



The first fossil replete ant worker establishes living food storage in the Eocene

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Abstract

Worker specialization extends the behavioral and ecological repertoire of ant colonies. Specialization may relate to colony defense, brood care, foraging, and, in some taxa, storage. Replete workers swell the crop and gaster to store liquid food, which can be accessed by other colony members through trophallaxis. This storage ability, known as repletism, has independently evolved across several ant lineages, but the temporal history of this trait has not yet been investigated. Here, we describe the first fossil replete in the extinct species *Leptomyrmex neotropicus* BARONI URBANI, 1980 preserved in Miocene-age Dominican amber. Together with new evidence of repletism in *L. neotropicus*' extant sister species, *Leptomyrmex relictus* BOUDINOT & al., 2016, we reconstruct the pattern of acquisition and descent in this storage-linked trait. Our ancestral-state reconstruction suggests that *Leptomyrmex* acquired replete workers in the Eocene and may therefore represent the earliest instance of so-called “honeypot” ants among all known ants, both living and extinct.

Key words: Palaeoentomology, repletism, *Leptomyrmex*, Hymenoptera, Formicidae.

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Introduction

Eusociality is a profound phenotypic phenomenon that shapes morphology as well as behavior. Division of labor is central to advanced sociality in insects such as ants, and workers may exhibit a range of behavioral or morphological specializations related to task performance (WILSON & HÖLLDOBLER 2005). A striking example of caste specialization in ants is repletism. Replete workers serve as living food storage within the colony by retaining liquid food within their gaster. Food storage takes place in the crop, a region of the alimentary canal in the foregut between the esophagus and the proventriculus. The crop swells to

accommodate large amounts of food, distending the gaster to large proportions via elastic intersegmental membranes located between each tergite and sternite (CARNEY 1969, WILSON 1974). This elasticity enables repletes to distend their gaster dramatically in some species, which renders replete individuals visibly distinct from other workers (CONWAY 1994) and may limit mobility (CHARBONNEAU & al. 2017). During times of scarcity, the stored contents of the replete crop are redistributed to colony members. Food is regurgitated from one ant to another, a process known as trophallaxis. Prior to trophallaxis, ants concentrate the

