

A primitive ant brood chamber with evidence of brood care in Burmese amber (Lower Cretaceous) – implications for brood care as the facilitating factor for true eusociality and dominance of ants

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Abstract: Ants are one of the most successful and ecological dominant organisms on Earth, owing their success and dominance to their advanced social structure, eusociality. While many new discoveries of primitive ants and studies have occurred, the origins of the true ants and their evolution of eusociality remains largely unexplained. Until now, evidence of eusociality in the primitive ants has been based on morphological features (presence of different castes and metapleural gland) with inference of the critical requirement of brood care. For the first time, direct evidence of brood care is observed in a Cretaceous ant specimen. A primitive ant of undetermined subfamily (though not Sphecomyrminae) occurs in a Burmite specimen along with nest material, an ant egg and food for ant brood (arthropod prey and ant eggs – oophagy). While this specimen containing an ant brood chamber answers questions as to the origin of eusociality in primitive ants, observations of this specimen compared to other primitive ants (specifically Sphecomyrminae) raises many new questions. Most of these questions center on: If primitive ants were eusocial, why did one lineage become extinct (Sphecomyrminae) while others survived and later explosively diversified into the dominant organisms that they are today? Interpretations of general morphological features of the worker caste coupled with their social roles allows for the postulation that brood care was the facilitating factor that helped establish the dominance of particular ant lineages originating in the Cretaceous. This non-Sphecomyrminae worker ants generally appears to be larger and more graceful (exhibits very long legs and slim body) with smaller eyes and simple mandibles, suggesting adaptation to specialized brood care within the nest. In contrast, Sphecomyrminae generally have stouter bodies and bigger eyes (compared to this new specimen) and likely development of non-traditional social roles, suggesting that they are better adapted to hunting and scavenging and activities outside the nest (and brood). While oophagy probably occurred in the specimen herein presented, it is also known to be common in many primitive ant lineages, thus providing an advantage to these non-Sphecomyrminae ants as well as an engine for evolutionary change. Concluding that more advanced social structure was attained compared to their counterparts (Sphecomyrminae), these non-Sphecomyrminae lineages were able to form more complex nests with larger populations. With these social and perhaps evolutionary advantages, these non-Sphecomyrminae lineages were poised to explode in diversity and numbers during the early ant radiations of the ever increasingly diversifying Cretaceous forests becoming the superorganisms that they are today.

Key words: Formicidae, sociobiology, evolution, oophagy, eusociality.

Santrauka: Skruzdėlės yra vieni sėkmingiausių ir ekologiškai dominuojančių organizmų Žemėje. Jų sėkmė ir dominavimas susiję su labai išsivysčiusia socialine struktūra, eusocialumu. Nors surandama ir ištiriama vis daugiau primityvių skruzdėlių, tačiau tikrųjų skruzdėlių atsiradimas ir jų bendruomeninės elgsenos susiformavimas dar iki galo neaiškūs. Iki šiol primityvių skruzdėlių bendruomeninio gyvenimo įrodymai iš esmės rėmėsi morfologiniais požymiais, pavyzdžiui, skirtingos kastos ir metapleuralinė liauka, bei būtinybe rūpintis jaunikliais. Pirm kartą rastus tiesioginius jauniklių priežiūros įrodymus atspindi kreidos periodo skruzdėlė. Nenustatytam pošeimui priklausanti primityvi skruzdėlė kartu su lizdo fragmentais, kiaušiniu ir maistu jaunikliui (grobis – nariuotakojis ir kiaušiniai – oofagija) rasti Birmos (Mianmaro) gintare. Nors šis pavyzdys su skruzdėlės vystymosi kamera atsako į klausimus, susijusius su primityvių skruzdėlių bendruomeninės elgsenos atsiradimu, tačiau pačios skruzdėlės palyginimas su kitomis primityviomis skruzdėlėmis (ypač *Sphecomyrminae*) iškelia daugybę naujų problemų. Iš principo jos siejasi su tokiais aspektais: ar primityvios skruzdėlės buvo bendruomeninės, kodėl viena linija išnyko (*Sphecomyrminae*), o kitos išliko ir net vėliau taip stipriai diversifikavosi, kad net tapo dominuojančiais organizmais, kokiais jos yra iki šiol? Svarbiausių darbininkių kastos morfologinių požymių interpretacijos, susietos su jų vaidmeniu bendruomenės gyvenime, leidžia teigti, jog rūpinimasis palikuonimis buvo svarbus faktorius, nulėmęs, jog tam tikros skruzdėlių linijos, kilusios kreidos periode, tapo dominuojančiomis. *Sphecomyrminae* nepriklausanti skruzdėlė darbininkė yra didesnė ir grakštesnė, mažesnėmis akimis ir paprastomis mandibulėmis. Iš to daroma išvada, kad ji buvo prisitaikiusi specializuotai jauniklių priežiūrai lizde. O *Sphecomyrminae*, pasižymintys tvirtesniu kūno sudėjimu ir didesnėmis akimis, manoma, turėjo netradicinius bendruomeninius vaidmenis. Galvojama, jog jos buvo geriau prisitaikiusios medžioti ir ieškoti maisto, t. y. veiklai už lizdo ribų, kuri tiesiogiai nesusijusi su jauniklių priežiūra. Oofagija tikriausiai buvo būdinga čia aptariamai

