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Review Article

Honeypots: a review of repletism across the ants

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Abstract

Honeypot ants are a fascinating case of the convergent evolution of an internal food-storage strategy. They are characterized by a subset of physogastric workers, called repletes, that store food long-term in their crops to support the colony in times of low resource availability. Despite their biological and evolutionary significance, information on honeypot ants remains scattered, and the trait itself has lacked a clear and unified definition. This review synthesizes current knowledge on replete morphology, physiology, and function, establishing a foundation for defining the repletism syndrome. Through our literature review, we confirm the occurrence of repletes in at least eight genera across three subfamilies (Formicinae, Dolichoderinae, and Myrmicinae). We also identify four genera with putative honeypot species that remain poorly studied and clarify cases of misidentification, where repletism has been confused with other internal storage strategies such as worker corpulence, trophic eggs, or thoracic crop expansion. We propose that repletism occurs along a spectrum across species, reflecting both morphological specialization and behavioral flexibility. In this review, we also demonstrate the global distribution of this extreme adaptation. Finally, we highlight future research directions into factors driving convergence of repletism and mechanisms and potential microbial interactions underlying this adaptation.

Key words: Worker specialization, convergent evolution, storage strategy, Hymenoptera, Formicidae.

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Introduction

Social insects have evolved diverse strategies to overcome resource-storage challenges, developing both internal and external mechanisms, often influenced by seasonal and life-cycle factors (Hölldobler & Wilson 1990). The beginning of a new colony and reproductive season, for example, are important periods where protein and high-energy resources are essential to produce new workers, brood, and reproductives (Hölldobler & Wilson 1990, Feldhaar 2014). In bees, these needs can be met by collecting and storing pollen and nectar in combs. Ants, on the other hand, do not have such structures but have developed external storage strategies, such as seed caching, stockpiling, and food burying (Reyes-López & Fernández-Haeger 2002, Smith 2007, Gayahan & Tschinkel 2008, Qin & al. 2019). They have also developed internal food storage via fat bodies (Rosell & Wheeler 1995), trophic eggs (Hölldobler & Wilson 1990), and the crop (i.e., the social stomach). Crop storage is rather common across ant subfamilies, usually as a short and temporary strategy where foragers collect and hold food to distribute it among nestmates (Eisner & Wilson 1952, Greenwald & al. 2018, Meurville & al. 2025).

Some ant species have developed a more extreme strategy in which specialized individuals, known as repletes, store great amounts of liquid food in their crops for long periods. Species that include these individuals, such as those from the genus *Myrmecocystus* Wesmael, 1838, are referred to as honeypot ants. Repletes are typically fed by regular workers, who collect and regurgitate fluids into their mouths through trophallaxis (Conway 1986, Meurville & LeBoeuf 2021). When nestmates require nutrients, repletes then regurgitate the stored fluid, which is distributed throughout the colony (Conway 1977, 1986). As repletes take in food, their crops become abnormally enlarged, stretching the intersegmental membranes and separating the exoskeletal plates. This physogastry (i.e., inflation of the gaster or parts of it; Weesner 1955, Kusnezov 1960, Haug & Haug 2022) can limit their activity by reducing mobility, with repletes varying from nearly immobile (e.g., *Myrmecocystus*) to highly mobile (e.g., some *Leptomyrmex* Mayr, 1862). Notably, the earliest use of the term physogastry was in reference to queens (Weesner 1955), but here, it is used in the context of trophic physogastry found in repletes (Kusnezov 1960, Haug & Haug 2022). These ants are specialized in food storage, relying on regular workers for other tasks; however, in *Leptomyrmex*, repletes appear to be less strictly specialized and have been observed foraging outside the nest (Wheeler 1915, Plowman 1981, Sawh & al. 2023). This interspecific variation in task specialization challenges the classification of repletes as a caste and suggests that their function can be context dependent.

The retention of the liquid food inside the crop is possible due to a valve-like structure, the proventriculus, which prevents food from passing into the midgut, where digestion occurs. Repletes can accumulate sugar or protein-rich fluids in their crops for weeks or even months (Stumper 1961, Marikovsky 1974, Conway 1990, Khalife & Peeters 2020), raising questions about how these resources remain viable for such extended periods. The mechanism behind the prolonged preservation of the liquids remains unknown but may be related to microbial activity (McCutcheon & al. 2009, Russell & al. 2009, Vásquez & al. 2012, Engel & Moran 2013, Dong & al. 2023), and the factors influencing the storage duration, such as species-specific traits or colony demands, have yet to be studied.

Most species of honeypot ants live in arid environments with distinct wet and dry seasons, where food availability fluctuates. Their long-term food storage is thought to ensure colony survival in periods of scarcity and has likely facilitated the colonization of novel ecological niches. Honeypot ants are considered a case of convergent evolution, where similar traits have arisen in independent lineages, possibly due to similar environmental pressures (Rocha & al. 2021, Wang & al. 2025).

Several morphological and behavioral traits characterize true honeypot ants, suggesting that this adaptation occurs along a spectrum and can be considered a syndrome. Key features of the repletism syndrome are: (1) the presence of physogastric workers specialized and dedicated to food storage; (2) food storage occurring specifically in the crop, rather than fat-bodies or trophic eggs; and (3) the ability to store food for extended periods, on the order of weeks and months.

A primary goal of this review is to substantiate repletism as a specialized long-term internal food-storage strategy in ants and evaluate the literature considering this definition. In doing so, we clarify the criteria for repletism, addressing prior misclassifications, and examine the current state of the research into honeypot ants, which has focused mainly on *Myrmecocystus*. Since key aspects of honeypot ants – including behavioral specialization, physiological and morphological variation, food-storage mechanisms, and evolutionary context – are still poorly understood, this review also lays the groundwork for future research. Finally, as global climate around the world becomes more extreme and ecosystems shift, studying evolutionary solutions for extreme environments is timely.

Replete morphology and physiology

As repletes are fed, their crops expand to fill most of the gaster (Fig. 1). This expansion stretches the gaster's intersegmental membranes to the point where their

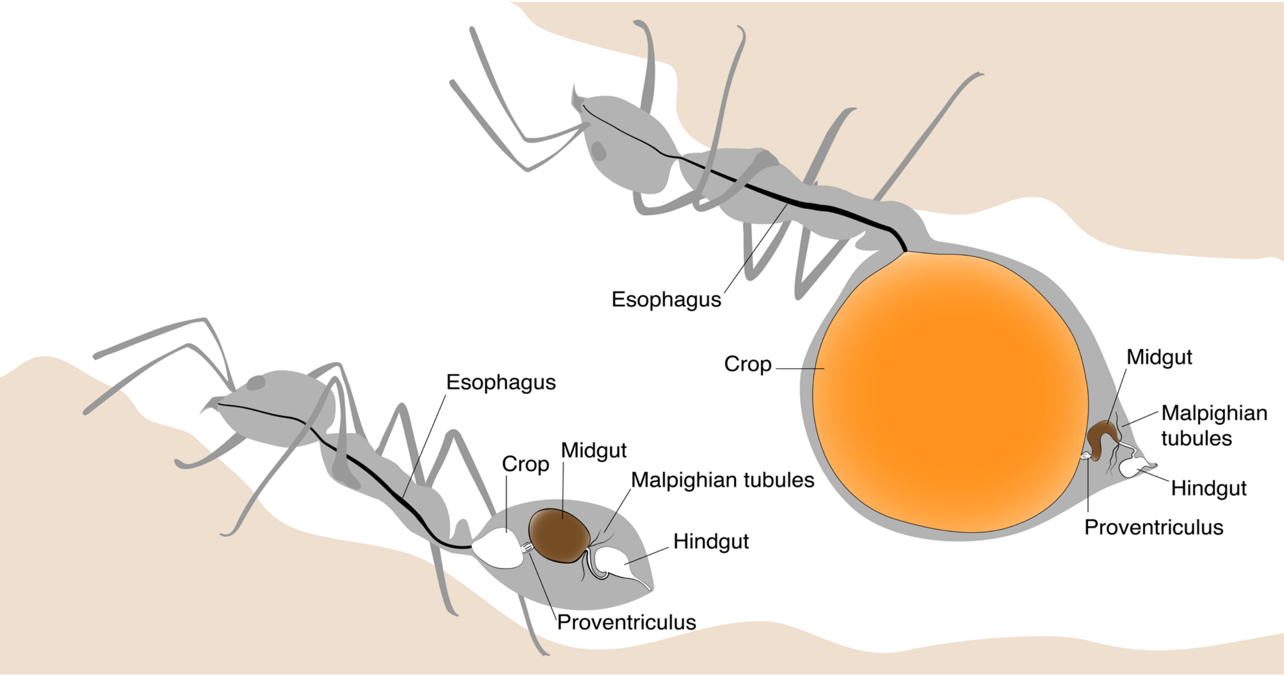

Fig. 1: Diagram of the digestive system of honeypot ants, showing key structures: esophagus, crop, proventriculus, midgut, Malpighian tubules, and hindgut. The bottom section illustrates a *Myrmecocystus* regular worker, while the top section shows a replete worker, highlighting differences in gut morphology between the two ants (drawing: © B. Nogueira).