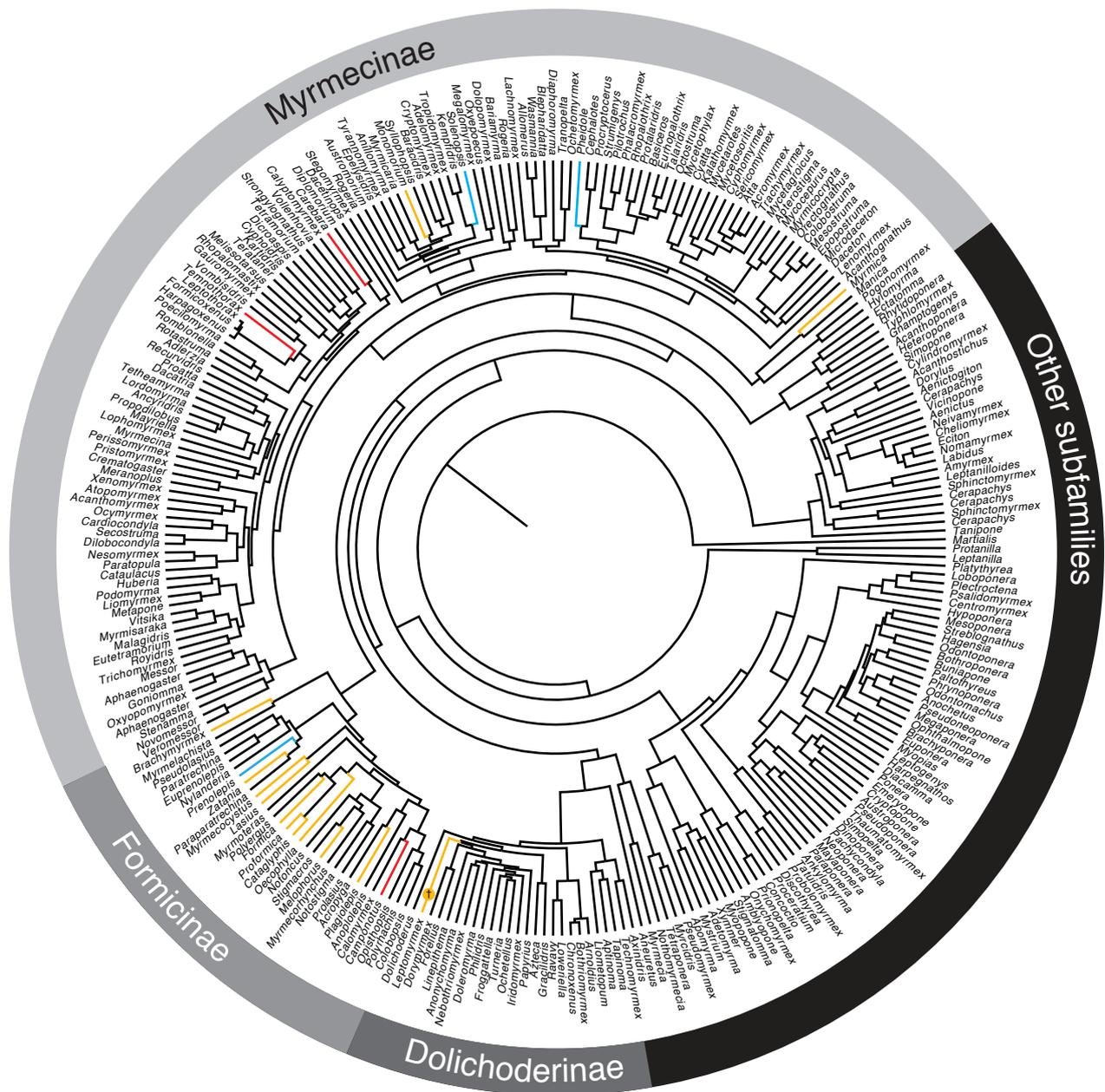


Fig. 1: Phylogenetic distribution of known repletes. Topology adapted from BLANCHARD & MOREAU (2017). Lineage color reflects presence of repletes (yellow: crop repletes; blue: fat body repletes; red: crop / fat body repletes). The fossil species *Leptomyrmex neotropicus* is denoted by the dagger symbol (†).

stored material by reducing its water content and they add components of their internal fluids in the crop (MEURVILLE & LEBŒUF 2021). This creates a network of fluid and nutrient exchange in the colony. Because trophallaxis is a common feature across ant lineages, many taxa have the capacity to distend the crop and gaster as part of a colony-wide “social stomach” (MEURVILLE & LEBŒUF 2021). Taxa with a replete caste are ostensibly less vulnerable to fluctuating resource availability, particularly during seasons when food sources are limited (VAN ELST & al. 2021). Trophallaxis may regulate the flow of nutrients among the colony with repletes, in particular, providing a reliable source of a “higher quality” of food (BØRGESEN 2000).

Repletism is a convergently evolved trait that has been observed in several ant lineages. While a precise definition of repletism is lacking, well-documented replete castes are reported from 20 genera (GLANCEY & al. 1973, COSENS & TOUSSAINT 1985, MOFFETT 1986, 1988, CONWAY 1992a, b, RUANO & TINAUT 1999, BØRGESEN 2000, ANDERSEN 2002, EYER & al. 2012, LORINCZI 2016, CASADEI-FERREIRA & al. 2020, KHALIFE & PEETERS 2020). Repletes are typically classified as either crop repletes, storing liquid carbohydrates in the social stomach (i.e., crop), or fat body repletes, containing lipids in hypertrophied fat bodies (TSCHINKEL 1987, CHARBONNEAU & al. 2017). Both types of repletes play a role in regulating nutrient storage in the colony and



