihood and Bayesian approaches, and estimate divergence dates. Three major clades of *Dorymyrmex* emerge with maximal support, corresponding to former genera: *Dorymyrmex sensu stricto*, *Araucomyrmex* Gallardo 1919, and *Conomyrma* Forel 1913. The *pyramicus* group (‘*Conomyrma*’) shows a recent, rapid radiation with minimal morphological differentiation, reaffirming the difficulty of species delimitation in this widespread clade. Finally, I observe a general south-to-north pattern of dispersal, likely by way of savanna ‘stepping stones’ across the tropics during cooler, drier periods. Intercontinental dispersal occurred after the hypothetical Caribbean landspan in the Miocene, but before the Pleistocene or the completion of the Panamanian isthmus, suggesting dispersal by flight. This corroborates patterns observed in other arid-adapted amphitropical New World taxa. Characterizing the major *Dorymyrmex* species groups is an important first step towards stable taxonomic definitions—which underpin active studies in behavior, chemical ecology, and physiology.

### Graphical Abstract



**Key words:** phylogenomics, ultraconserved elements, biogeography, taxonomy, phylogeny

Terrestrial biodiversity on Earth is most concentrated in tropical moist forests such as those in Amazonia, but arid and semi-arid ecoregions harbor remarkable diversity as well (Cloudsley-Thompson 1975, 1993; Byrne et al. 2008). Nonetheless, the wet tropics have attracted most efforts of taxonomy and species and habitat conservation, leaving dry habitats more poorly characterized and thus perceived as less valuable (Redford et al. 1990). Ants, the world's most species-rich and 'biologically eclectic' social insects (Ward 2010), are one example of many that exemplify these patterns. Their described diversity peaks in the Neotropics (Fisher 2010), yet the total size of the ant fauna of arid Australia has been estimated by some to rival, if not surpass, that of the Amazon basin (Andersen 2016). In the Americas, dry regions cover an immense latitudinal range and dozens of habitat types, from the prairies of North America, coastal grasslands of Central America, and sandy dunes in the Antilles, to the cerrado of Brazil and scrublands extending south to Patagonia. Arid and semi-arid habitats in the New World could certainly harbor greater ant diversity than currently acknowledged.

The ant subfamily Dolichoderinae, while one of the four largest subfamilies, encompasses only ~712 of ~14,000 described ant species (28 of 338 genera; Bolton 2021). It is quite likely that many more dolichoderine species exist but await formal description. There are several reasons for this: Many species within the Dolichoderinae appear superficially similar, with most species lacking spines, tubercles, or elaborately developed sculpture, leading many taxonomists to direct their attentions to morphologically more diverse groups (Shattuck 1992). Since securing clear-cut external characters even for generic boundaries within the subfamily was such a challenge (Creighton 1950, Shattuck 1992), there are certainly cryptic species within dolichoderine genera that are not immediately evident by morphology but form independently evolving units. Furthermore, Dolichoderinae have a precedent for being under-described. A recent revision of the genus *Iridomyrmex* Mayr 1862, which is ecologically dominant in arid Australia, recognized 79 species, of which 31 were new (Heterick and Shattuck 2011). Other observers have suggested that the total number of morphospecies may be closer to ~350 (Andersen 2007, Andersen et al. 2013), but without genetic analysis, it is extremely difficult to distinguish individual variation from interspecific variation in the dolichoderines, much less infer if morphospecies are indeed true species.

At the confluence of these conditions—New World ants which are in the subfamily Dolichoderinae and adapted to xeric environments—we find the genus *Dorymyrmex* Mayr 1866 and its sister group *Forelius* Emery 1888. *Dorymyrmex* ants favor deserts, roadsides, and open grasslands, and are frequently encountered in open habitats across the Americas. The expansive range of *Dorymyrmex*, together with its moderate age (~23 My; Boudinot et al. 2016), makes the genus a prime candidate for studies of New World biogeography. It features a curious amphitropical distribution, in which the greatest population density and species richness of the genus occurrence are not centered around the equator, in concert with latitudinal diversity gradient theory (Pianka 1966), but rather concentrated in the temperate regions to the north and south. Of the 61 currently valid species of *Dorymyrmex*, 18 were described from North America, 1 from Central America and the Antilles, and 42 from South America (Bolton 2021). Other desert-dwelling pan-American groups are known to share this 'bimodal' or 'inverse' latitudinal gradient, including the sister genus *Forelius*, the plant genus *Larrea* Cavanilles 1800 (creosote bush), and bees in the genus *Diadasia* Patton 1879 (Hymenoptera: Apidae; Raven 1963, Lia et al. 2001, Sipes and Wolf 2001, Wilson et al. 2014). Indeed, a recent

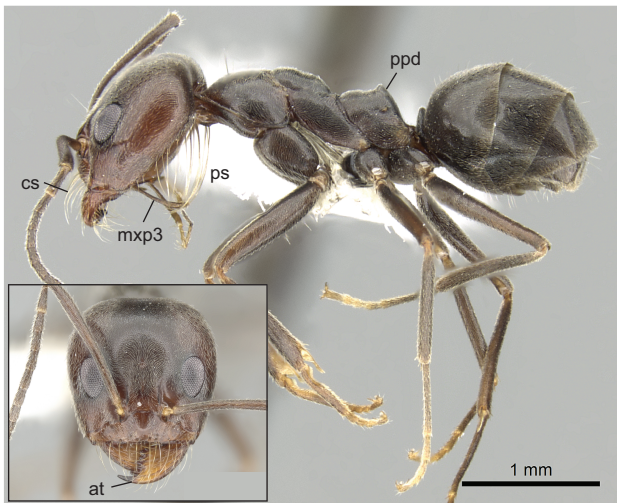
analysis found that global bee richness peaks in xeric, non-forested areas and areas of notable faunal turnover such as the southwestern United States and southeast Brazil (Orr et al. 2021). Based on the apparent similarity of present distributions, the paleodistributions and dispersal timing of these taxa may inform similar processes in *Dorymyrmex*.