Fig. 2: Three repletes from the same *Myrmecocystus mexicanus* colony, with different crop contents. The contents of the left-most ant are considered "milky" in the literature, the middle ant would be considered dark amber and the right-most would be considered light amber (Conway 1990). The milky ant crop is protein- and lipid-rich, while the two amber ant crops are carbohydrate-rich (photo: © L. Khadempour).

exoskeletal plates (tergites and sternites) separate and make the crop's contents visible (Fig. 2). The storage capacity of repletes varies considerably across taxa. In *Myrmecocystus*, larger species such as *Myrmecocystus mexicanus* Wesmael, 1838 can hold up to 112 µl, while smaller species like *Myrmecocystus arenarius* Snelling, 1982 reach at least 10 µl; by contrast, repletes of the much smaller *Tapinolepis* sp. store around 2 µl (B. Nogueira, D. Nguyen, L. Khadempour, pers. obs.).

The gastral intersegmental membranes of *Myrmecocystus mexicanus* contain resilin and folds that allow this extreme distension; and once repletes are full, the folds are completely stretched, leaving the surface smooth (Varman 1981). It has been observed both in field and in laboratory colonies that partially emptied repletes, or "depletes", exhibit sagging gasters, flaccid intersegmental membranes, and deformed abdominal sclerites (Conway 1986; L. Khadempour, pers. obs.). This suggests that once membranes are fully unfolded in repletes, they cannot return to their folded state, preventing the gaster from shrinking back to normal size. In termites, differential expression of cuticle proteins across castes and body parts enables the extreme physogastry of queens (Rasheed & al. 2019, Costa-Leonardo & al. 2025). Whether similar cuticular modifications underlie repletism is unknown. Folding mechanisms also occur in the crops of other insects and regular ant workers, where folds stretch when the organ is full (Chapman 1998, Solis & al. 2013). It is possible that in honeypot ants, replete crops are not only folded, like the gastral intersegmental membranes, but are also more elastic (Caetano 1984). More histological observations are needed to determine the specific modifications in the intersegmental gastral membranes of other honeypot ants and castes and how crop tissue accommodates this level of expansion.

The retention of fluids in repletes' crops is facilitated by the proventriculus (Fig. 1). This organ has a valve-like function and regulates both storage and controlled release of liquid food into the midgut (Fig. 1). In adult Hymenoptera, the crop content is slowly passed into the midgut, likely to guarantee proper digestion and nutrient absorption in the latter (Eisner & Wilson 1952). In ants, however, the proventriculus also functions as a dam, allowing food to be retained in the crop and shared with nestmates through trophallaxis (Meurville & LeBoeuf 2021). The proventriculus structure differs among ant subfamilies; in some taxa it is very simple, while in others it is highly elaborate and, in addition to regulating passage through the digestive tract, also works as a suction pump that facilitates food retention and transfer during trophallaxis (Eisner & Wilson 1952).

Additional structural features may also contribute to this regulation. Many insects possess spinule-like projections within the crop that can help direct food toward the midgut (Chapman 1998). For example, in *Monomorium* Mayr, 1855, similar structures have been reported at points where the crop connects with the esophagus and proventriculus (Solis & al. 2013), while in *Solenopsis saevissima* (Smith, 1855) and *Camponotus pennsylvanicus* (De Geer, 1773), they are present along the esophagus to the connection with the crop, oriented toward the midgut (Forbes 1938, Walker & Clower 1961). These structures are thought to sift and ensure directional food flow through the digestive tract.

Whether honeypot ants rely on similar mechanisms to prevent the large quantities of liquid stored in their crops from unwantedly returning to the esophagus is unknown. In sap-sucking hemipterans, an esophageal valve lies between the cibarium (i.e., food pouch) and the esophagus, ensuring a one-way passage of liquid to the esophagus under positive pressure (Backus & McLean 1983, Almeida & al. 2005, Ruschioni & al. 2019, Clark & al. 2023). By contrast, in ants and other hymenopterans, the crop appears continuous with the esophagus, and no comparable valves are known to regulate reverse flow of liquid (Forbes 1938, Walker & Clower 1961, Caetano 1991). Our own observations in honeypot ants have not revealed any structures between the crop and esophagus that would control flow; however, we have not specifically searched for this, and much closer observations and anatomical studies are needed to determine whether a valve-like structure exists.

Replete development

Repletes can develop early in the colony's life cycle in a lab setting (Bartz & Hölldobler 1982; J. Gadau, pers. comm.), but they are not seen amongst the first-brood workers, even when given sugary fluids (Conway 1981). In the cooperative colony-founding ant *Myrmecocystus mimicus* Wheeler, 1908, repletes develop after most queens have been killed and the worker population stabilizes, their formation likely depending on a surplus of food and resources (Bartz & Hölldobler 1982). Whether the onset of replete production occurs at the same time in colonies fed ad libitum as those under a strict diet in natural settings is uncertain. Rissing (1984) observed repletes developing after two weeks in a field-collected *Myrmecocystus mexicanus* colony. These individuals were significantly larger than regular workers. When repletes were removed and before the colony could produce the largest caste, the second-largest workers transitioned into repletes (Rissing 1984). This suggests that worker size may set a constraint in which individuals can become repletes, but colony condition, more than size or age, may provide a trigger for replete assignment. This task flexibility is seen in honey bees – when foragers are removed, younger individuals are recruited to replace them, and foragers can revert to brood care if nurse workers are lacking (Robinson & al. 1992).

While major workers are generally the individuals most likely to become repletes (Rissing 1984, Eyer & al. 2013, Khalife & al. 2023), mated and virgin queens are also known to store liquids and can serve as repletes in a colony (Morgan 1991, Khalife & al. 2023). In addition to size, it has also been proposed that callows are more prone to develop into repletes due to their greater membrane elasticity after eclosion (Snelling 1976, Schmid-Hempel & Schmid-Hempel 1984). However, *Myrmecocystus* colonies can be experimentally induced to produce repletes even without the presence of callows (Rissing 1984, Conway 1990). *Myrmecocystus* is by far the best-studied genus of honeypot ants, but little is known about replete formation in other taxa, and caste-specific patterns may vary across the Formicidae.

Functions of repletes in the colony economy

Task specialization

In *Myrmecocystus* species, once a replete becomes fully distended, the gaster's intersegmental membranes can no longer return to their original state, limiting the ant from performing a different functional role. Depleted repletes have been observed refilling in laboratory colonies (Conway 1986; L. Khadempour, pers. obs.), but whether this occurs in the wild remains unclear. The fate of repletes after full depletion or how many cycles of filling they can undergo is also unknown, raising questions about their longevity once emptied. In general, lifespan in ants varies with caste and task (Chapuisat & Keller 2002, Giraldo & Traniello 2014). Longevity can be shorter for foragers engaged in out-of-nest tasks and longer for workers performing internal tasks (Schmid-Hempel & Schmid-Hempel 1984, Gordon & Hölldobler 1987, Oettler & Johnson 2009). Because repletes are restricted to internal, restricted roles, they may live longer than regular workers.

Considered trophic physogastric workers (Kusnezov 1960, Haug & Haug 2022), repletes' enlarged size and weight limits their mobility. Their movement likely carries a high energetic cost. Although the burden of load carriage has been studied in regular foragers of *Myrmecocystus mendax* Wheeler, 1908 and *Myrmecocystus mexicanus* (see Duncan & Lighton 1994), it has not been quantified in repletes. Restriction of movement likely explains why repletes often hang from the ceilings of deep underground chambers (Wheeler 1908). However, the degree of mobility varies across honeypot ant genera. In *Leptomyrmex*, for example, repletes appear to be mobile and have been observed foraging outside the nest (Plowman 1981), in contrast to *Myrmecocystus* repletes, which are largely immobile (Conway 1986). Such variability suggests that while extreme distension generally reduces behavioral flexibility once workers assume the role of food storage, the degree of restriction depends on morphology and may differ among honeypot ant lineages.

Despite some inherent variability between species and individuals, these physical and behavioral constraints indicate that once an ant assumes the role of food storage, it is unlikely to return to other colony tasks, though it may have performed them earlier in life (Rissing 1984). Repletes have been described as a caste or sub-caste (Rissing 1984), but current knowledge on the variability in task specialization across genera is not enough to establish this status. However, it undoubtedly represents a unique phenomenon in ants, which is a compelling example of convergent evolution and warrants further study.

Repletism vs regular trophallactic behavior

Both repletism and regular trophallactic behavior within an ant colony involve liquid food stored in the crop, but they differ fundamentally in scale, duration, and role. For regular trophallactic behavior, ant species display a broad range of trophallaxis frequencies, from some species that are capable of trophallaxis but use it rarely (e.g., *Diacamma* cf. *indicum* Santschi, 1920) to many ant species that circulate their crop contents across the colony even outside the context of food (e.g., *Camponotus floridanus* (Buckley, 1866)) (Hakala & al. 2021, Fujioka & al. 2023). In the former, trophallaxis is used only in the context of feeding, but in the latter, it appears to have other roles (Meurville & LeBoeuf 2021). Regular within-colony trophallaxis behavior has only been explored in depth in a famine-release context (Greenwald & al. 2015, Planckaert & al. 2019, Baltiansky & al. 2023). Typically, ant foragers fill their crops and retain fluids for minutes before sharing resources with nestmates upon their return to the nest (Wilson & Eisner 1957, Howard & Tschinkel 1981, Buffin & al. 2009, Greenwald & al. 2015). Such short-term storage is part of routine food transport and does not constitute repletism nor does it create a distinct worker role.