skruzdėlei, ji taip pat įprasta daugeliui primityvių skruzdėlių linijų. Ji laikoma šių *Sphecomyrminae* nepriklausančių skruzdėlių pranašumu ir, manoma, kad būtent ji skatino evoliucinius pokyčius. Daroma išvada, jog šių skruzdėlių bendruomeninė struktūra buvo pažangesnė negu *Sphecomyrminae*; jos galėdavo pasistatyti sudėtingesnius lizdus su daugiau gyventojų. Kadangi *Sphecomyrminae* nepriklausančios skruzdėlėms būdingi bendruomeninės elgsenos, turbūt ir evoliuciniai privalumai, joms buvo lemta patirti įvairovės ir gausumo „sprogim“ ankstyvųjų skruzdėlių radiacijų metu vis labiau įvairėjančiuose kriedos periodo miškuose. Galiausiai jos tapo superorganizmais, kokie yra ir dabar.

Raktiniai žodžiai: Formicidae, sociobiologija, evoliucija, oofagija, eusocialumas.

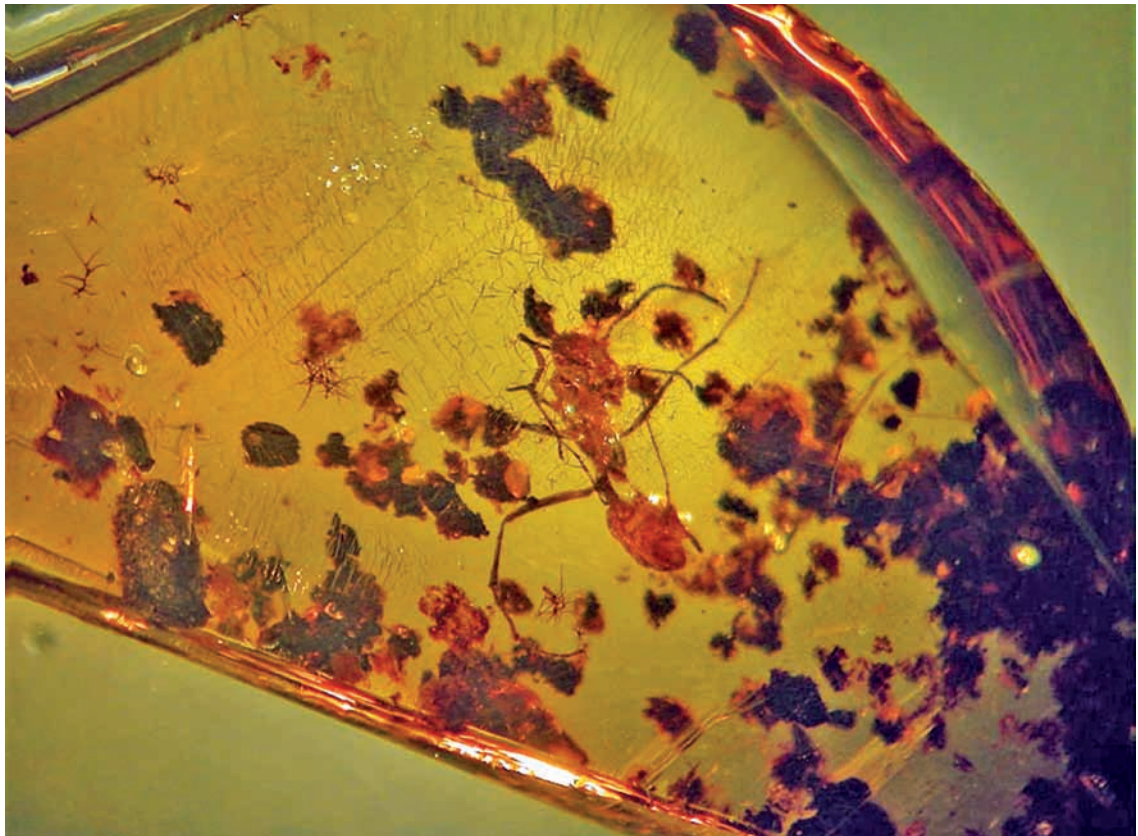


Fig. 1: Overview of Burmite specimen containing primitive ant with larval brood chamber, ant egg and evidence of brood care.

Introduction

Ants are one of the most successful and ecological dominant organisms on earth, occupying a significant portion of the total global biomass while being just a small percentage of the insect fauna. Worldwide, they occupy a wide variety of niches and play an important role in many ecosystems, acting as predators, scavengers and even herbivores (HÖLLDOBLER & WILSON 1990). Ants owe their success and dominance to their advanced social structure (being eusocial), typically forming intricate and vast colonies that are often referred to as superorganisms (HÖLLDOBLER & WILSON 1990; WILSON & HÖLLDOBLER 2005b). Recently, the number of studies of primitive ants that focused on their possible origins (both morphological and social) has greatly increased due to many exciting discoveries in Cretaceous ambers of France, Canada, the USA and Myanmar (DLUSSKY 1996, 1999; GRIMALDI et al. 1997; NEL et al. 2004; ENGEL & GRIMALDI 2005; PERRICHOT et al. 2008b). Most of these studies tend to focus on either the systematic

placement of the specimens into extant or extinct subfamilies or the geological and ecological occurrences of these subfamilies in order to better understand their origins and success. Eusociality of both the very primitive extinct subfamily *Sphecomyrminae* (generally considered the most basal subfamily) and primitive members of the extant subfamily *Formicinae* and the poneromorph group of subfamilies (WILSON & HÖLLDOBLER 2005b) has been based on morphological features. Emphasis has been placed on morphological characteristics (metapleural gland and length of antennal segments) (DLUSSKY 1987, 1996; GRIMALDI et al. 1997; NEL et al. 2004; ENGEL & GRIMALDI 2005; PERRICHOT et al. 2008a). Even with the plethora of studies on ants and their social structure, the origin of true ants and their evolution of eusociality still remain largely unexplained.

In this paper, an ant brood chamber, with a morphologically primitive ant of undetermined subfamily, containing an ant egg with evidence of arthropod prey feeding and possible oophagy in Burmese amber (approx-

mately 100 Ma) is discussed. While this discovery of care for the young (larvae) shows that primitive (and potentially basal) ants were eusocial, it also raises many new questions, especially surrounding the very primitive extinct subfamily Sphecomyrminae. Consideration is given to division of labor of the primitive castes (of all primitive ant lineages) in relation to evolutionary success. Based on these considerations, tentative conclusions are presented to help explain the global dominance of ants today and the extinction of the very primitive yet highly specialized and eusocial Sphecomyrminae.

Materials and Methods

Burmite (amber from Myanmar) is dated to the late Albian (~100-110 Ma) based upon palynomorphs obtained from the lignitic seams where the amber occurs within sandstone-limestone deposits in the Hukawng Valley (CRUICKSHANK & KO 2002). Placement within the late Albian makes Burmite Early Cretaceous in age and thus, of great interest for the inclusions it contains.

All inclusions within the piece were primarily examined under a trinocular/stereo dissecting scope, utilizing a variable zoom range of 15 to 90 times magnification. Lighting was supplied from above (direct) and below (backlighting) in varying intensities and with a dual-channel fiber optic light source, also utilizing various intensities. Photography was performed utilizing the trinocular port equipped with a 10 times Zarf lens adapter (LNS-30DWF©) with a Nikon Coolpix E995 digital camera connected directly to the lens. Use of the freeware program CombineZ5 allowed the images taken at slightly different focal planes to be combined into one composite image. Measurements were taken with a standard ruler calibrated in millimeters.