Although *Dorymyrmex* do not dominate the landscape like their Australian relatives in the genus *Iridomyrmex*, they are quite conspicuous in open habitats when present. *Dorymyrmex* build ground nests usually marked by craters or cones of soil, predominantly forage during daylight hours when they can be conveniently observed, and actively scavenge (opportunistically and omnivorously) and tend hemipterans (Hölldobler and Wilson 1990). All ants of arid zones, *Dorymyrmex* included, constitute a very important group of animals in terms of abundance, biomass, and nutrient turnover (MacKay 1991, Rojas and Fragoso 2000). *Dorymyrmex* frequently appear in recent surveys and reviews as members of local ant faunas (Jory and Feitosa 2020, Fernández et al. 2021, Melo et al. 2021), or as a small proportion of the subjects in ecological studies, e.g., the feeding guild or native ant community (Chalcoff et al. 2019, Devegili et al. 2020, Juárez-Juárez et al. 2020, Braman et al. 2021, Burrow et al. 2021). In addition, quite recently, *Dorymyrmex* has been established as a model organism for social evolution. Colony size, foraging patterns, and relative brain investment of several sympatric *Dorymyrmex* species offer a window into their division of labor and behavior of individuals—findings which may be instrumental in understanding ants as superorganisms more generally (Godfrey and Gronenberg 2019). This wave of recent publications is a promising indication of scientific interest in *Dorymyrmex*, but at the heart of all experimental studies are key hypotheses easily overlooked: the very identities of the species concerned.

Despite their wide distribution, commonness in collections, and unmistakable diagnosis (at the genus level), *Dorymyrmex* ants are undoubtedly neglected with respect to their species-level taxonomy. Taxonomic descriptions of the group date back to the mid-nineteenth century, and 61 species are recognized as valid today (Roger 1863, Mayr 1866, Bolton 2021), but these greatly need revision. As with many dolichoderine groups, *Dorymyrmex* species are morphologically conserved, but they all share an unmistakable trait diagnostic of the genus: a single medial tubercle on the propodeum of the worker (Fig. 1; Bolton 1994). This tubercle varies in shape throughout the genus and seems like a prime candidate for species delineation, but differentiating species by their appearance in this group is fraught with uncertainty, as it appears that similar forms may have evolved convergently and intraspecific variation can equal or surpass interspecific variation for some characters (Kusnezov 1952). Nonetheless, many species have been described based on morphological characters such as color, the shape of the propodeal tubercle, the prominence of the psammophore, alate wing venation, and/or worker body size.

*Dorymyrmex* has been divided into as many as seven genera and subgenera (Kusnezov 1959) (full list of generic and subgeneric changes enumerated in Supp Table S1 [online only]):

Genus *Dorymyrmex* Mayr 1866  
 subgenus *Psammomyrma* Forel 1912  
 subgenus *Ammomyrma* Santschi 1922  
 Genus *Conomyrma* Forel 1913  
 Genus *Biconomyrma* Kusnezov 1952  
 Genus *Araucomyrma* Gallardo 1919  
 Genus *Spinomyrma* Kusnezov 1952



**Fig. 1.** Diagnostic characters of *Dorymyrmex* workers (Shattuck 1992; Bolton 1994). Angle of propodeum (*ppd*) with single medial dorsal spine/tooth; psammophore (*ps*) present; segment 3 of maxillary palp (*mxp3*) elongate; numerous elongate, curved clypeal setae (*cs*) extending from the anterior margin of the clypeus forward over the mandibles; apical tooth (*at*) of mandibles greatly elongate. Specimen: *D. richteri*, CASENT0249680, phot. Ryan Perry.

Much like the species boundaries, these morphologically defined ‘genera’ prove inconsistent under scrutiny. For many seemingly diagnostic characters, there are exceptions: several species possess mixed characteristics that prevent their unequivocal placement in one genus or another (Shattuck 1992). This is true for even *Dorymyrmex* + *Conomyrma*, the two-genus arrangement most consistent over time and most recently valid (Hölldobler and Wilson 1990). Thus, all other genera are considered indistinct and have been synonymized into *Dorymyrmex* (Shattuck 1992).

Recent (since 2000) contributions to the species-level taxonomy of *Dorymyrmex* include elevations of *D. antillanus* Snelling 2005 and *D. paranensis* Santschi 1922 to the species level (Snelling 2005, Wild 2007) and a treatment of the *Dorymyrmex* of Colombia (Cuezzo and Guerrero 2012). The most recent partial revision of the genus, including a key to Nearctic species, was published in 1995 (Snelling 1995). Overall, contributions to *Dorymyrmex* classification have been isolated species descriptions, rather than identification keys or revisions, and are typically limited to a region or country—resulting in relative chaos at the species level. Global, comprehensive approaches are certainly superior to parochial taxonomy when reviewing and revising poorly resolved groups (Bolton 2007, Prebus 2017). The *Dorymyrmex* fauna of the Nearctic is better characterized than that of the Neotropics, even integrating natural history data such as social parasitism to describe species (Trager 1988, Johnson 1989, Deyrup 2017), but there are a number of species in western North America which still need confirmation and/or description (Fisher and Cover 2007). The Nearctic *Dorymyrmex* lineages as a whole are frustratingly similar in appearance, yet their reproductive isolation is suggested by differing ecologies and alate morphologies, among other features (Snelling 1995, Deyrup 2017). Resolving these patterns and the degree of inter- and intraspecific variability will require extensive sampling, careful morphological scrutiny, natural history knowledge, and algorithmic species delimitation empowered by (selectively applied) phylogenomic data.