Foragers generally share food in proportion to how much non-foragers can receive, and the amount left in their crops often determines whether they resume foraging activity (Greenwald & al. 2015, 2018, Baltiansky & al. 2023). This means that food distribution is shaped by crop capacity and suggests that ants can perceive the tension and limitations of their full crop (GREENWALD & al. 2018). Non-foraging workers, in turn, can engage in food intake until their crops are full or contribute to food distribution to other nestmates, including foragers (GREENWALD & al. 2015). Food distribution can be heterogeneous within colonies, with food concentrated in certain workers positioned centrally, likely due to logistical dynamics (BUFFIN & al. 2009, GREENWALD & al. 2018). In short, general trophallaxis creates a dynamic and transient flow in which storage is constrained by crop fullness and logistical position within the colony.

In repletes, crop capacity is far greater than that of regular workers, and rather than acting as transient carriers, they function as long-term storage specialists (STUMPER 1961, MARIKOVSKY 1974, CONWAY 1990, KHALIFE & PEETERS 2020). In *Myrmecocystus*, repletes can retain liquid food for weeks to months and in some cases up to a year (CONWAY 1990; A. LeBoeuf, pers. obs.), likely accumulating surplus during periods of abundance (e.g., wet-season nectar flows) and releasing it during scarcity (e.g., the dry season) (CONWAY 1986). The duration of storage remains poorly documented across honeypot ant species, likely varying among taxa and relative to worker lifespan, and requires further investigation.

Another key distinction is that repletes not only store large quantities of liquid but also hold it without spontaneous release. In other ants, workers may regurgitate liquid unintentionally when overfed (CAMMAERTS 1996), and it appears that a higher concentration and viscosity of fluids make consumption and retention more energy-intensive and difficult (LOIS-MILEVICICH & al. 2021). By contrast, we have no record of unrequested regurgitation by repletes, highlighting a physiological ability to retain food when there is no immediate trophallactic demand. This ability sets them apart from non-honeypot ant species and emphasizes their role as living reservoirs. It is the large volume and long-term storage, rather than the act of crop-filling alone, that defines repletism as a unique form of task specialization.

Storage content

The term honeypot comes from the fact that most repletes store carbohydrate-rich sugary liquids such as nectar and honeydew (SNELLING 1976, CONWAY 1986, MEURVILLE & al. 2025). *Myrmecocystus mimicus, Myrmecocystus mexicanus* (see BURGETT & YOUNG 1974), *Camponotus inflatus* LUBBOCK, 1880 (ISLAM & al. 2022), and *Melophorus bagoti* LUBBOCK, 1883 (BADGER & KORYTNYK 1956) primarily store glucose and fructose and sometimes maltose and sucrose. However, there are also records of repletes storing lipids and proteins (BURGETT & YOUNG 1974, ISLAM & al. 2022). Individual repletes were even observed with two phases of liquid, one that is sugary and another that contains lipids (BURGETT & YOUNG 1974, CONWAY 1990). Similar within-colony variation has also been observed in *Myrmecocystus mendax* (see SNELLING 1976, CONWAY 2003) and *Myrmecocystus bagoti* (see CONWAY 1992, SCHULTHEISS & al. 2010).

Different crop contents are reflected in color variation observed between replete gasters (Fig. 2). In *Myrmecocystus*, darker amber indicates more tannins, glucose, and fructose, while milky-colored repletes correspond to a higher protein content (CONWAY 1990). Some repletes, particularly those with clear crop contents, may primarily function as water-storage vessels (SNELLING 1976). In theory, repletes that store different materials could become hubs for specific nutrients. However, we do not yet know if this is the case. It is uncertain if the resource partitioning across different repletes leading to these striking asymmetries is driven by worker behavior (i.e., differential feeding of the repletes), replete behavior (i.e., the repletes choose to specialize), or resource variations over time. We also do not know if, after a replete is filled, the crop composition changes over time.

The stored crop fluid is acidic in both *Myrmecocystus* (WHEELER 1908) and *Camponotus* MAYR, 1861 repletes, measured to have a pH of 3.85 (ISLAM & al. 2022), consistent with other formicine ants (TRAGUST & al. 2020). In the formicine subfamily, acidic crops are due to ingestion of poison-gland secretions and can select beneficial microbes (TRAGUST & al. 2020). It is unclear if the acidity of honeypot ants comes from formic acid, microbial metabolism, or both. Microbes are often associated with animals' extreme feeding strategies (SAPOUNTZIS & al. 2015, DUPLAIS & al. 2021, CHANSON & al. 2023), and so, repletes' gut microbiome is thought to contribute to the preservation of their stored food (DONG & al. 2023). This would mean that microbial activity could have been a key factor in the evolution of repletism. We do not know what the pH is of crops of non-formicine honeypot ants, and this could be an important phenotype to explore as we examine convergent evolution of repletism.

Replete crop content distribution and contribution to colony fitness

Across many ant species, most colony members do not forage and are fed through trophallaxis or other secondary food-sharing behaviors. Resources brought by different foragers are blended with existing crop contents to ensure nutritional balance across the colony (CASSILL & TSCHINKEL 1995, BOULAY & al. 2000, COOK & al. 2010, GREENWALD & al. 2019). This mixing also mediates information exchange, odor signaling, and hormonal regulation (BOULAY & al. 2000, LEBOEUF & al. 2016). In honeypot ants, repletes may influence this network by modifying circulating trophallactic fluid composition, adding another layer of complexity to colony nutrient management (HAKALA & al. 2021, KHALIFE & al. 2023).

Different sub-groups within ant colonies have distinct nutritional demands (FELDHAAR 2014). For example, larvae and queens require more protein-rich diets whereas workers rely more on carbohydrates. How repletes fit in this partitioning is poorly understood. They could mirror the general trophallactic composition or serve as specialized reservoirs for different nutrients, which would involve a mechanism to regulate the proportions of repletes with specific contents. Seasonal changes could also cause a dynamic shift (Wheeler & Martinez 1995, Ashcraft & Judd 2014). For example, reproductive periods may increase protein demand, potentially altering both use and composition of repletes' crop contents.

Generally, in species that rely heavily on trophallaxis, workers will use this method to feed larvae (Meurville & LeBoeuf 2021, Matte & LeBoeuf 2025). This brood food is often a nutritive secretion made of endogenously produced proteins and processed metabolites (LeBoeuf & al. 2016) similar to bee royal jelly. Conway (1981) observed that in *Myrmecocystus*, sugary liquids were delivered to larvae via trophallactic networks, but for protein, larvae were more frequently found feeding on dead workers rather than provided mealworms. Compared with other, relatively passive larvae of most formicine ants, *Myrmecocystus* are unusually active (Snelling 1976, Conway 1981). They have unique morphology that corresponds with their high activity levels (Matte & LeBoeuf 2025). They have even been observed begging (i.e., waving their mouthparts) and feeding on living repletes that fall to the chamber floor (A. LeBoeuf, pers. obs.). The necessary behavioral observations to determine the prevalence of this phenomenon in other honeypot ant genera have not been conducted. It is also unclear whether it is part of the suite of phenotypes associated with the convergent evolution of repletism.

Repletes' primary food-storage function appears especially relevant in arid or seasonally fluctuating environments (Froggatt 1896, Conway 1992, Duncan & Lighton 1994, Sankey-Alamilla & al. 2024). Ant foraging strategies are associated with the availability and distribution of resources across space and time (Lanan 2014), and storage strategies appear to follow the same principle. Across ants, storage management and food distribution are regulated by colony hunger level and logistic dynamics (Josens & Roces 2000, Buffin & al. 2012, Greenwald & al. 2018). For example, in laboratory colonies, *Solenopsis* Westwood, 1840 prioritizes food storage only once the colony has been satiated and when food is abundant, particularly following an extended period of starvation (Qin & al. 2019). Repletes may function in a comparable way, storing liquids when a surplus is available and having them redistributed during scarcity, aligning with their association with environments with high resource variability. In seed-storing *Messor* Forel, 1890 ants, storage saturation influences foraging selectivity, with less discrimination as storage increases (Reyes-López & Fernández-Haeger 2002). It would be interesting to investigate whether existing reserves could also shape future replete crop-content composition.

By acting as "living pantries" for carbohydrates, proteins, or water, repletes likely buffer the colony against scarcity, linking the distribution of crop contents directly to colony fitness. The specific patterns of nutrient flow among repletes and their impact on colony survival, however, have not been tested.