The dimension of the specimen is approximately 30 mm long by 17 mm wide by 9 mm high, being mostly triangular in shape. Thickness tapers generally along the length of the specimen, increasing from a minimum of 5 mm to 9 mm. Portions of both flat surfaces currently exhibit minor surface crazing, with some areas being penetrated by fractures approximately 1 mm in length.

Results

Evaluation of ant brood chamber

Numerous inorganic and organic inclusions occur within the piece, ranging in size from less than 0.5 mm to in excess of 5 mm, as seen in Fig. 1. Soil consisting of both individual sand grains and clumps occur throughout the piece. Several frass pellets also occur with one being nearly 5 mm in length. Numerous wood and vegetation fragments occur (typically less than a few mm in length) as well as unidentified plant hairs. While some-

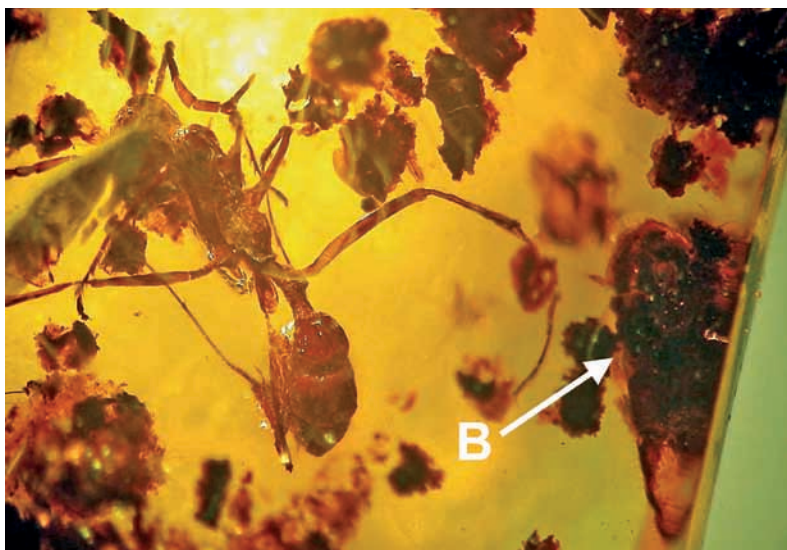


Fig. 2: Anterior view of primitive ant in Burmite showing head, alitrunk, petiole and gaster. Also present is hollow carcass of a beetle (B = hollow beetle carcass).



Fig. 3: Anterior view of primitive ant in Burmite showing close-up of petiole and gaster.

what infrequent, there are also very fine fibrous fungus filaments, as well as what may be minute (less than 1 mm) resin fragments scattered throughout the piece.

As observed in Fig. 1, the primitive ant is the central inclusion within the piece. Whereas most of the primitive ant is intact and complete, portions suffer deformation (dominantly flattening). Additionally, outgassing of internal fluids occurred, particularly near the apex of the head. The ant is approximately 5 mm in length from the tip of the head to the posterior of the abdomen while the lengths of the legs are also approximately 5 mm. The width of the body is approximately 2 mm. Overall, these observations results in an ant that appears both sleek and graceful with a long slender body and very long legs.