*Dorymyrmex* has not been examined comprehensively using phylogenetics. Since the advent of molecular phylogenetics as

standard procedure for systematics, several studies of ant phylogeny have sampled the genus, albeit quite superficially (Moreau et al. 2006, Ward et al. 2010, Moreau and Bell 2013, Boudinot et al. 2016, Economo et al. 2018). These have each included 1–3 of the following three species: *D. planidens* Mayr 1868, representing *Dorymyrmex* s. str. (*‘Psammomyrma’*), and *D. elegans* (Trager 1988) and *D. bicolor* Wheeler 1906, both representing *Dorymyrmex* (*‘Conomyrma’*).

Consequently, in *Dorymyrmex* today, both species boundaries and the phylogenetic relationships among species are unclear. Although over 150 years have passed since Mayr’s original description of the genus, and nearly 30 yr since Shattuck synonymized *Araucomyrmex* and *Conomyrma* under *Dorymyrmex*, little progress has been made towards resolving the phylogeny of the genus, even at the level of major lineages. The species-level taxonomy of *Dorymyrmex* greatly needs revision, and determining phylogenetically supported species groups is an important first step in this process. Here I present the first molecular phylogeny of *Dorymyrmex* based on systematic sampling of representative taxa, compare it to previous conceptions of the genus, and outline avenues for future systematic research.

## Materials and Methods

### Taxon Sampling and Naming Conventions

For this first phylogeny of *Dorymyrmex*, I sampled 28 specimens to explore species-level relationships within the genus, including four outgroup taxa and 24 *Dorymyrmex* (approximately 22 species: 13 described and 9 undescribed). Undescribed putative species are given species codes (e.g., ‘*pr01*’, ‘*jto03*’, ‘*bc02*’) but formal designation is outside the scope of the present work. The included outgroup taxa are two species of *Forelius*, the sister genus of *Dorymyrmex*, and two *Leptomyrmex* Mayr 1862, the sister of *Dorymyrmex* + *Forelius* (Ward et al. 2010). The sampled *Dorymyrmex* were collected between 1993 and 2020, and cover a wide geographical range, from the central and eastern United States to Bolivia, Argentina, and southern Chile (Fig. 3; Supp Table S2 [online only]). All specimens were preserved in 95% ethanol or point-mounted on pins in dry collections.

### UCE Sequencing

DNA were extracted using a QIAGEN DNeasy Blood and Tissue Kit, deviating from the manufacturer protocol in several ways: 1) incubating the Proteinase K solution overnight, 2) eluting using RT nuclease-free water or 56°C Buffer AE, 3) incubating the water or buffer in the spin column filter for 2 min at RT, and 4) eluting in two rounds of 65 µL, yielding a final DNA extraction volume of ~130 µL. For most samples, DNA was extracted nondestructively by removing the specimen from its paper point (if necessary), placing the specimen loosely in a microcentrifuge tube for overnight incubation in the Buffer ATL + Proteinase K solution, and after extraction, washed with ethyl acetate and 95% ethanol before re-mounting. Six samples were destructively extracted by grinding whole specimens in Buffer ATL with a pestle prior to incubation. DNA concentration values were estimated using a Qubit fluorometer, after which samples were diluted to ≤50 ng DNA and sheared to a target fragment size of 400–600 bp using a Diagenode Bioruptor or Qsonica Q800R2 acoustic sonicator. Library preparation for targeted genomic enrichment was completed following Faircloth et al. (Faircloth et al. 2014) as modified by Branstetter et al. (Branstetter et al. 2017), using the iTru dual-indexing adapter system (Glenn et al. 2019). Libraries were pooled and 2,524 UCE loci were enriched using the ‘ant-specific hym v2’ bait set, designed by Branstetter et al. (2017),

and custom adapter blockers. A final check on enrichment success and DNA concentration was completed using a Bio-Rad CFX96 qPCR machine. The final pool was sequenced on an Illumina HiSeq 2500 at the University of Utah High Throughput Genomics Center in Salt Lake City, Utah, or an Illumina HiSeq X at Novogene, Inc., Sacramento, California. For 8 of 28 samples, after extraction and sonication, specimen DNA samples were sent to RAPiD Genomics LLC (Gainesville, FL, USA) for library preparation, enrichment, and sequencing using comparable protocols.

### Data Processing and Matrix Assembly

Sequence data were processed using the package *PHYLUCE* v1.6.7 and its associated programs (Faircloth 2016). Within the *PHYLUCE* pipeline, raw reads were trimmed using *illumiprocessor* (Faircloth 2013), incorporating *trimmomatic* (Bolger et al. 2014), and assembled using *Trinity* or *SPAdes* (Grabherr et al. 2011, Bankevich et al. 2012). Assembled contigs were matched to UCE probes under default parameters and compiled into a FASTA file in *PHYLUCE*. Alignment was completed using the L-INS-i algorithm in *MAFFT* v7.407 (Katoh and Standley 2013), and poorly aligned portions were trimmed in *Gblocks* (Talavera and Castresana 2007) under relaxed settings (--b1 0.5 --b2 0.5 --b3 12 --b4 7). Four matrices were assembled with variable taxon coverage, removing any UCE loci that were not represented by a minimum of 80, 90, 95, or 99% of taxa. Finally, additional alignment statistics were summarized using *AMAS* v1.0 (Borowiec 2016). The 90% matrix selected for use in downstream analyses contains 28 taxa, 1891 genetic loci, 1,591,128 total base pairs, 183,183 parsimony informative sites, and 18.15% total missing data, which accounts for all gaps and ambiguities.