Fig. 2: Photomicrograph of *Leptomyrmex neotropicus* replete specimen BALDR-0155 preserved in Miocene-age Dominican amber. Lateral view with distended gaster visible. Scale = 1 mm.

can provide sustenance to the colony during times of scarcity (BØRGESEN 2000, CHARBONNEAU & al. 2017, KHALIFE & PEETERS 2020). Crop repletes are often referred to as “honeypot ants” or “honey ants”, while fat body repletes are referred to as “corpulents” or “false honeypot ants” (BØRGESEN 2000, LORINCZI 2016). Nearly all origins of repletism occur in the subfamilies Formicinae and Myrmicinae, while a single dolichoderine genus – *Leptomyrmex* MAYR, 1862 – exhibits honeypot workers (Fig. 1).

While most of the 29 described species are endemic to Australia, New Guinea, and New Caledonia, two species are known from the Neotropics: a single fossil species from the Dominican Republic and a recently discovered extant species in Brazil (LUCKY & WARD 2010, BOUDINOT & al. 2016, BARDEN & al. 2017). Numerous Australasian *Leptomyrmex* species exhibit replete workers, which are frequently found outside of the nest and apparently use their distended crops for liquid food transport as well as storage (WHEELER 1915). Until now, the replete status of Neotropical *Leptomyrmex* species has remained unknown, obscuring the temporal and biogeographic

origin of this trait. Following the recent discovery of *Leptomyrmex relictus* in the Brazilian cerrado (BOUDINOT & al. 2016), *Leptomyrmex* is hypothesized to have originated in the Neotropics during the Eocene before dispersing to Australasia prior to the glaciation of Antarctica (BARDEN & al. 2017), a route that has been documented in other lineages (SANMARTÍN & RONQUIST 2004, DLUSKY & RADCHENKO 2013). We sought to determine whether repletism originated recently in Australasia or if there was an older origin in the Neotropics prior to the long-distance migration and diversification of the genus. In this study, we test the hypothesis that there was a single origin of repletism in *Leptomyrmex*.

Here, we report new fossil and extant evidence of repletism in the Neotropics. Through microCT imaging, we confirm the replete status of the now extinct Caribbean species *Leptomyrmex neotropicus* BARONI URBANI, 1980 and report replete workers in the extant sister species *Leptomyrmex relictus* BOUDINOT & al., 2016 for the first time. With these natural history data, we estimate the approximate age and retention of repletism in the genus