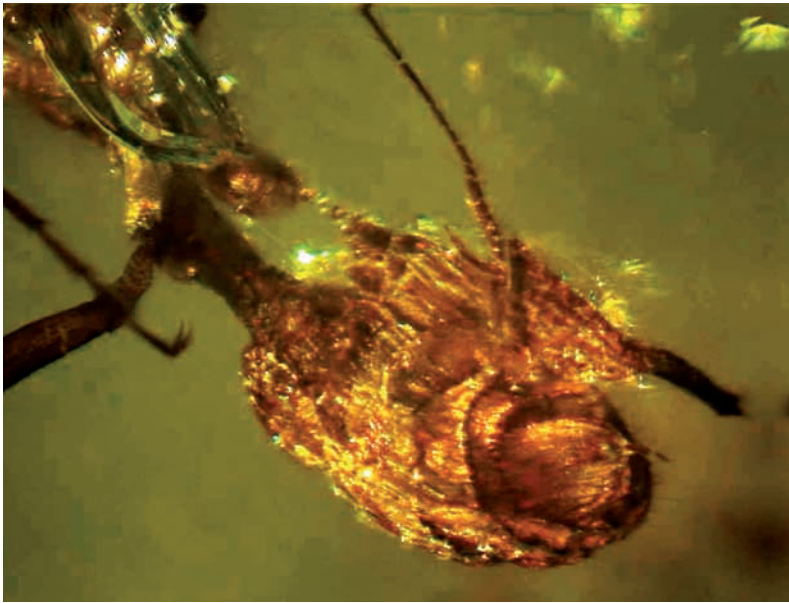


Fig. 4: Details of gaster of primitive ant showing ventrites and well developed sting.

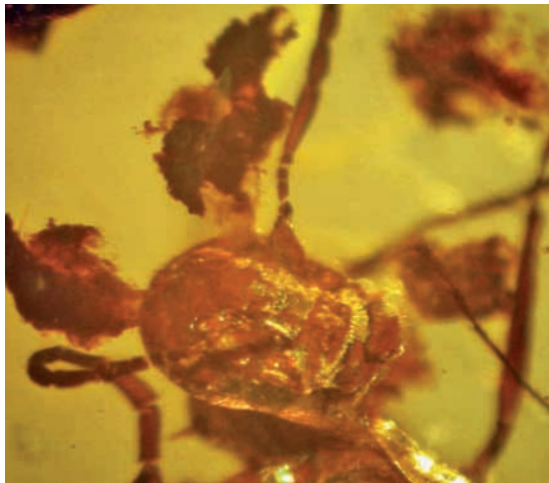


Fig. 5: Details of the head of the undetermined primitive ant showing simple mandibles, modest sized compound eyes and elongated funicular article 2, typical of primitive ants in Cretaceous ambers.

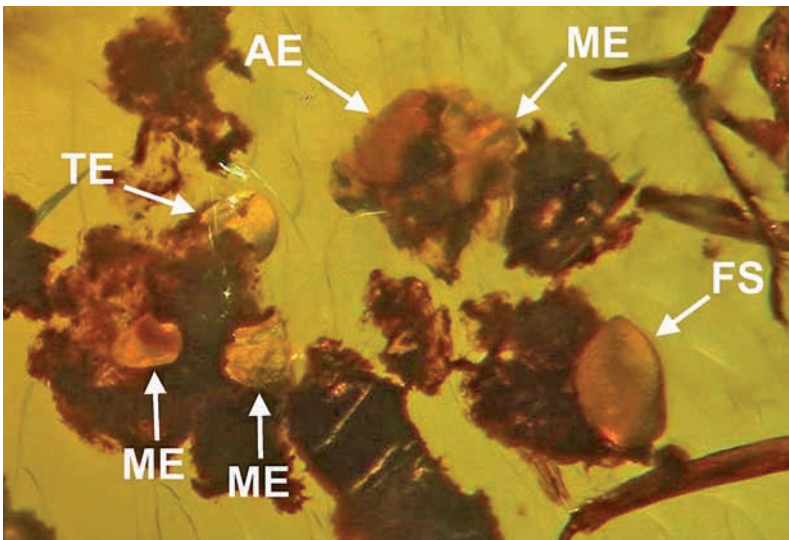


Fig. 6: Ant egg, malformed/misshapen eggs and possible trophic egg contemporaneous with primitive ant. AE = ant egg, ME = malformed/misshapen eggs, TE = trophic egg?, FS = fungal sporangia.

A formal systematic description of the ant is currently being prepared (POINAR, pers. comm.) and is therefore not provided here. However, key observations indicate its primitive condition. Figure 2 presents an anterior view of the ant where principle morphological features can be observed (head, alitrunk, petiole and gaster). A small opening to the metapleural gland is present (just above hind coxa) while fine setae occur on the propodeum. A long propodeal spine is also apparent. Figure 3 shows the petiole and gaster regions. A high rounded petiole is attached in approximately the mid-point position along a very long, narrow, tubular second metasomal segment. Two deep constrictions in the gaster occur, one between the second and third metasomal segments and the other between the third and fourth metasomal segments. The terga and sterna are telescoped and the sting is very well developed and nearly fully extended, as observed in Fig. 4. Also observed in Fig. 4 (and in Fig. 3), the pygidium supports long fine setae.