Other internal food-storage strategies in Formicidae

Certain ant species display alternative internal food-storage strategies that may resemble repletism, leading to potential misclassification. Our literature review shows that terms often used to describe repletes based on appearance or function (e.g., "physogastric workers", "honey-bags", "swollen gasters", "stretched membrane", and "crop repletes") sometimes refer to other workers with enlarged gasters, including corpulent workers or those storing energy in trophic eggs. Here, we will examine the most frequently misidentified cases (Tab. 1), highlighting the key differences between repletism and other internal food-storage strategies within ant colonies.

Fat body

Corpulent workers develop hypertrophied fat-body deposits outside their digestive tract for internal nutrient storage. These enlarged deposits result in pronounced abdominal distension and separation of the exoskeletal plates, giving them a superficial resemblance to repletes. Since distinction cannot always be made externally, dissection and examination are required to determine whether swelling results from liquid food retained in the crop (i.e., repletism) or reserves stored in the fat body. The fat body of insects is an essential metabolic and endocrine organ. Its cells synthesize proteins and metabolites involved in morphogenesis, lipid transport, egg maturation, and hormone regulation (Keeley 1985, Arrese & Soulages 2010). Ants accumulate fat-body reserves when resources are abundant and mobilize them during scarcity, with storage levels influenced by colony condition and environmental variation (Bernadou & al. 2020).

Fat-body deposits consist of lipids, proteins, and carbohydrates (Rosell & Wheeler 1995), which can be redistributed to nestmates through oral secretions from the postpharyngeal gland, or via trophic eggs derived from metabolized reserves (Hölldobler & Wilson 1990). The fat-body tissue lies in close contact with the hemolymph, which facilitates circulation and transport of metabolites (Chapman 1998, Arrese & Soulages 2010, Roma & al. 2010). Corpulent ants may have a restricted behavioral repertoire, functioning mainly as nutrient stores and showing reduced tendencies to forage or engage in aggression compared with regular major workers or soldiers (Blanchard & al. 2000, Dussutour & al. 2016, Bernadou & al. 2020).

Fat-body storage differs from repletism in that ingested food must first be processed and assimilated before storage. Because it does not rely on retaining undigested liquid in the crop, it also avoids the spoilage risks observed in repletes. Moreover, corpulent workers provide primarily individualized storage; their nutrients must also be metabolized before they can be shared with the colony, whereas repletes provide colony-level storage by directly regurgitating fluids on demand.

These fundamental distinctions highlight that abdominal distension alone cannot be used to diagnose the

Tab. 1: Species previously classified as repletes but that do not fulfill the criteria defining repletism and therefore should not be considered repletes. Distribution information was obtained from the publications that described repletism in each species. * When occurrence data were not available in the original sources, we used AntWeb (2025). [1]*Leptothorax albipennis* is included under its current classification as *Temnothorax albipennis*.

Taxa	Reason for exclusion from confirmed repletes	Distribution	References
Formicinae			
Lasius flavus (Fabricius, 1782)	Reversible brood-tending workers	Nearctic and Palearctic regions *	Børgesen (2000)
Lasius mixtus (Nylander, 1846)	Reversible brood-tending workers	Palearctic region *	Børgesen (2000)
Lasius niger (Linnaeus, 1758)	Insufficient data	Indomalaya, Nearctic, and Palearctic regions *	Børgesen (2000)
Lasius japonicus Santschi, 1941	Thoracic crop	Japan	Kurihara & al. (2022)
Prenolepis imparis (Say, 1836)	Fat body	United States	Talbot (1943), tschinkel (1987)
Myrmicinae			
Crematogaster difformis Smith, 1857	Thoracic crop	Indomalaya region *	Wheeler (1908)
Crematogaster inflata Smith, 1857	Thoracic crop	Singapore; Malaysia	Froggatt (1896), Wheeler (1908)
Leptothorax acervorum (Fabricius, 1793)	Reversible brood-tending workers	Indomalaya, Nearctic, and Palearctic regions *	Børgesen (2000)
Leptothorax muscorum (Nylander, 1846)	Reversible brood-tending workers	Nearctic and Palearctic regions *	Børgesen (2000)
Myrmica rubra (Linnaeus, 1758)	Reversible brood-tending workers	Nearctic, Neotropical, and Palearctic regions *	Børgesen (2000)
Myrmica ruginodis Nylander, 1846	Reversible brood-tending workers	Indomalaya and Palearctic regions *	Børgesen (2000)
Myrmica scabrinodis Nylander, 1846	Reversible brood-tending workers	Palearctic region *	Børgesen (2000)
Pheidole pallidula (Nylander, 1849)	Fat body	France	Lachaud & al. (1992)
Pheidole aberrans Mayr, 1868	Thoracic crop	Brazil	Casadei-ferreira (2020)
Pheidole deima Wilson, 2003	Thoracic crop	Guiana Francesa	Casadei-ferreira (2020)
Pheidole morrisii Forel, 1886	Fat body	United States	Yang (2006)
Solenopsis invicta Buren, 1972	Oil storing questioned in previous works	Australasia, Indomalaya, Nearctic, Neotropical, and Oceania regions *	Glancey & al. (1973)
Temnothorax interruptus (Schenck, 1852)	Reversible brood-tending workers	Neotropical and Palearctic regions *	Børgesen (2000)
Temnothorax nylanderi (Foerster, 1850)	Reversible brood-tending workers	Palearctic region *	Børgesen (2000)
Temnothorax tuberum (Fabricius, 1775)	Reversible brood-tending workers	Neotropical and Palearctic regions *	Børgesen (2000)
Temnothorax albipennis (Curtis, 1854)	Fat body	UK	Blanchard & al. (2000)

repletism syndrome. In fact, several ant species described as honeypot ants rely on fat body hypertrophy for storage: *Colobopsis nipponica* (Wheeler, 1928), *Pheidole morrisii* Forel, 1886, *Pheidole pallidula* (Nylander, 1849), *Temnothorax albipennis* (Curtis, 1854), and *Prenolepis imparis* (Say, 1836) (Talbot 1943). Upon dissection, Tschinkel (1987) observed that in the winter-active ant *Prenolepis imparis*, young workers develop hypertrophied fat bodies up to twice their normal size to provide for the brood, while older workers focus on foraging. Similarly, *Pheidole pallidula* and *Pheidole morrisii* major workers display swollen abdomens due to hypertrophied fat bodies (Yang 2006) and remain inside the nest without foraging (Lachaud & al. 1992).

Thoracic crop

Some ant species have evolved an alternative method of internal food storage through a specialized structure known as the thoracic crop (Petersen-Braun & Buschinger 1975). This adaptation involves the expansion of the cavity around the thoracic region and the portion of the esophagus within it, enabling the storage of nutritious liquid (Petersen-Braun & Buschinger 1975, Casadei-Ferreira & al. 2020, Kurihara & al. 2022). In queens, the cavity is likely a result of the histolysis of flight muscles (Petersen-Braun & Buschinger 1975), which are metabolized along with fat-body reserves stored in this compartment (Kurihara & al. 2022). Since individuals that rarely engage in trophallaxis, such as some Ponerinae, also possess a thoracic crop, its function is thought to serve in individual short-term storage rather than long-term such as observed with repletism (Caetano 1988, 1991).

In some species, like *Pheidole aberrans* Mayr, 1868 and *Pheidole deima* Wilson, 2003, this adaptation is caste-specific, where only major workers possess this trait while minor workers do not (Casadei-Ferreira & al. 2020). Queens of *Lasius japonicus* Santschi, 1941 and *Lasius niger* (Linnaeus, 1758) also possess a thoracic crop, suggesting a shared adaptation within the genus (Matte & Billen 2021, Kurihara & al. 2022). Early observations of *Crematogaster difformis* Smith, 1857 and *Crematogaster inflata* Smith, 1857 misinterpreted their enlarged thoracic region as a thoracic crop, leading to their classification as repletes (Froggatt 1896, Wheeler 1908). However, subsequent studies clarified that this swelling is due to the presence of metapleural glands, which contribute to the structural modification of the thoracic region (Billen & al. 2011).

Honeypot ants, such as *Carebara perpusilla* (Emery, 1895), may also exhibit a thoracic crop, which may serve as a means to slightly enhance their storage capacity (Khalife & al. 2023). Unlike gastral crop storage, which cannot be combined with trophic-egg production or fat-body storage because of finite space in the gaster, the thoracic-crop strategy can be integrated with either of these other storage methods (Khalife & al. 2023). This adaptation could be particularly advantageous for individuals that cannot develop enlarged crops or gasters, such as egg-laying queens that must prioritize egg production (Peeters & al. 2013). In such cases, the thoracic crop could significantly contribute to overall individual storage capacity (Khalife & al. 2023).

In repletism, physogastric workers typically function as living storage units, specializing in food storage at the cost of performing other colony tasks. In contrast, ants with thoracic-crop expansion may be able to engage in multiple activities within the colony while simultaneously storing food, offering a more flexible and dynamic storage strategy (Casadei-Ferreira & al. 2020, Khalife & al. 2023). This flexibility means that the strategy does not exhibit the same limitations as repletism. Although individuals displaying this trait have been termed thoracic-crop repletes (Khalife & al. 2023), this internal food storage does not fall under our current definition of the repletism syndrome.