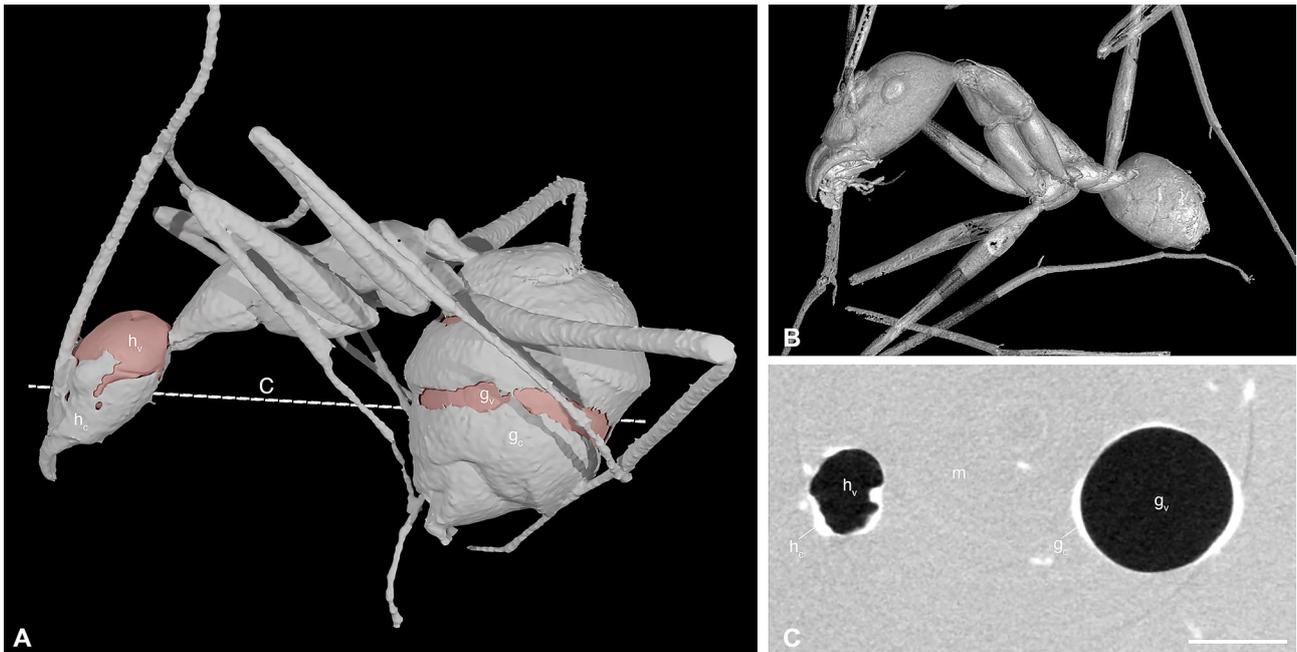


Fig. 3: X-ray computed tomography images of *Leptomyrmex neotropicus*. (A) Lateral view of replete *L. neotropicus* worker specimen BALDR 0155. (B) Lateral view of a non-replete *L. neotropicus* worker (AMNHDR-13-85 modified from BARDEN & al. 2017). (C) Z-stack cross section of specimen BALDR 0155, head and gaster denoted by dotted line in sub-panel A; h_c = head cuticle, h_v = voidspace of head, m = amber matrix, g_c = gaster cuticle, g_v = voidspace of gaster. Scale = 1 mm.

Leptomyrmex through ancestral-state reconstruction. Our approach illuminates the evolutionary history of extreme morphology-assisted food storage in ants.

Material and methods

Fossil imaging

Photomicrographs were taken using a Nikon SMZ25 stereomicroscope (Tokyo, Japan) equipped with a DS-Ri2 digital camera (Tokyo, Japan). Individual images were digitally stacked using Nikon NIS Elements v5.02.00 64-bit to generate a high-resolution extended focus montage image. X-ray computed tomography data were generated at the New Jersey Institute of Technology Otto H. York Center for Environmental Engineering and Science using a Bruker SkyScan 1275 micro-CT scanner (Kontich, Belgium). The fossil specimen was scanned at a voltage of 38 kV and current of 190 μ A for 65 ms exposure time averaged over four frames per rotation with a voxel size of 8.00 μ m. Z-stacks were generated using NRecon (Micro Photonics, Allentown, PA), segmented using 3D Slicer v.4.9 (FEDOROV & al. 2012), and rendered in Blender v.3.2.1.

Ancestral-state reconstruction

Ancestral repletism states were reconstructed across *Leptomyrmex* using the phylogeny of BARDEN & al. (2017) and a compilation of natural history observations. Worker replete codings were derived from a literature survey, new observations reported here, as well as published iNaturalist accounts of reliably identified *Leptomyrmex* species (Data S1, as digital supplementary material to this