Figure 5 shows a close-up view of the head of the primitive ant. The mandibles are approximately 1/3 to 1/2 the length of the head, and are generally rounded with possibly a very short, blunt apical tooth and very fine setae near the external margin. Modest sized (less than 25% head length) and well developed elongate oval to roundish compound eyes, ocelli not observed. Antennae long, nearly half of total length of ant with 12 segments. The scape is very short with triangular inset into antennal fossa while funicular article 1 is shortest and 2 is longest (approximately twice length of other segments).

Systematic placement of this ant is difficult and not the intent of this paper. The obvious deep constrictions in the gaster as well as the lack of ocelli strongly indicate that this specimen could be within Ponerinae (perhaps near Amblyopone) or Myrmeciinae (Myrmecia). Overall body form, long simple nearly toothless mandibles and particularly the tubular, elongated petiole area also suggests Nothomyrmeciinae. In any case, the overall morphological features clearly indicate that this is a very primitive ant (most likely a basal ant to an extant subfamily), particularly the elongated second funicular article, a feature shared with Sphecomyrminae.

Of special interest are the approximate 10 tiny (1 mm or less) inclusions found adjacent to the ant. Figure 6 shows six of these inclusions. While similar in size and overall shape, physically and morphologically, there are at least three (possibly four) distinct types of inclusions (identified in Fig. 6). Perhaps of greatest interest among these inclusions is a possible ant egg. Figure 7 shows a close-up view of this inclusion. This potential ant egg is approximately 1 mm in length by approximately 0.5 mm in width, essentially elongate oval in

shape and somewhat flattened. The surface of the egg appears to be covered by a rough meshwork structure, although precise details are difficult to ascertain given the position of the egg within the amber and the angle of occurrence. It is clear, based on the observations, that the surface is not smooth. Additionally, the egg appears to be pigmented (not translucent), although the original color is unknown. On the egg apex is a rough dome-like structure approximately 0.1 mm in radius with what appears to be a central depression. This structure is interpreted to be the micropyle of the egg, based on data for ponerine ant eggs as outlined by GOBIN et al. (1998).

Adjacent to the ant egg is a generally elongate oval-rectangular structure of similar size as the egg. The surface structure is irregular yet appears to be consistently covered with a polygonal-like meshwork. While pigmentation occurs within the structure and on the surface, it is not uniform throughout since much of the inclusion is essentially translucent. Two similar inclusions occur very close (approximately 5 mm) to the first, as observed in Fig. 8. The close-up view provided in Fig. 8 further exemplifies the general irregular, misshapen surfaces yet still covered by a polygonal like meshwork. The translucent nature of the inclusions as well as minor areas with pigmentation is clearly visible. Based on these observations, it is plausible that these structures are malformed or misshapen ant eggs. It is also entirely possible that they attained this shape by either feeding activities of ant larvae or preparation by worker ants for feeding to the ant larvae (BARONI URBANI 1991). If they are ant eggs, it is not known whether these were viable or non-viable (trophic) eggs. One confounding aspect of these inclusions is that two of them exhibit an almost flattened and bent orientation along their entire length. If these are ant eggs, they may be dominantly shells, with minor amounts of internal egg material. However, they also resemble fungal sporangia.

As seen in Fig. 8, adjacent to the malformed/misshapen ant eggs is what appears to be a discarded shell-like structure. Overall dimensions of this inclusion are approximately 0.5 mm round while the thickness is quite thin (exact dimensions not known, but qualitatively appears thinner than the other egg inclusions). The surface is fractured and exhibits a strong polygonal meshwork pattern, similar to the malformed/misshapen ant eggs. On the exposed broken edge, a general pattern occurs that appears to conform to bite marks rather than ripping or breaking (which would be more irregular). Based on the characteristics, this is likely an ant egg shell (chorion), possibly even a trophic egg. Trophic eggs are generally round compared to viable eggs that are elongate-oval. Larvae do not always consume the chorion of either viable or trophic eggs (BARONI URBANI 1991).