Temporary crop-filling status

Distinguishing replete workers from regular workers with a full crop can be challenging in some species, leading to misconceptions in the literature regarding the identification of repletism. This is especially true for small-bodied ant species, where distension may not be clearly visible to the naked eye. Additionally, the term "replete" is often used to describe recently-fed workers with distended crops filled with liquid food, as observed in *Formica aquilonia* Yarrow, 1955, *Acromyrmex subterraneus* (Forel, 1893), *Acromyrmex octospinosus* (Reich, 1793), *Linepithema humile* (Mayr, 1868), and *Carebara overbecki* (Viehmeyer, 1916) (Cosens & Toussaint 1985, Moffett 1986, Lamb & Ollason 1994, Halley & Elgar 2001, Richard & Errard 2009).

One interesting case of temporary food storage can be seen in *Lasius flavus* (Fabricius, 1782) (Cammaerts 1996). After consuming excessive amounts of liquid food, full workers remain mostly motionless in the nest with their mandibles spread apart and their gasters visibly swollen. These workers regurgitate food spontaneously even with no external stimulation. Within a few hours, most overfed workers return to their normal size, further emphasizing the temporary nature of their food storage, in contrast to honeypot ant repletes. The uncontrolled regurgitation also contrasts with the regulated trophallactic exchanges seen in true honeypot ants, raising questions about the mechanisms that prevent liquid food from being expelled uncontrollably in repletes.

Another interesting case is that of *Solenopsis invicta* Buren, 1972, where Glancey & al. (1973) reported that major workers could retain oil in their crops for many months (6 - 18). Subsequent studies, however, countered this interpretation (Ricks & Vinson 1972, Wilson 1978, Howard & Tschinkel 1981). While morphological differences between large and small workers have been noted, with majors showing larger gasters (Tschinkel & al. 2003) and retaining food for longer (Howard & Tschinkel 1981), they do not appear to be physogastric, and there is only partial support for a storage function. Instead, the relatively larger gaster in major workers is likely linked to their capacity for fat storage (Tschinkel 1993).

Børgesen (2000) described replete-like behavior of brood-tending workers in lab colonies of *Monomorium pharaonis* (Linnaeus, 1758), calling them brood-tending crop repletes. This study describes the replete-like behavior to be labile and reversible. The workers who filled their crops for temporary storage would quickly (within five days) revert to looking and behaving just like the other workers. Thus, storage of crop fluid appears to be temporary and the gaster distension reversible. Børgesen (2000) also listed several species as having brood-tending crop, without providing additional specific descriptions. These include *Lasius flavus*, *Lasius mixtus* (Nylander, 1846), *Lasius niger*, *Leptothorax acervorum* (Fabricius, 1793), *Leptothorax muscorum* (Nylander, 1846), *Myrmica rubra* (Linnaeus, 1758), *Myrmica ruginodis* (Nylander, 1846), *Myrmica scabrinodis* (Nylander, 1846), *Temnothorax interruptus* (Schenck, 1852), *Temnothorax nylanderi* (Foerster, 1850), and *Temnothorax tuberum* (Fabricius, 1775). With the given definition, we do not think these species should be categorized as having repletism (Tab. 1).

Status of repletism across the ant phylogeny

Putative repletes

Some cases of repletism reported in the literature remain ambiguous; more experimental and observational studies are needed to determine if these ants can be considered true honeypot ant species (Tab. 2). In each of the cases that follow, we are unable to identify these species as containing repletes based off our flow chart (Fig. 3), but the missing information varies for different species. Future studies may reveal that these species can be categorized as honeypot ants.

In some taxa, workers show swollen abdomens, but it is unclear whether their condition matches the physogastry that restricts task performance and reversibility observed in confirmed honeypot ants. For instance, potential repletes of *Cataglyphis cursor* (Fonscolombe, 1846) are part of the major worker caste, with distended intersegmental membranes, separated chitinous plates, and a tendency to remain inside the nest (Eyer & al. 2013); however, only head sizes have been reported, and there is no mention of whether crops were used for storage or whether their gasters expanded beyond the range seen in normally-filled workers. Similarly, *Cataglyphis bicolor* (Fabricius, 1793) appears to have storage-specialized workers, but there is no information on whether these individuals represent a long-term, non-reversible storage role (Schmid-Hempel & Schmid-Hempel 1984).

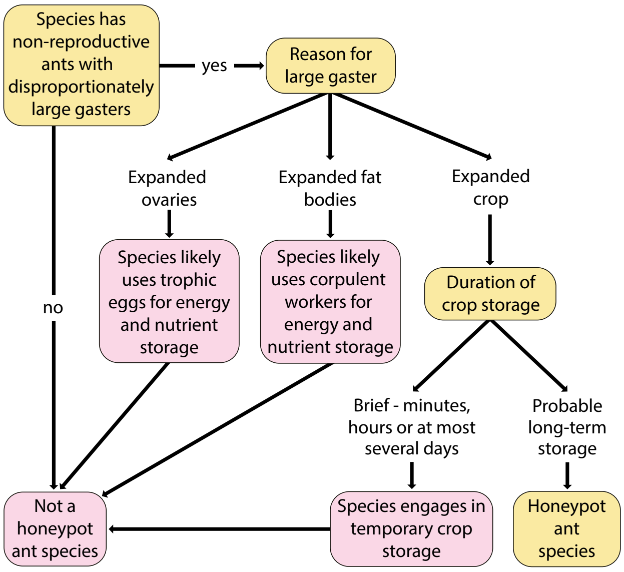

Fig. 3: Decision tree to identify honeypot-ant species with specialist replete workers. This decision tree is meant to differentiate between honeypot ants and other species that have workers with enlarged gasters for other types of nutrient storage. The final decision point of duration of crop storage is somewhat nebulous as the duration has not been measured in many species.

In other cases, the swollen appearance is documented, but the underlying storage organ has not been confirmed.

Tab. 2: List of species considered putative repletes that require further study and additional information to confirm this classification. * *Erebomyrma nevermanni* is included under its current classification as *Carebara urichi*. Distribution information was obtained from the publications that indicated repletism in each species.

Taxa	Evidence gap	Distribution	References
Formicinae			
Cataglyphis cursor (Fonscolombe, 1846)	No confirmation on the storage organ. The level of gaster distension is uncertain.	France	Eyer & al. (2013)
Cataglyphis bicolor (Fabricius, 1793)	No confirmation on the storage organ or whether it is a temporary behavior.	Tunisia	Schmid-Hempel & Schmid-Hempel (1984)
Proformica longipilosa Galkowski & al., 2017	No confirmation on the storage organ or whether it is a temporary behavior.	France	Galkowski & al. (2017)
Zatania darlingtoni (Wheeler, 1936)	No confirmation on the storage organ.	Haiti	Wheeler (1936)
Myrmicinae			
Carebara jajoby Azorsa & Fisher, 2018	A single photo as evidence of gaster distension.	Madagascar	Azorsa & Fisher (2018)
Carebara urichi (Wheeler, 1922) *	No confirmation on the storage organ. The level of gaster distension is uncertain and has been described as semi-replete.	Costa Rica	Wilson (1986)
Pheidole ryukyuensis Ogata, 1982	Dissection confirmed a transparent liquid inside the crop, with no confirmation on whether it is a temporary storage behavior.	Japan	Tsuji (1990)

Proformica longipilosa Galkowski & al., 2017 is reported to possess repletes, yet there is no evidence on whether food is stored in the crop or for how long (Galkowski & al. 2017). For *Carebara urichi* (Wheeler, 1922) and *Zatania darlingtoni* (Wheeler, 1936), the distinction between crop-based storage, fat-body reserves, or other mechanisms is not clear (*Carebara urichi* was previously named *Erebomyrma nevermanni* Mann, 1926 in Wilson 1986, Wheeler 1936). *Zatania darlingtoni* is described as having repletes with greatly distended gasters like *Prenolepis imparis* corpulent workers, but it remains unclear whether the species possesses fat-body reserves.

Even when crop storage is confirmed, the long-term nature of storage remains uncertain. In *Cataglyphis bicolor*, the permanence of the storage role has not been demonstrated (Schmid-Hempel & Schmid-Hempel 1984). In *Carebara jajoby* Azorsa & Fisher, 2018, a single photograph shows a swollen, translucent gaster suggesting a replete function, while in *Carebara urichi* "semi-repletes" swell when colonies are abundantly fed (Wilson 1986, Azorsa & Fisher 2018). For both species, swollen gasters may reflect temporary or reversible storage, and the storage organ is uncertain. *Pheidole ryukyuensis* Ogata, 1982, dissections have revealed transparent liquid inside a swollen crop (Tsuji 1990), but it is still unclear whether individuals serve as long-term storage units comparable with other repletes.

In some genera, the broader occurrence of repletism is unresolved. While some *Carebara* Westwood, 1840 species have confirmed repletes, it is not yet clear how widespread the trait is across the genus (Wilson 1986, Azorsa & Fisher 2018). Likewise, although *Pheidole ryukyuensis* might exhibit crop storage, other species from the genus use other strategies such as thoracic crops or fat-body reserves (Lachaud & al. 1992, Helms 1995, Yang 2006, Casadei-Ferreira & al. 2020). This suggests multiple storage strategies may evolve among species within the same genus.