### Data Partitioning

To examine effects of partitioning, the 90% matrix was analyzed under three schemes: unpartitioned, partitioned by UCE locus (1891 partitions), and partitioned with the Sliding-Window Site Characteristics method based on Entropy (SWSC-EN; Supp Figs. S1–S2 [online only]; Tagliacollo and Lanfear 2018). This algorithm divides each genetic locus into three regions, the slowly evolving ‘core’ and two more variable ‘flanks’ observed in ultraconserved element sequences. These 5673 partitions were merged by similarity in PartitionFinder 2 (Lanfear et al. 2016) using a separate GTR+G model for each partition, linked branch lengths, and the *rcclusterf* search scheme to optimize performance when analyzing 30,649,490 subsets. PartitionFinder 2 ultimately yielded a final set of 960 partitions for the SWSC-EN scheme, a matrix now referred to as the *960-swsc-part* dataset.

### Phylogenetic Analyses

I selected the partitioning scheme *960-swsc-part*, which best partitions the variation in evolutionary rate across each UCE locus, for analysis in a Bayesian framework. Bayesian inference (BI) was completed using ExaBayes v1.5.1 (Aberer et al. 2014) on the CIPRES Science Gateway (Miller et al. 2010) operated by the University of California San Diego. For large datasets with many partitions, ExaBayes restricts the number of possible models of sequence evolution; each of the 960 partitions was therefore analyzed under its own GTR+G model. The Metropolis-coupled MCMC was called with four independent runs of two chains each (one heated, one cold); branch length parameters across all partitions were linked. MCMC continued for 1.5 million generations (most parameter effective sample sizes [ESS] > 1000; all ESS values over 400). The first 150,000 generations (10%) were discarded as burn-in. Posterior

probability density estimates were opened in Tracer v1.7.1 (Rambaut et al. 2018) and visually assessed for convergence.

Maximum likelihood (ML) phylogenies were inferred using the program *IQ-TREE* version 2.1.2 (Nguyen et al. 2015), including the algorithms for ultrafast bootstrapping, ModelFinder, and partitioned models (Chernomor et al. 2016, Kalyaanamoorthy et al. 2017, Hoang et al. 2018). Preliminary *IQ-TREE* analyses ran the *960-swsc-part* dataset under a GTR+G model of sequence evolution, 1000 ultrafast bootstrap replicates, and three independent runs per scheme. For final analysis, *IQ-TREE* used the *960-swsc-part* dataset but employed ModelFinder to determine the best-fit substitution model for each partition, and also reduced the total number of partitions to 904. Three independent runs of 1000 ultrafast bootstrap replicates were completed, compared, and summarized.

Divergence dates were inferred using MCMCTree as included in PAML v4.9 (Yang 2007). MCMCTree can estimate and utilize an approximation of the likelihood function, making MCMC calculations feasible on genome-scale data. Two soft calibration points were used. The root node was assigned a uniform prior distribution ranging from 59 to 42 million years ago (Ma). This calibration is based on the 95% highest posterior density (HPD) for the same clade, *Leptomyrmex* + (*Dorymyrmex* + *Forelius*), found in Boudinot et al. (2016). Additionally, the crown age of *Dorymyrmex* (Node 1) was assigned a range of 33–13 Ma, the 95% HPD for (*D. planidens* + *D. bicolor*) reported in Ward et al. (2010). Three independent runs were completed using an unpartitioned alignment, the independent-rates clock model, and other default parameters. As indicated in the control file, MCMCTree sampled every 100 iterations up to 1 million samples—i.e., 100 million total iterations. The first 25% was discarded as burn-in and trace logs were visualized to check convergence in Tracer v1.7.1. Results from the three runs were combined into a single log file and summarized using the ‘Print = -1’ option.

### Data Availability

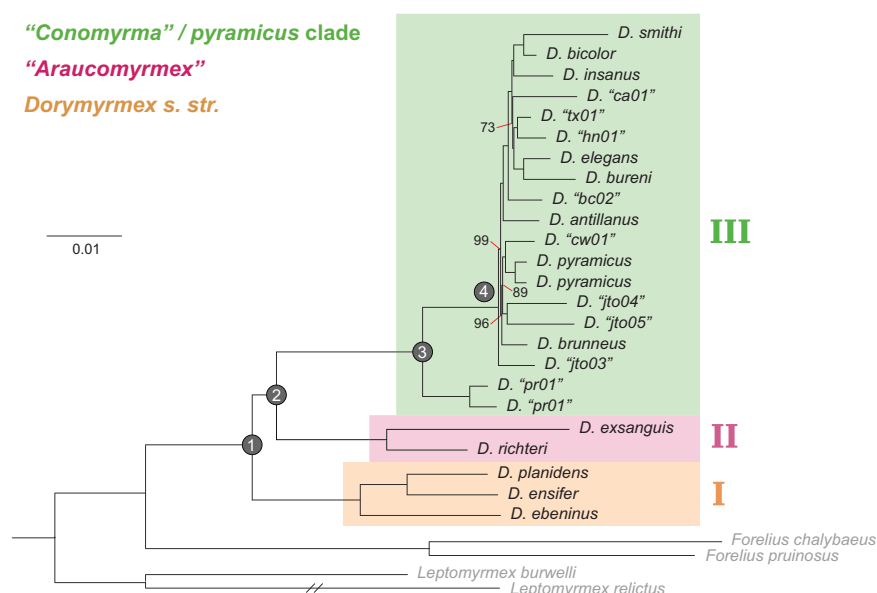
Specimen collection data and images, when applicable, are publicly accessible on the AntWeb database (www.antweb.org) by searching for CASENT numbers. Voucher specimens are located at the University of California Davis insect collection (UCDC) unless indicated otherwise on AntWeb. Raw sequence reads have been archived in the NCBI Sequence Read Archive (SRA) under BioProject ID PRJNA759281.