article, at the journal's web pages). The taxonomic identities of Australasian iNaturalist observations were verified using the criteria of LUCKY & WARD (2010). There is only one fossil *Leptomyrmex* species known, *Leptomyrmex neotropicus*; the fossil replete specimen reported here was compared with the morphology of a known series of this species and determined to be conspecific. There is one known extant Neotropical species of *Leptomyrmex*, *Leptomyrmex relictus*; newly observed replete workers from Brazil were identified by Lívia Pires do Prado of the Museu Paraense Emílio Goeldi and determined conspecific based on the criteria of BOUDINOT & al. (2016). iNaturalist derived codings were based on photographs that depicted *Leptomyrmex* workers with clearly distended gasters. Given the uncertainty associated with some species regarding the presence of repletes, species were coded in a probability matrix: Terminals were assigned a 1 / 0 replete / non-replete status if known to have repletes, a 0 / 1 replete / non-replete status if known to not have repletes, and assigned 0.5 / 0.5 if the presence of repletes was uncertain. A flat, uninformative prior probability distribution was assumed for uncertain states rather than attempting to assess the probability of repletes vs non-repletes in uncertain species, given the lack of natural history information for many species. Ancestral-state reconstruction was conducted using stochastic character-state mapping implemented with the prior probability matrix for character states. The reconstruction was inferred under the equal rates (ER) model, based on prior comparisons of the Akaike information criterion (AIC) using different character-state evolution models (symmetrical (SYM) and