Confirmed honeypot-ant genera

The following is a list of genera confirmed to exhibit repletism, meeting our requirements of long-term food storage in the crops of specialized physogastric workers. Additional details are provided in Table 3, their geographic distributions are displayed in Figure 4, and their phylogenetic distribution is displayed in Figure 5.

***Myrmecocystus* Wesmael, 1838:** *Myrmecocystus* exhibits an extreme case of repletism, likely present in all species of this genus of 30 species (Bolton 2025), with some being among the most well-documented cases. Individuals that become repletes are significantly larger than the average nestmates and have a significantly greater gastral-to-head width ratio than regular workers (Rissing 1984, Eriksson & al. 2019). The repletes have low mobility and are most often fed by other workers (Wheeler 1908, Burgett & Young 1974, Rissing 1984). *Myrmecocystus* workers can feed on insects, nectar, honeydew, and occasionally dead vertebrates (Snelling 1976). They inhabit arid, semi-arid, and desert regions, including coastal dunes, stream drainages, mountain slopes, and sandy riverbeds, often at low to moderate elevations (Wheeler 1908, Snelling 1976, Sankey-Alamilla & al. 2024).

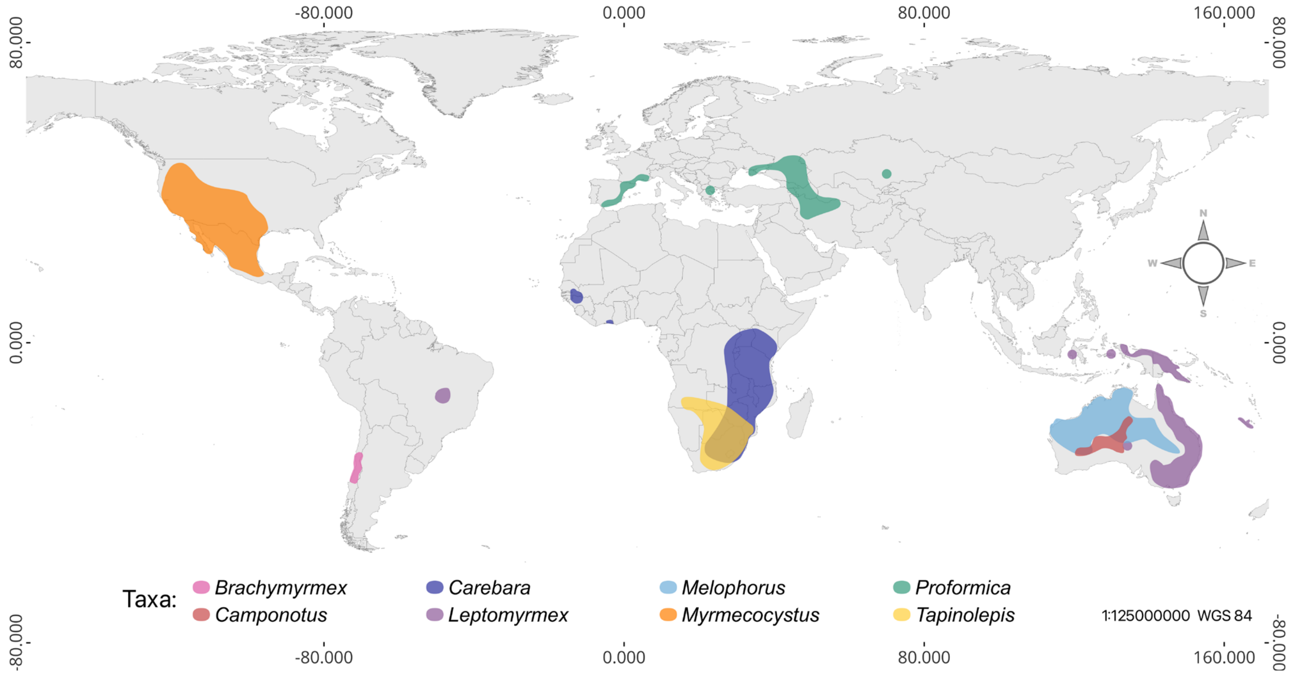

Fig. 4: Global distributions of honeypot ants. Map of honeypot-ant distributions with different colors representing the eight different confirmed genera of honeypot ants. Occurrence data were retrieved from GBIF using the rgbif package in R (Derived dataset GBIF.org 2025), based on our curated list of confirmed replete species. The final map was generated using QGIS, ensuring accurate spatial visualization of species distributions.

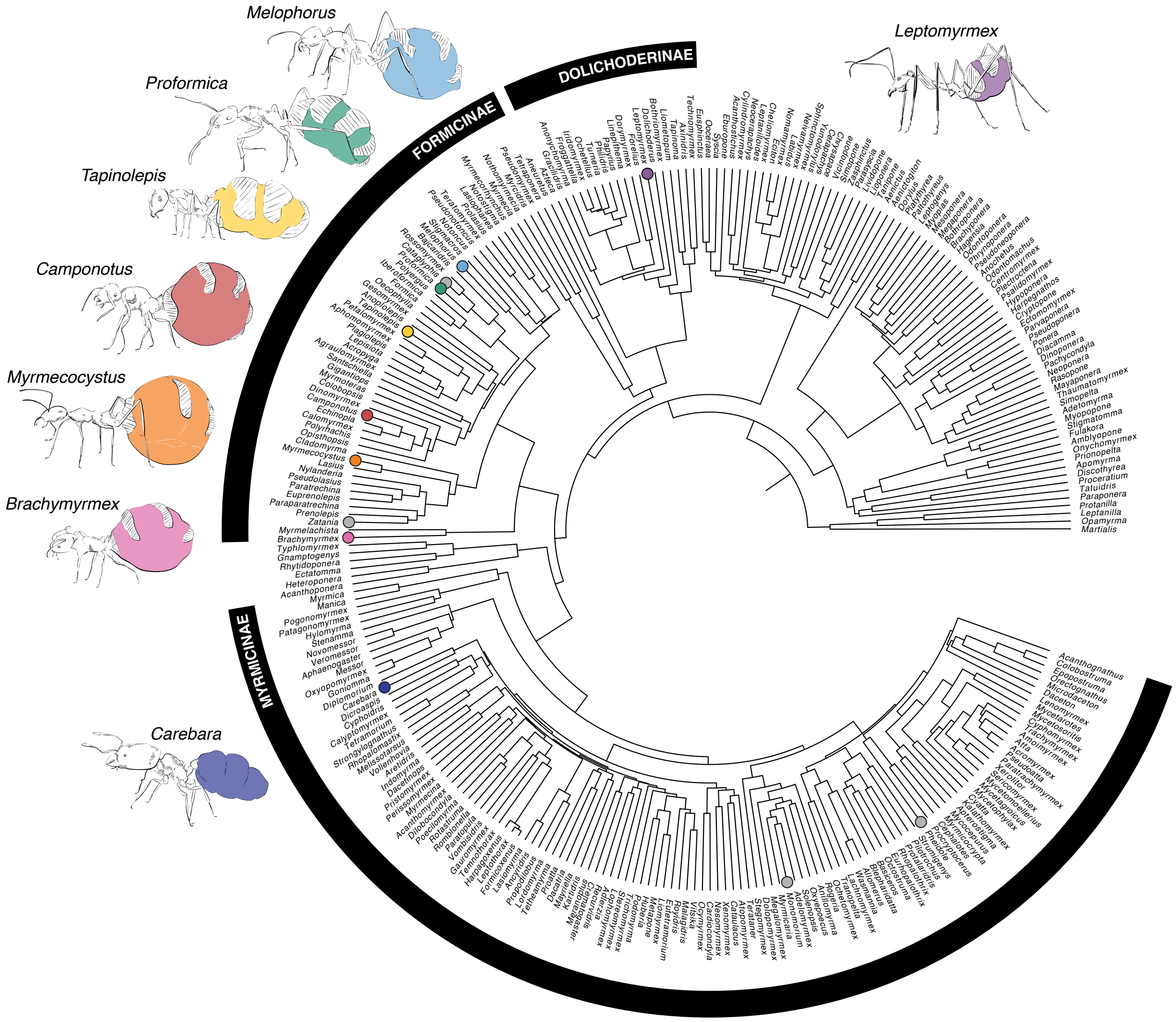

Fig. 5: Phylogenetic distribution of repletism across ants. Genus-level tree topology from Borowiec & al. (2025); confirmed repletes denoted in color corresponding to replete drawings, putative repletes in grey. Replete images © D. Nguyen – not to scale. Reference material for illustrations derived from Froggatt (1896), Wheeler (1915), Stumper (1961), Burgett & Young (1974), de Zolessi & al. (1976), Galkowski & al. (2017), Azorsa & Fisher (2018), Islam & al. (2022), and Sawh & al. (2023).

Different levels of turgidity and gas bubbles can be observed in *Myrmecocystus* repletes. The reason for the presence of bubbles inside the repletes' crops and their eventual fallout is unknown, but it possibly indicates microbial activity and liquid spoilage. Bubbles can occupy most of the crop and are more common in milky repletes (Conway 1990). Most ants have a homogeneous liquid phase in their crop, but some display two distinct liquid layers: one containing mostly lipids and the other carbohydrates (Burgett & Young 1974).