## Results

The maximum likelihood (ML) phylogeny is recovered with 100% bootstrap support for all major clades (Fig. 2). These basal support values and the tree topology are robust across all sets of filtered data and all partitioning schemes. *Dorymyrmex* and *Forelius* are reciprocally monophyletic, as inferred previously (Ward et al. 2010, Moreau and Bell 2013, Boudinot et al. 2016).

Three mutually monophyletic clades of *Dorymyrmex* also emerge. The first of these (‘Clade I’), sister to all remaining *Dorymyrmex*, consists of *D. ebeninus* Forel 1914, *D. ensifer* Forel 1912, and *D. planidens* Mayr 1868, all collected in Argentina. Clade II includes *D. exsanguis* Forel 1912, also from Argentina, and *D. richteri* Forel 1911, which was collected in southern Chile. Clade III is the most thoroughly sampled clade. It contains representatives of two nests of an undetermined species (*D. ‘pr01’*) from Paraná, Brazil, frequently misidentified in collections as *D. brunneus* Forel 1908. The sister group to *D. ‘pr01’* is a species-rich group including *D. brunneus* and *D. pyramicus* (Roger 1863), which shows a rapid radiation marked





**Fig. 2.** Maximum likelihood (ML) phylogeny of *Dorymyrmex* inferred in IQ-TREE v2.1.2., with an identical topology to the Bayesian phylogeny (Supp Fig. S3 [online only]) inferred in ExaBayes v1.5.1. Clades are highlighted by color and main nodes and clades are numbered for easy reference in the text. All support values are at maximum (100% bootstrap, posterior probability of 1) except where indicated. For ML analysis, IQ-TREE included three independent runs, each with 1000 ultrafast bootstrap replicates, drawing on the data matrix of 904 partitions determined using the SWSC-EN method and using the best-fit models chosen by IQ-TREE ModelFinder. For Bayesian analysis, ExaBayes included 4 independent runs of 2 chains each, which continued for 1.5 million generations (first 100,000 generations discarded for diagnostics), under the same SWSC-EN partitioning scheme and a GTR+G model (full details in Methods).

by short branch lengths (Fig. 2). Clade III will also be referred to as the ‘*pyramicus* clade’ after the oldest available species name, one which has also gained a reputation as the ‘wastebasket taxon’ to which *Dorymyrmex* specimens from Clade III are often assigned.

At the base of the apparent radiation is *D. 'jto03'*, a species from Bolivia sequenced from males and whose workers have not yet been identified. The remaining phylogeny bifurcates into a clade of generally South American species and a clade of generally North American species. The former contains *D. brunneus* from southern Brazil and ‘*jto04*’ and ‘*jto05*’ of eastern Bolivia, sister to three others: *D. 'cw01'* (cf. *pyramicus*) from Curaçao and two *D. pyramicus* from French Guiana. In the latter, generally North American clade, the first to diverge is *D. antillanus* from the Dominican Republic, followed by *D. 'bc02'* from Baja California, a trio including *D. insanus* (Buckley 1866) + (*D. bicolor* + *D. smithi* Cole 1936), *D. 'ca01'* from southern California, and finally two pairs: *D. elegans* and *D. bureni* (Trager 1988), both collected in Florida, and *D. 'tx01'* from Texas and, unexpectedly, *D. 'hn01'* from Honduras. For a complete list of collection localities and specimen information, please see Supp Table S2 (online only). The internal topology of the *pyramicus* clade was recovered identically under all data sets and analyses and usually with maximal support values (bootstrap value 100%/posterior probability 1), although several nodes varied slightly in support (Supp Figs. S1–S3 [online only]).