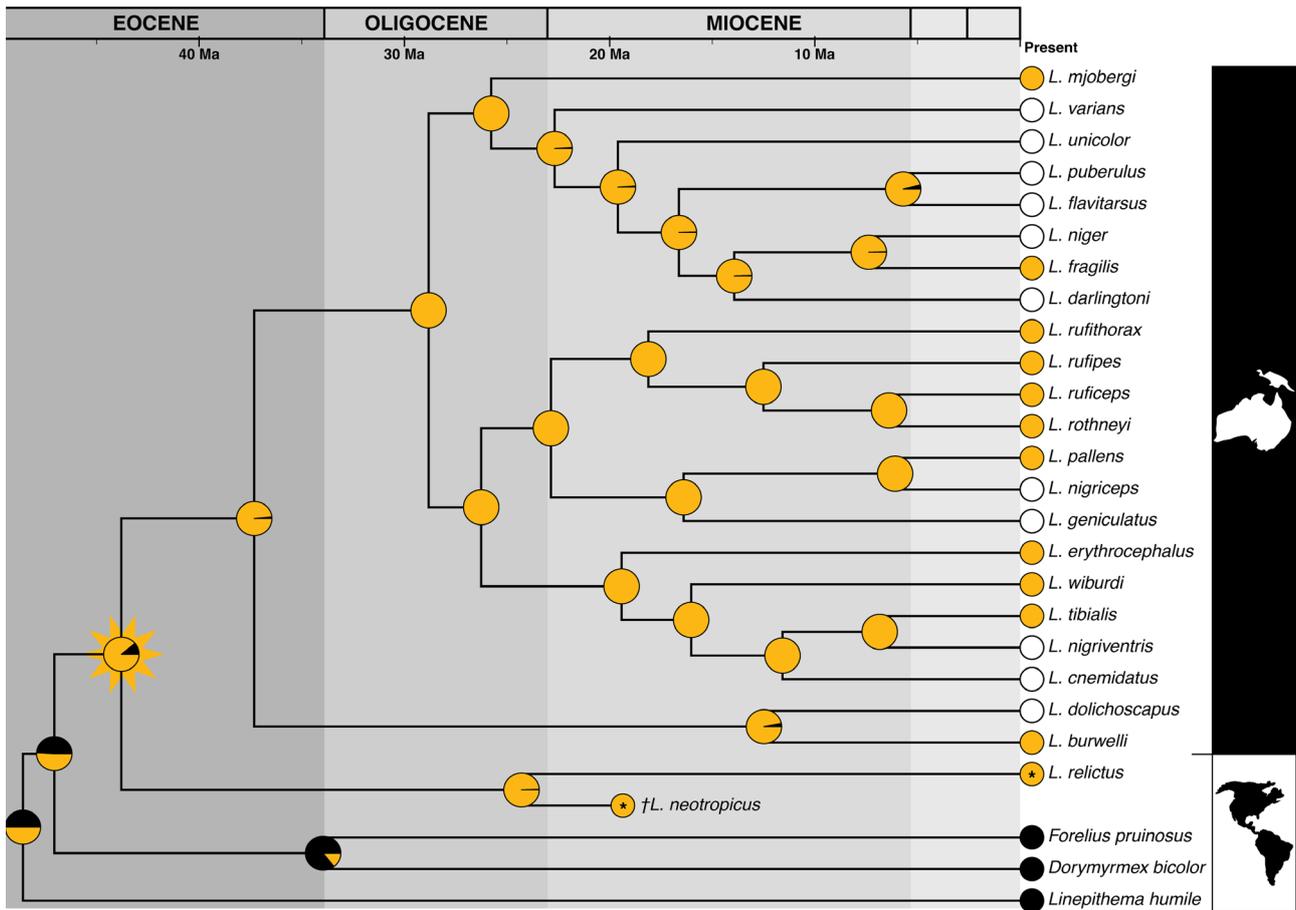


Fig. 4: Ancestral-state reconstruction of replete workers across *Leptomyrmex*. Summary of 200 simulated stochastic character histories under an equal rates (ER) model. Node pie charts represent posterior probabilities of states at each node. Yellow = replete; black = no replete; white = unknown, these were coded as ambiguous in ancestral-state reconstruction. The most recent common ancestor of all *Leptomyrmex* is indicated with the star icon. Topology and mean node ages from BARDEN & al. (2017). Asterisks denote new observations reported here.

all rates different (ARD)), and ran across simulations of 200 trees (number of simulations = 200). State changes were summarized across all 200 trees. Ancestral-state reconstruction was conducted in R version 4.2.0 using the package phytools (REVELL 2012).

Results

A fossil replete

Specimen BALDR-0155 is a *Leptomyrmex neotropicus* worker preserved as an inclusion within amber dated to the Upper Miocene (~ 16 Ma; ITURRALDE-VINCENT & MACPHEE 1996) from the Northern mines of near La Cumbre, Dominican Republic. The gastral elastic intersegmental membrane is significantly distended (Fig. 2) while there are no signs of taphonomic distortion across the cuticle. X-ray computed tomography recovers a sharp difference in inclusion density in the region of the gaster and head (Fig. 3), consistent with air. This heterogeneous density is the result of void space within the cuticle, a common feature recovered through X-ray imaging as internal features degrade after an insect is entombed in resin (DIERICK & al. 2007).

Extant repletes in the Neotropics

We (LC, HMM) observed replete workers of *Leptomyrmex relictus* entering and exiting a disturbed nest entrance, with some repletes carrying brood or plant and soil fragments in their mandibles. Replete gasters were conspicuously enlarged and distended relative to nearby non-repletes. This documentation in *L. relictus* confirms mobility and multiple task performance of repletes, as described in other *Leptomyrmex* species (PLOWMAN 1981). Observations took place across the months of July, August, and September 2020 in an urban forested park, Parque Cesamar (10° 12' 35.4" S, 48° 19' 22.5" W), city of Palmas, state of Tocantins, Brazil. Two videos were recorded from the same nest within the park (Videos S1, S2). A nest survey revealed 47 non-replete workers (exemplars in Fig. S1), 10 replete workers, six males, and 83 brood individuals; specimens are currently housed at the Federal University of Maranhão, Brazil.

The evolution of repletism in *Leptomyrmex*

We found strong support for repletism as the ancestral condition of *Leptomyrmex* (Fig. 4; posterior probability for

Tab. 1: Summary of major replete lineages and their estimated crown ages. Lineage dates are derived from published molecular-based divergence estimates and indicate the age of the last common ancestor for each genus, except where otherwise noted. Lineage dates denoted with (divergence) correspond with the last common ancestor of the focal genus and its closest living relative sampled in the corresponding phylogeny – such instances reflect inadequate sampling to confidently estimate crown ages and are therefore overestimates. Instances of single-species repletes are excluded; it is not possible to estimate the age of these lineages with currently available data. Note that some genera, such as *Camponotus* and *Monomorium*, have been recovered as polyphyletic in phylogenetic analyses.