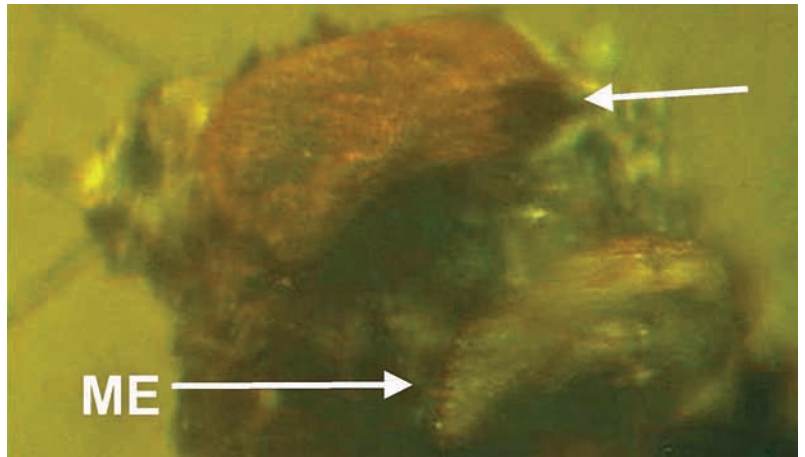


Fig. 7: Ant egg (arrow depicts micropyle) and malformed/misshapen egg (ME).

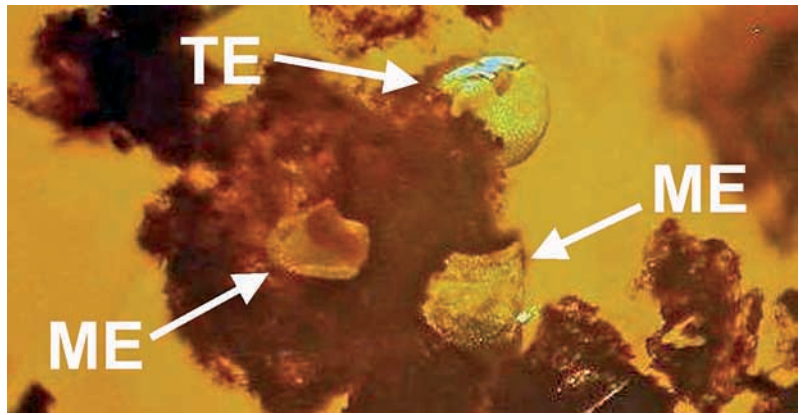


Fig. 8: Malformed/misshapen eggs and egg shell (possible trophic egg?) with bite marks. See Fig. 6 for identifications of individual inclusions.

The sixth inclusion noted in Fig. 6 appears to be fungal sporangia. While roundish, it is larger than the egg-shell inclusion and also lacks an apparent polygonal meshwork pattern. Additionally, the structure appears to have a hinge.

The final key inclusion in the piece is a hollow beetle carcass (Fig. 2). The beetle is approximately 3 mm long with an elongate slender body. Since it is only a hollow shell, no efforts were made to identify it further. Interestingly, near the apex of the head are very fine fibrous, fungi filaments.

Based on all of the inclusions described above, this specimen appears to be a portion of a primitive ant nest with one of the ants still resident. This interpretation of ant nest is not unique, it was recently determined by POINAR & POINAR (2008). It is not known definitively whether the nest was an arboreal/wood nesting or resided within the ground litter; however, the presence of soil and fine vegetation within the nest suggests that it was from the ground litter (or potentially from a hollowed root?). The combined evidence of brood care, a worker ant with ant egg and evidence of feeding (whole

insect prey and potentially oophagy) suggests that this specimen represents the brood chamber portion of a primitive ant nest.

Eusociality in basal ant lineages

There have been quite a few publications by a variety of authors concerning the origin of ants and/or their social status (DLUSSKY 1987, 1996, 1999; HÖLLDOBLER & WILSON 1990; SCHULTZ 2000; ENGEL & GRIMALDI 2005; GRIMALDI & ENGEL 2005; WILSON & HÖLLDOBLER 2005a; BRADY et al. 2006; MOREAU et al. 2006; PERRICHOT et al. 2008a). Generally speaking, while quite a few of the publications are centered on molecular analyses and dating first occurrences of true ants and their diversification into the subfamilies observed today, others address whether or not the primitive ants that occurred within the Cretaceous were eusocial. Eusociality is a very rare level of social development for any colonial organism (WILSON & HÖLLDOBLER 2005b). To meet the definition of eusocial, several key characters are required: overlapping generations must occur within the nest/colony, division of labor (reproduction, hunting/gathering, mating, etc.), and perhaps most important, brood-care by non-reproductive adults (CHOE & CRESPI 1997; WILSON & HÖLLDOBLER 2005b).