After established colonies are collected from the field, repletes of different filling levels can be observed hanging from chamber ceilings after two weeks (Rissing 1984, Conway 1990). Semi-repletes (i.e., partially filled repletes) may take about four weeks to become fully distended (Conway 1975, 1977), suggesting that a continuous food supply over this period is sufficient to fill replete workers. However, this timeline can vary as repletes have been reported to form from both callow and mature workers within 24 to 42 days (Conway 1975, Rissing 1984). Replete abundance in *Myrmecocystus mendax* and *Myrmecocystus mexicanus* colonies can reach approximately 600 individuals or 22 - 25% of the colony (Conway 1983, Rissing 1984, Conway 1990, 2003).

While there are no published reports of repletes in *Myrmecocystus kathjuli* Snelling, 1976, *Myrmecocystus romainei* Snelling, 1975, and *Myrmecocystus yuma* Wheeler, 1912, reports from ant husbandry hobbyists confirm their presence.

***Leptomyrmex*:** *Leptomyrmex* is the only honeypot ant in the Dolichoderinae subfamily, and repletism likely occurs in all species of the genus (28 valid species; Bolton 2025). The repletes have noticeably enlarged gasters compared with non-repletes, with stretched intersegmental membranes and crops filled with transparent liquid or honey. Plowman (1981) describes workers of

Tab. 3: Confirmed honeypot-ant species and genera. [1]Referred to as *Brachymyrmex melensis* in reference given. [2]Referred to as *Camponotus cowlei* in Froggatt 1896. [3]Referred to as *Plagiolepis trimenii* in reference given. [4]*Carebara perpusilla* known to display both gastral and thoracic crop repletism. Distribution information was obtained from the publications that described repletism in each species. * When occurrence data were not available in the original sources, we used GBIF (Derived dataset GBIF.org 2025).

Taxa	Replete mobility; storage duration	Distribution	References
Dolichoderinae			
Leptomyrmex Mayr, 1862 (likely the entire genus)	Mobile; storage duration unknown	Australia, Brazil, Dominican Republic, New Caledonia, New Guinea	Wheeler (1908, 1915), Plowman (1981), Sawh & al. (2023)
Formicinae			
Brachymyrmex giardi Emery, 1895[1]	Mobility unknown; storage duration unknown	Uruguay	de Zolessi & al. (1976)
Camponotus inflatus Lubbock, 1880	Low mobility; long / seasonal storage duration	Australia	Froggatt (1896), Dong & al. (2023)
Melophorus bagoti Lubbock, 1883[2]	Low mobility; possible long storage duration but unconfirmed	Australia	Froggatt (1896), Conway (1992), Schultheiss & al. (2010)
Myrmecocystus Wesmael, 1838 (entire genus)	Low mobility; long / seasonal storage duration	Mexico, United States	Wheeler (1908), Burgett & Young (1974), Snelling (1976), Bartz & Hölldobler (1982), Snelling (1982), Rissing (1984), Conway (1990, 2003), Eriksson & al. (2019), Sankey-Alamilla & al. (2024)
Proformica epinotalis Kuznetsov-Ugamsky, 1927	N / A; storage duration unknown	Palearctic region *	Marikovsky (1974)
Proformica nasuta (Nylander, 1856)	Low mobility; storage duration unknown	France	Stumper (1961), Galkowski & al. (2017)
Tapinolepis trimenii (Forel, 1895)[3]	Mobile; probable long / seasonal duration	South Africa	Wheeler (1908)
Myrmicinae			
Carebara perpusilla (Emery, 1895)[4]	Low mobility	Mozambique	Khalife & Peeters (2020), Khalife & al. (2023)

Leptomyrmex fragilis (Smith, 1859) and *Leptomyrmex niger* Emery, 1900 foraging and returning replete, which may be a misapplication of the term, referring instead to individuals with crops full of recently foraged liquid. However, since repletes in this genus are known to be mobile, they could potentially forage and collect their own fluids for storage. Wheeler (1915) suggests that *Leptomyrmex unicolor* Emery, 1895 is possibly the only species in the genus without this trait. He attributes its absence to the species' plesiomorphic traits, as indicated by its unmodified larval type and its presence in coastal rainforests, which may reflect the genus' past distribution. However, a Neotropical fossil replete was found by Sawh & al. (2023), suggesting that the trait evolved once in a common ancestor and may have been retained as the genus dispersed to Australasia. The species *Leptomyrmex relictus* Boudinot & al., 2016 and its repletes were recently described in Brazil (Boudinot & al. 2016, Sawh & al. 2023), providing insight into the biogeographical history of the genus.

Unlike other honeypot ants, the contemporary distribution of *Leptomyrmex* is not restricted to dry environments, challenging previous assumptions about the ecological conditions that favor repletism. It is worthwhile to investigate the historical context in which repletism evolved in this genus to understand the role of the environment in shaping this phenotype. *Leptomyrmex* species inhabit a range of environments, including eucalyptus forests, montane rainforests, and even urban forested parks in Australia, Brazil, Indonesia, New Caledonia, and New Guinea (Wheeler 1908, Plowman 1981, Sawh & al. 2023). These ants typically nest in the ground beneath boulders, within tree roots, or inside rotten logs, often occupying the central part of the wood. It is believed that *Leptomyrmex* utilizes pre-existing cavities, as no signs of excavation or debris have been observed near their nests. Wheeler (1915) documented a soil-nesting ant gallery extending about 10 cm underground, leading to a chamber approximately 13 cm long, 8 cm wide, and 2.5 cm high.

Unlike extreme cases of repletism, *Leptomyrmex* repletes may perform various tasks within the colony rather than serving exclusively as food reserves. It remains unknown whether immobile workers exist deep within the nest. WHEELER (1915) describes repletes as being closely associated with the brood and possibly hanging from the ceiling while holding a larva or pupa in their jaws, which was confirmed by BURCHILL (2021). The development of repletes can be observed from the moment individuals eclose, before their exoskeleton fully hardens (WHEELER 1915), but further observations are required to confirm if that would be the only condition for repletes formation. The composition of replete-crop contents remains largely unknown, though the stored liquid appears clear. *Leptomyrmex* workers are monomorphic (LUCKY & WARD 2010), making it unclear if and under which circumstances individuals may be more likely to become repletes within this genus. The repletism status remains unreported for the species *Leptomyrmex aitchisoni* SMITH & SHATTUCK, 2009, *Leptomyrmex burwelli* SMITH & SHATTUCK, 2009, *Leptomyrmex darlingtoni* WHEELER, 1934, *Leptomyrmex dolichoscapus* SMITH & SHATTUCK, 2009, *Leptomyrmex flavitarsus* (SMITH, 1859), *Leptomyrmex garretti* SMITH & SHATTUCK, 2009, *Leptomyrmex melanoticus* WHEELER, 1934, *Leptomyrmex pilosus* SMITH & SHATTUCK, 2009, *Leptomyrmex puberulus* WHEELER, 1934, and *Leptomyrmex ramorniensis* SMITH & SHATTUCK, 2009.

***Camponotus* MAYR, 1861:** *Camponotus* is one of the most speciose genera within Formicidae (1100 valid species; BOLTON 2025); however, true repletism has been confirmed in only one species (*Camponotus inflatus*), although it is suspected in others (B.L. Fisher, pers. comm.). Despite this, fat-body storage is known in the genus (ROSELL & WHEELER 1995, HAHN 2006). The repletes of *C. inflatus* resemble those of *Myrmecocystus*, with large, semi-transparent gasters, tensely distended intersegmental membranes, and separated tergites and sclerites, resulting in low mobility. *Camponotus* worker castes are polymorphic, but it is uncertain if repletism is expressed mostly in larger individuals. *Camponotus inflatus* can be found in Australia's hard sandy plains and Mulga scrub areas (FROGGATT 1896, DONG & al. 2023). Indigenous Australian communities often use them for food and cultural traditions (ISLAM & al. 2022). DONG & al. (2023) analyzed the antimicrobial properties of *C. inflatus* honey, comparing it with honeybee honey. The study suggested they have different antimicrobial action modes, with *C. inflatus* honey showing strong inhibition of *Staphylococcus aureus*. They also sequenced the microbiomes of whole ants but mostly found *Candidatus* Blochmannia endosymbiotic bacteria (DONG & al. 2023). These bacteria are not found in the crop of ants (DE SOUZA & al. 2009) and so are unlikely to be responsible for the antimicrobial properties of the crop fluid.

***Melophorus* LUBBOCK, 1883:** *Melophorus bagoti* is the only species within this genus of 92 species (BOLTON 2025) known for its extreme food-storage adaptation. The repletes in *M. bagoti* are known to be mobile (CONWAY 1992, SCHULTHEISS & al. 2010). Replete gasters vary in color from light amber to milky white, which may indicate the storing of different substances (SCHULTHEISS & al. 2010). Workers forage for materials, including dead insects, seeds, and sugary plant exudates. They are found in branching passages near the surface, under small blocks of quartzite. The nests of *Melophorus* can span up to 2.3 m² with as many as 160 chambers, some as deep as 1.75 m. These ants are found in desert regions in Australia, particularly in sandy floodplain alluvium and gorges (FROGGATT 1896, CONWAY 1992, SCHULTHEISS & al. 2010).