Subfamily	Replete genera	Type of repletism	Mean lineage age (Ma)	Age reference	Replete reference
Formicinae	<i>Agraulomyrmex</i>	Fat body	~23	BLAIMER & al. (2016)	PRINS (1983)
	<i>Brachymyrmex</i>	Crop	~17 [27.5 – 7.5]	BOUDINOT & al. (2022)	COVELO DE ZOLESSI & al. (1978)
	<i>Camponotus</i>	Crop	~24 [30 – 13]	BOUDINOT & al. (2022)	LUBBOCK (1880), FROGGATT (1896), HETERICK (2022)
	<i>Cataglyphis</i>	Crop	~15 (divergence)	BLAIMER & al. (2015); TINAUT & RUANO (2021)	EYER & al. (2013)
	<i>Colobopsis</i>	Crop	~24.5 [35 – 15]	BOUDINOT & al. (2022)	WILSON (1974), HASEGAWA (1993)
	<i>Lasius</i>	Crop	~21.9 [28.6 – 15.3]	BOUDINOT & al. (2022)	CAMMAERTS (1996)
	<i>Melophorus</i>	Crop	~44.2 [51 – 20] (divergence)	BLAIMER & al. (2015)	CONWAY (1992b), HETERICK (2017)
	<i>Myrmecocystus</i>	Crop	~14.1 [19.9 – 10.2]	VAN ELST & al. (2021)	FROGGATT (1896), SNELLING (1976)
	<i>Plagiolepis</i>	Crop	~11.2 [24 – 3] (low sample size)	BLAIMER & al. (2015)	HETERICK (2022)
	<i>Prenolepis</i>	Fat body	~15 [19 – 9]	BOUDINOT & al. (2022)	TSCHINKEL (1987)
	<i>Proformica</i>	Crop	~20 (divergence)	BLAIMER & al.; TINAUT & RUANO (2021)	GALKOWSKI (2017)
		<i>Zatania</i>	Crop	~15 [18.5 – 9]	BOUDINOT & al. (2022)
	<i>Formica</i>	Crop	~17 [21 – 4]	BOUDINOT & al. (2022)	COSENS & TOUSSAINT (1985)
Dolichoderinae	<i>Leptomyrmex</i>	Crop	~43.8 [54 – 35.2]	BARDEN & al. (2017)	See Data S1
Myrmicinae	<i>Solenopsis</i>	Fat body	~39.1 [31.4 – 47.1]	WARD & al. (2015)	GLANCEY & al. (1973)
	<i>Leptothorax</i>	Crop	[~48 – 25]	WARD & al. (2015)	BØRGESEN (2000)
	<i>Myrmica</i>	Crop	~34	JANSEN & al. (2010)	BØRGESEN (2000)
	<i>Monomorium</i>	Crop	[~50 – 30]	WARD & al. (2015)	BØRGESEN (2000)
	<i>Carebara</i>	Crop	~43 [50 – 30]	WARD & al. (2015)	AZORSA & FISHER (2018)
	<i>Pheidole</i>	Fat body	35.2 [46.6 – 24.9]	WARD & al. (2015)	TSUJI (1990)

repletism 0.89). State changes were relatively infrequent; across all trees, we estimated the average number of gains and losses as 2.5. Our reconstruction suggests that once repletism evolved in *Leptomyrmex*, it infrequently or perhaps never reverted. The preponderance of ancestral nodes estimated as replete suggests that many *Leptomyrmex* species are likely to have a replete caste upon further study, though because our probability matrix used a flat uninformative prior due to lack of ecological data, this may have biased some more recent ancestral nodes towards repletism.