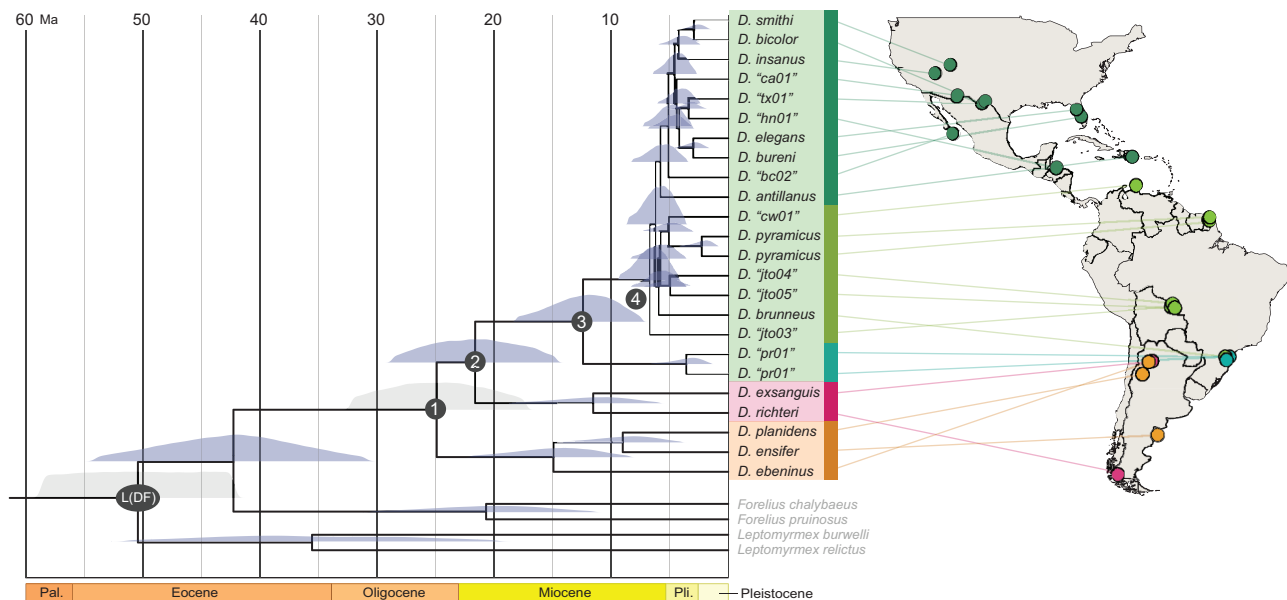
The ages of the root node ‘L(DF)’ and crown *Dorymyrmex* (node 1) were both inferred within the soft bounds of their assigned ranges: L(DF) at 50.4 Ma and node 1 at 24.9 Ma (Fig. 3). The crown ages of the following nodes were newly estimated as shown in Fig. 3: Node 2, approximately 22 Ma (95% HPD: 29.2–13.8 Ma); node 3, 12.5 Ma (95% HPD: 17.7–7.3 Ma); and node 4 (crown of rapid radiation), 6.7 Ma (95% HPD: 9.5–4.1 Ma). All estimated node age ranges can be viewed in Supp Fig. S4 (online only); all estimated ages, Supp Fig. S5 (online only). The bulk of Clade III appeared from approximately 8 to 5 Ma, and diversification events that resulted in

definitive extant species—i.e., taxonomically valid and consistently diagnosable using present species concepts—are as young as 3.0 Mya (e.g., *D. elegans* and *D. bureni*).

## Discussion

This broad molecular phylogeny of *Dorymyrmex* establishes the evolutionary trajectory of the genus and provides the first evidence toward resolving persistent questions. While based solely on sequence data, it addresses our understanding of *Dorymyrmex* from multiple angles: taxonomic classification, the congruence between morphological and molecular data, and historical biogeography. The topology is congruent with previously published analyses that included Dolichoderinae and extends the sampling tenfold. Moreover, the major lineages of *Dorymyrmex* seem to correspond to (sub) genera established historically by morphology—not necessarily all seven, or as defined per their original designations, but rather the arrangement of three genera most consistently upheld in taxonomic treatments of *Dorymyrmex* over the 20th century: *Dorymyrmex s. str.* (syn. *Psammomyrma* and *Spinomyrma*), *Araucomyrmex* Gallardo 1919 (syn. *Ammomyrma*), and *Conomyrma* Forel 1913 (syn. *Biconomyrma*). These three genera were recognized by Snelling and Hunt (1975) in their survey of the ants of Chile, although one of the three, *Conomyrma*, is absent from that country. Later Snelling (1995) concurred with Shattuck’s (1992) synonymy of *Araucomyrmex* and *Conomyrma* under *Dorymyrmex*.

Indeed, the worker-based morphological characters used by Snelling and Hunt to differentiate the three groups appear largely consistent in the set of species sampled for the current study. In particular, *Dorymyrmex s. str.* possesses a prominent propodeal tooth or spine, a psammophore, a nodiform petiole, a marked or notable indentation at the metanotal groove, and usually a preapical attachment of the fifth maxillary palpomere to the fourth. *Araucomyrmex* workers differ from *Dorymyrmex* in their apical

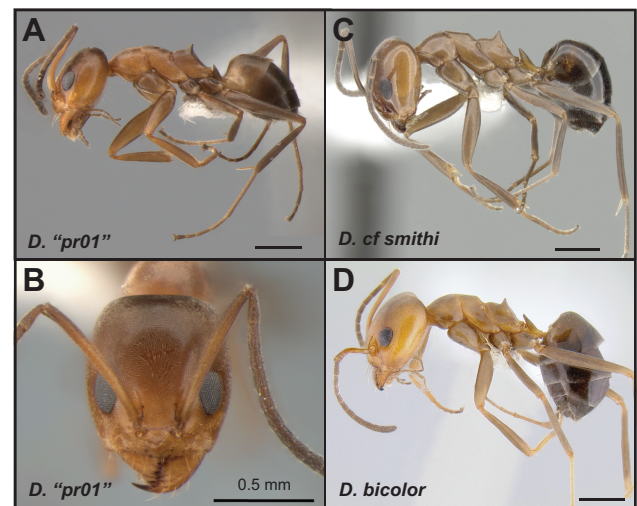


**Fig. 3.** Divergence dates of *Dorymyrmex* and outgroups as estimated in MCMCTree (in PAML v4.9), with a map of specimen collection localities. Estimated node ages are displayed with 95% highest probability density (HPD) distributions. Two soft calibration points were used, indicated with grey HPD distributions: (i) The root node 'L(DF)', uniting *Leptomyrmex* + (*Dorymyrmex* + *Forelius*), was assigned a range of 59–42 Ma, and (ii) the divergence between *D. planidens* and *D. bicolor* (Node 1) was assigned a range of 33–13 Ma, both based on previous studies incorporating other dolichoderine genera and fossil calibrations (Ward et al. 2010; Boudinot et al. 2016). For full collection details, please see [Supp Table 2 \(online only\)](#); for all HPD distributions, [Supp Fig. S4 \(online only\)](#); for all node age estimations, [Supp Fig. S5 \(online only\)](#). Figure was created using the R packages MCMCTreeR and phytools (phylo.to.map function).