***Brachymyrmex* MAYR, 1868:** *Brachymyrmex giardi* EMERY, 1895 is the only known honeypot-ant species in its genus of 40 species (BOLTON 2025). It has been described as having physogastric workers with highly dilated crops, a trait likely developed in response to a previously dry environment and retained after the species spread to more humid areas (DE ZOLESSI & al. 1976). The species generally occurs near streams, where floods are common, and in grazing fields with sparse grasses. Repletes were noted to have a larger thorax than non-replete workers (DE ZOLESSI & al. 1976), even though *Brachymyrmex* species are often monomorphic (ORTIZ & FERNÁNDEZ 2014). The species is native to and can be found in the regions of Uruguay, Argentina, and Chile (DE ZOLESSI & al. 1976).

***Proformica* RUZSKY, 1902:** The genus *Proformica* also exhibits examples of repletism, with certain species developing specialized workers to store liquid food for extended periods. *Proformica epinotalis* KUZNETSOV-UGAMSKY, 1927, is found in stony, saline, and clayey desert environments. Workers in this species serve as repletes, often hanging from the ceilings of their nests (MARIKOVSKY 1974). Similarly, *Proformica nasuta* (NYLANDER, 1856), found in xerothermic environments, produces repletes that store liquid in their crops for prolonged periods and become nearly immobile (STUMPER 1961, GALKOWSKI & al. 2017). As with *P. epinotalis*, repletism in *P. nasuta* is primarily observed in larger workers. It is likely that more species within the genus, such as *Proformica splendida* DLUSSKY, 1965, *Proformica ferreri* BONDROIT, 1918, and *Proformica longipilosa*, also exhibit this trait, but information is lacking to confirm this (GALKOWSKI & al. 2017). *Proformica epinotalis* and *P. nasuta* are currently the only known replete-producing ants in Europe.

***Tapinolepis* EMERY, 1925:** The species *Tapinolepis trimenii* (FOREL, 1895), previously classified under the *Plagiolepis* MAYR, 1861 genus (WHEELER 1908), exhibits replete workers with greatly distended crops and the intersegmental membranes tensely stretched. Unlike other repletes, these individuals retain some mobility, despite their swollen abdomens. *Tapiniolepis trimenii* is found in arid habitats in southern Africa, such as the Kalahari Desert. At least one other species of *Tapinolepis* is known to exhibit repletism (undescribed species; L. Khadempour, pers. obs.), suggesting that this trait may be shared across the genus.

***Carebara* WESTWOOD, 1840:** The Myrmicinae subfamily contains 148 valid genera (BOLTON 2025), but only one, *Carebara*, is confirmed to contain repletes. In *Carebara perpusilla*, both the gastral and thoracic crops are involved in food storage (Khalife & Peeters 2020, Khalife & al. 2023). Queens and major workers express repletism, with both displaying low mobility. These ants are found in riverine forests in southern and central Africa. Other species of *Carebara* might also demonstrate repletism (Tab. 2) but have yet to be confirmed.

The uneven phylogenetic distribution of repletes

We have identified a total of eight ant genera that exhibit replete workers, while a further four genera await confirmation (Fig. 5). Based on current natural-history data, the genus-level prevalence of repletism suggests a minimum of eight independent origins of replete workers across ants. Repletism is conspicuously absent or relatively underrepresented in some ant lineages; origins are most common among formicine genera, and the syndrome is an occasional feature of two dolichoderine and myrmicine taxa. The relative lack of repletism in the Myrmicinae – even as this subfamily comprises nearly 50% of all described ant species – suggests that lineage-specific traits may underpin the capacity for some taxa to evolve worker food storage. A predisposition toward repletism also appears to be linked to diet and use of trophallaxis (Meurville & al. 2025). No repletes have been reported in the predominantly predatory subfamilies Ponerinae and Dorylinae, which perform trophallaxis less frequently. While the association between trophallaxis and repletism might seem intuitive, our review confirms this pattern across lineages.

One other feature that may underpin this uneven distribution is the proventriculus. Ants display a greater diversity of proventriculus structures than any other hymenopteran group, likely reflecting the central role of liquid food transfer in their social organization (Eisner & Wilson 1952, Caetano 1988, Bution & al. 2010). In some taxa (e.g., *Atta* Fabricius, 1804, *Acromyrmex* Mayr, 1865, *Solenopsis*, *Ectatomma quadridens* (Fabricius, 1793), *Labidus praedator* (Smith, 1858), *Monomorium floricola* (Jerdon, 1851)), the proventriculus lacks a muscular bulb, and fluids are retained in the crop mainly through petiole constriction and circular muscle contraction (Caetano 1991, Solis & al. 2013). Where the proventriculus is more elaborate and the bulb is present, crop contents can be held passively by fluid pressure without muscular effort, enabling long-term storage at low energetic cost (Caetano 1991).

Formicinae, the subfamily containing most honeypot ants, possess especially elaborate proventriculi (Eisner & Wilson 1952, Bution & al. 2010); and in the dolichoderine *Leptomyrmex*, the proventriculus has a cross-shaped occlusory tract with a narrow, hair-lined passage that resists backward pressure from stored liquid, improving fluid retention in the crop (Eisner 1957). Consistent with this, Davidson & al. (2004) found that Formicinae and small-bodied Dolichoderinae with more complex proventriculi carried larger liquid loads. These structural innovations likely explain why repletism has repeatedly evolved in Formicinae but rarely in other lineages.

Defensive morphology may also have a role in the trait distribution. Several ant species have experienced sting reduction or have lost the ability to sting (Kugler 1979). This is seen more frequently in the subfamilies Formicinae and Dolichoderinae, the former having evolved the acidopore (Hung & Brown 1966, Aili & al. 2014). There is support for the hypothesis that trade-offs between defensive traits, like sting defense loss, have influenced the diversification of ants (Blanchard & Moreau 2017). Our findings suggest it could have facilitated the evolution of food-storage strategies as well. Future field observations and phylogenetic reconstructions will be crucial to clarify the origins, reversals, and temporal history of repletism.

Knowledge gaps and open questions

Indigenous peoples in North America and Australia have known about honeypot ants and consumed them as a culturally important delicacy for millennia (Meyer-Rochow & Changkija 1997, Melo-Ruíz & al. 2017). Western science has also documented these ants for centuries (Lubbock 1880). However, much remains unknown about them, including the full extent of their global and phylogenetic distributions. To determine whether a species possesses designated physogastric replete workers that engage in long-term crop food storage, careful excavation and close observation are required. Studying repletes in their natural environment is particularly challenging due to the need for invasive excavation techniques, which are labor-intensive and can disrupt colony dynamics. Retrieving live repletes from deep nest chambers is especially difficult for species inhabiting hard or compact soils. The inaccessibility of nests can introduce data biases, potentially overlooking key behaviors and ecological conditions influencing repletism. Despite these challenges, targeted excavations remain essential to reveal whether additional species harbor repletes that have not yet been documented.

Repletism is an example of convergent evolution, yet no formal study has been completed to understand the extent and mechanisms of the convergence. Without a clearer understanding of replete development, behavior, morphology, and physiology, it remains uncertain whether repletism arose through similar genetic and developmental mechanisms across independent lineages or via distinct evolutionary paths. Additionally, we do not know the selective factors that drive the evolution of repletism or if certain taxa have a predisposition to evolving repletes. We also do not know the extent of plasticity in repletism. If a species has the capacity to form repletes, will it always do so, or only when the environment requires it? While arid habitats are strongly associated with repletism, data linking specific abiotic variables to the emergence of this trait are lacking.

As animals with specialist diets and life histories, we would expect that honeypot ants would have a specialized gut microbiome. Dong & al. (2023) discovered that the crop fluid of *Camponotus* honeypot ants has antimicrobial properties, and this is likely due to the members of the ants' gut microbiome. However, it is not yet known what microbes may be conferring this phenotype. With *Myrmecocystus* ants in North America, we have identified that there appears to be a resident gut microbiome in this genus. However, we are still merely scratching the surface in understanding what function these community members may serve for their host ant, if any (D. Nguyen & al., unpubl.). If honeypot ants have a mutualistic relationship with certain gut-microbiome members, it would be interesting to compare these functions across the ant phylogeny to see if they converge in a parallel manner to the ants themselves. Furthermore, there is much to uncover about how microorganisms move throughout and between colonies and what role the ants play in controlling their movement. These are some of the unresolved questions about honeypot ants and repletism, and we hope this review lays the groundwork for future studies into these fascinating ants.

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Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence (AI) tools in any part of the composition of this manuscript except that during its preparation, BRN used ChatGPT to correct spelling and grammar and to enhance clarity. AI was not used to generate any of the content of the manuscript or to review the literature. After using this tool / service, the authors reviewed and edited the content as needed and take full responsibility of the content of the manuscript in every detail.

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