In extreme cases of repletism (e.g., *Myrmecocystus* WESMAEL, 1838), replete workers tend to be immobile and confined to the nest, solely serving as subterranean food storage (CONWAY 1977). In fat repletes, once workers have depleted the resources in their fat bodies, usually during the season after storage, they also become foragers (WILLIAMS & LUCKY 2020). In other taxa, repletes are mobile, performing other tasks, such as carrying brood or foraging

(SKINNER 1980, PLOWMAN 1981, COSENS & TOUSSAINT 1985, CONWAY 1992b). Several species of *Leptomyrmex* are documented as mobile repletes, foraging on plants and transporting liquid food to the nest (PLOWMAN 1981, DAVIDSON & al. 2004). Our report of mobile repletes in *Leptomyrmex relictus* and the presence of a *Leptomyrmex neotropicus* replete worker in fossil amber suggest that mobility and replete foraging were ancestral in this lineage.

Discussion

We recover a single origin of replete workers in the last common ancestor of all extant and extinct *Leptomyrmex* species in the Eocene ~ 45 Ma (Fig. 4) (BARDEN & al. 2017). Our results suggest that living food storage was present in a Neotropical ancestor and that this trait was retained as the genus expanded into Australasia. The expansion of grasslands and increases in global temperatures during the Eocene-Miocene transition may have contributed to the retention of repletism even across continents and tens of

millions of years (DLUSSKY & RADCHENKO 2013, AZEVEDO & al. 2020). The retention of this trait in *Leptomyrmex* is unexpected because repletism is frequently ascribed to species that inhabit dry climates or are winter active (HÖLLDOBLER & WILSON 1990, KRONAUER & al. 2004), whereas some replete species in *Leptomyrmex* are found in wet forests. Several other genera, including *Pheidole* WESTWOOD, 1839 (see TSUJI 1990), exhibit repletes within species that are endemic to wet habitats; even though climate is strongly linked to living food storage in some lineages, it does not appear to be a requirement for repletism. Future work focusing on the relative contributions of climatic pressure, the full distribution of replete ants across continents, and potential costs associated with replete worker capacity may reveal a more complete picture of selection pressures associated with living food storage.

It is notable that in our ancestral-state reconstruction (Fig. 4) and throughout ant lineages that contain repletism (Tab. 1), there remain many species with an unknown status. Repletism is often difficult to detect if the replete workers are immobile and confined to the nest. These ants can be difficult to extract from underground, and nestmates often move repletes to deeper chambers to avoid exposure. There is therefore a bias toward underreporting replete castes where they may exist, and it is more likely that fossilized lineages will exhibit evidence of mobile repletes since taxa with immobile repletes are unlikely to be aboveground and therefore caught in resin- or sediment-based preservation modes.

This study marks the first ancestral-state reconstruction of repletes in any genus of ants, and the estimated ages of lineages that contain replete species provide an opportunity to assess the temporal distribution of living food storage (Tab. 1). Molecular-based divergence estimates suggest that crown group *Carebara* WESTWOOD, 1840, *Leptothorax* MAYR, 1855, and *Monomorium* MAYR, 1855 each originated in the early Eocene, prior to *Leptomyrmex* (see BØRGESEN 2000, BARDEN & al. 2017, AZORSA & FISHER 2018). Repletism is present but not pervasive in these older taxa, which prevents a clear reconstruction of replete origins – it is not yet known whether repletes evolved once early in the history of these lineages and were subsequently lost in several descendants or if repletism was recently acquired across multiple distantly related species. Although *Leptomyrmex* is not the oldest lineage to contain repletes, the definitive reconstruction of ancestral repletism here establishes the first clear indication that ants with “honeypot” repletes were present in the Eocene. Future ancestral reconstructions of replete workers across ant lineages will further reveal the tempo of replete evolution as a striking case of morphology-enabled division of labor.

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