palpomere attachment, reduction in depression of the metanotal groove, and a shorter, knoblike propodeal protuberance (Gallardo 1919, Kusnezov 1952). *Conomyrma*, meanwhile, has a drastically reduced psammophore compared to *Dorymyrmex* s. str. and *Araucomyrmex*. In addition, the propodeal tubercle is neither spine-shaped as in *Dorymyrmex*, nor a smooth knob as in *Araucomyrmex*, rather tending toward a pointed or conelike shape. The shape of the propodeal process is arguably subjective and may vary considerably within a species (Snelling 1973, 1975).

Shattuck (1992) did find definite exceptions to the boundaries described by Snelling and Hunt, such as *D. bruchi* Forel 1912, which 'has the nodiform scale used to diagnose *Dorymyrmex* s. str., but the metanotal groove is only weakly depressed and the fifth maxillary palp segment is attached apically', characters diagnostic of *Conomyrma* and *Araucomyrmex*. However, the extent of the metanotal groove may be masked, especially in lateral view, by the spiracles associated with it, which in many *Dorymyrmex* s. str. have formed tubercles and migrated to the dorsal face of the mesosoma. The entire metanotal region warrants further study. With the exception of the subjective metanotal groove character, *D. bruchi* differs from *Dorymyrmex* s. str. only in palpomere attachment. Similarly, *D. ebeninus* possesses *Dorymyrmex* s. str. features but apical palpomere attachments, and molecular evidence has now placed *D. ebeninus* with *Dorymyrmex* s. str. (Fig. 2).

While acknowledging the imperfections of the current morphological delimitation, Clade I may be considered as an approximation of *Dorymyrmex*; Clade II, *Araucomyrmex*; and Clade III, *Conomyrma*—the puzzling *pyramicus* group. Further sampling of *Araucomyrmex*, e.g., *D. tener*, the type species, will likely provide further evidence supporting the concordance between these clades and the former generic boundaries. It must be emphasized that the evidence presented here is still insufficient to establish or reinstate any formal taxonomic rank, but the consistency of these groups will be tested with more extensive taxon sampling and morphological analysis.



**Fig. 4.** Profile and head of *Dorymyrmex* 'pr01' as compared to representatives of the *pyramicus* clade. Note the striking similarity. All scale bars measure 0.5 mm. (A and B) *Dorymyrmex* 'pr01', CASENT0841114, phot. JTO. (C) *D. cf smithi*, CASENT0249673, phot. Ryan Perry. (D) *Dorymyrmex bicolor*, CASENT0106031, phot. Michael Branstetter.

It is also worth noting that with respect to position and branch lengths, *D. 'pr01'* differs from the remainder of the *Conomyrma* species. Morphological diagnosis, however, places *D. 'pr01'* unequivocally as part of this clade, which is otherwise closely inter-related (Fig. 4). Some undetermined factors may make it unique from the rest of the former *Conomyrma*, but it is more likely that the phylogeny is simply missing other relevant taxa. If all extant *Dorymyrmex* were included in this tree, any number of unsampled lineages similar in appearance could arise on the branch between nodes 3 and 4—Kempf's (1972) catalog of Neotropical ants lists 40 species and subspecies of *Conomyrma*. Given the rapid radiation

and richness bias in the *pyramicus* clade, it is likely that ecological release, penetration of novel niche space, or morphological innovation occurred somewhere between nodes 2 and 4. Another possibility (not mutually exclusive) is that extended sampling may reveal the radiation began much earlier, encompassing *D. 'pr01'* and other South American *Conomyrma*.

The internal topology and species limits of the *pyramicus* clade are difficult to resolve confidently, especially when compared with the older, unambiguous branching events and strong support within Clades I and II. Although most nodes are statistically well-supported, the branch lengths within Clade III are dramatically shorter than those across the rest of the tree. This uncertainty recapitulates morphological difficulty. Occasionally, high levels of morphological variation are observed among workers of a colony that appear to exceed diagnostic features typically used to distinguish Nearctic species: color, pubescence, and shape of the cephalic vertex and propodeal tubercle (as in Snelling 1995). Moreover, delimitation has always been notoriously difficult in the globally widespread *pyramicus* clade, but particularly so in the Northern Hemisphere (Trager 1988, Johnson 1989, Snelling 1995). Unpublished results suggest that when Nearctic species are sampled more sparsely, branches within the *pyramicus* clade are still relatively shorter than in Clades I and II. Conversely, when Clade III is sampled more densely, the support values drop, branches get yet shorter, and species boundaries are even less certain. This could in part be an effect of outgroup sampling, but even *Dorymyrmex*-only analyses and Nearctic-only analyses do not show significantly more resolution, i.e., better-supported branches (unpublished data). It is clear that Clade III is still diversifying rapidly and will require more targeted attention.

The estimated divergence dates underline the recency and speed of this diversification (Fig. 3). Some consistently upheld species have diverged within the last 5 My, such as *D. elegans* and *D. bureni*, but other terminals presumed to be conspecific show genetic divergence at similar timescales, such as two sympatric *D. 'pr01'*. It is possible that some 'conspecific' pairs may be separate, cryptic species, or, conversely, some 'heterospecific' pairs may belong to a single species with dramatic morphological variation. Patterns of evolutionary conservation and acceleration in *Dorymyrmex* appear to occur over unpredictable timescales, both genetically and morphologically.

The phylogeny presented here supports the radiation of *Dorymyrmex* from a South American ancestor, corroborating a Neotropical origin for *Dorymyrmex*, *Forelius*, and the *Leptomyrmex* (*Dorymyrmex* + *Forelius*) clade, as inferred by Boudinot et al. (2016) (Fig. 3). With regard to morphology, the early-diverging lineages in the Southern Cone (South America south of the Tropic of Capricorn; Clades I and II) show high morphological variability, but give rise to a widespread and relatively undifferentiated ingroup, suggesting that *Dorymyrmex s. str.* and *Araucomyrmex* (Clade I-II) are older and more specialized, while *Conomyrma* (Clade III) is too young to have noticeably diverged. Other noted amphitropical desert taxa in the New World—*Diadasia* bees and *Larrea* creosote bush—also originated in South American deserts and made their way northward to arid regions of North America, where *Diadasia* diversified 'explosively' (Lia et al. 2001, Sipes and Wolf 2001, Wilson et al. 2014).

Furthermore, tracing the stem of the phylogeny highlights lineages from the Southern Cone, then the mosaic savannas and forests of southeastern Brazil and Bolivia, part of the South American 'dry diagonal' hypothesized to be a Pleistocene arc of seasonal woodland (Prado and Gibbs 1993). This is not to be confused with the South American Arid Diagonal (SAAD) first described by Martonne, which extends from Peruvian coastal desert southeast to Patagonia (Martonne 1935). After the emergence of *D. jto03*, however, the

*pyramicus* clade shows two paths northward: one group spreading through Brazil, Bolivia, French Guiana, and Curaçao—relatively straightforward—and the other through the Dominican Republic, Baja California, and a smattering of other North American localities—a more complicated story. Particularly surprising is the placement of the *D. 'bn01'* collected in coastal Honduras, which appears nested within a clade of eastern United States species and may indicate a subsequent dispersal from the Gulf states or the Caribbean islands. Incidentally, one of the colonies sampled in French Guiana was from an isolated grassy helicopter pad surrounded by rainforest and 97 kilometers inland, attesting to a high dispersal capacity in *Dorymyrmex*. While the exact movements of *Dorymyrmex* are still uncertain, the overall south-to-north pattern is quite clear.

The radiation of *Dorymyrmex* in Neotropical savannas and its arrival in North America both occurred during the Miocene-Pliocene transition ~8–3 Ma, which predates the Pleistocene grassland expansions first hypothesized by Haffer (1969). Indeed, some researchers have strongly argued that the importance of Quaternary events in South American biodiversification has been overestimated (Colli 2005, Werneck 2011). The desiccating Miocene-Pliocene climate created grasslands throughout the New World, possibly allowing *Dorymyrmex* to use 'stepping stones' of grassland across moister landscapes. A stepwise dispersal seems more likely than a long-distance dispersal event based on the 'soft' nature of its bimodal distribution, which is not as starkly disjunct as, for example, its ecologically similar sister genus *Forelius* (Shattuck 1992). But would *Dorymyrmex* need a long-distance dispersal to reach North America?

The two prominent hypotheses regarding North/South America connections are the uplift of the Antilles landspan (GAARlandia) ~33 Ma (Iturralde-Vinent and MacPhee 1999) and the full closure of the Isthmus of Panama (IP) ~3 Ma, which resulted in the Great American Biotic Interchange (GABI) (Marshall et al. 1982, Stehli and Webb 1985). Some research has suggested an earlier, more complex emergence of the IP, with pulses of terrestrial dispersal between 23–20 and 8–6 Ma (Bacon et al. 2015). Moreover, Wilson et al. (2014) proposed that *Diadasia* bees (~20–15 Ma) traversed the ocean by 'jumping' between the islands destined to become the Panamanian Isthmus—the Panamanian Archipelago, as it were—in the Miocene. With regard to dispersal strategy, *Dorymyrmex* is similar to *Diadasia* bees, which are exclusively ground-nesting but have winged reproductives, thus forming an apt comparison to ants. However, Clade III *Dorymyrmex* traveled from South to North America between ~8 and 5 Ma (Fig. 3); thus, as for the timing of dispersal, *Dorymyrmex* may be better compared to a fellow ant genus, *Eciton* Latreille 1804, a Neotropical genus of army ants (~7–4 Ma) (Winston et al. 2017). Interestingly, however, *Eciton* ants disperse only over continuous landmasses, due to their wingless queens, whereas *Dorymyrmex* alates are capable of longer-distance dispersal over seaways. Despite their difference in vagility, it appears that *Dorymyrmex* ants did not disperse northward significantly earlier than *Eciton*, while *Diadasia* bees did. These speculations will be addressed in future studies by more densely sampling the Neotropics and performing comprehensive, dedicated analyses of historical biogeography.

Until now, *Dorymyrmex* ants have been known to myrmecologists mainly as a taxonomic headache in the subfamily Dolichoderinae and have thus been neglected for decades. Through revisiting the genus in a molecular genetic context, it emerges that some of the previous genus-level taxa that had been recognized by earlier investigators appear to be phylogenetically robust while others are not. Struggles in differentiating the North American species are actually

the result of an ongoing radiation—one which hints at still-cryptic diversity. Furthermore, *Dorymyrmex* has undergone an intercontinental journey that predates the Panamanian isthmus and concurs with patterns of dispersal found in other amphitropical arid-adapted taxa in the New World. Truly, as suggested by Deyrup (2017), ‘*Dorymyrmex* provides enough taxonomic and biogeographical puzzles to keep myrmecologists happily engaged for decades.’

## Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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