Given the extreme rarity of Cretaceous ant specimens found to date (DLUSSKY 1987, 1996, 1999; ENGEL & GRIMALDI 2005; GRIMALDI & ENGEL 2005; BRADY et al. 2006; PERRICHOT et al. 2008a), evidence to support the social status of primitive ants was based primarily on physical and morphological evidence. With the relatively recent discovery of both an alate gyne and worker of *Haidomyrmodes mammothus*, the first direct evidence of the first two requirements of eusociality were met (PERRICHOT et al. 2005a, b). This was the first example of two morphological castes within the same genus although workers and gynes were known in primitive subfamilies previously, just not within the same genera. Until now, the final requirement for true eusociality has been based on morphological characteristics such as the presence of the metapleural gland or relative lengths of the antennal segments (GRIMALDI et al. 1997; PERRICHOT et al. 2005a), characteristics that extant ants have which do enact in brood care by non-reproductive adults. Additionally, the final requirement for true eusociality has been based on observations of two workers being present within the same amber specimen – both New Jersey and French ambers (GRIMALDI & ENGEL 2005; PERRICHOT et al. 2005a), demonstrating social foraging for brood care and nestmates. Therefore, until now, brood care was inferred, but not directly observed. With the discovery of this specimen, the final requirement for true eusociality has been met with direct observation rather than inference.

Discussion and conclusions

While the discovery of an ant brood chamber with an ant egg and evidence of brood care (feeding) by a primitive, probably basal extant subfamily of ant is exciting, it also raises new questions. Were all primitive ants in the Cretaceous eusocial? What were the primary nesting types? How large were the nests (colony size, complexity of construction, etc.)? If all primitive ants were eusocial, why did Sphecomyrminae become extinct? This paper will entertain most of these questions in one fashion or another. In light of the new discovery, some tentative hypotheses concerning the several key areas within the origin of ants and the cause for their dominance today are also proffered.

It is generally accepted that primitive ants arose in the rapidly diversifying angiosperm/gymnosperm forests within the leaf and ground litter, being dominantly hunters (and scavengers) of arthropods, forming relatively simple nests of low total colony size (WILSON & HÖLLDOBLER 2005a; BRADY et al. 2006; MOREAU et al. 2006; PERRICHOT et al. 2008a). Compared to modern ant lineages (particularly the more socially advanced ants that engage in harvesting or fungus growing), it was a tough life, constantly full of dangers from other predators while trying to supply food to the colony. Due to the rapidly diversifying flora and fauna around them, they quickly became successful and began to specialize both morphologically and socially, ultimately increasing the complexity of the nests both socially and physically (larger, higher populations). While eusociality is the key to ants domination, it is herein proposed that brood care played an initial integral role in helping determine which lineages of ants ultimately survived to become the dominant superorganisms that they are today. This was accomplished through specialization of the castes (both morphologically and socially), particularly the worker, resulting in larger colony sizes and eventual dominance of certain lineages over others (essentially fundamental evolutionary theory of survival of the fittest).

Interestingly, a similar route may have assisted the evolution of social life in the Vespidae subfamily Stenogastrinae. Stenogastrinae are considered to be primitively eusocial, a sister group to the highly social Polistinae and Vespinae (GRIMALDI & ENGEL 2005). While Stenogastrinae feed their brood with masticated remains of prey (GRIMALDI & ENGEL 2005), a jelly-like substance secreted from the Dufour's gland is also fed to the brood (TURILLAZZI 1989). This nourishment with liquid food (a specialized food source) is thought to greatly contribute to the evolution of social life by increasing interactions between adults thereby allowing for the advancement of evolutionary behavioral mecha-

nisms (TURILLAZZI 1989). However, unlike the ants, further social advancements such as larger colony sizes and more advanced social structures (specialization of the castes) is hindered by various negative factors such as poor quality of nest construction, low egg-laying capacity and absence of defensive strategies of the colony (TURILLAZZI 1989). The facilitating factor to their success appears to be the specialized food source for their brood, suggesting brood care plays an important role in evolutionary success of eusocial insect lineages.

Understanding the origins of eusociality in ants is somewhat complex and not completely understood yet. For the intents of this paper, taking a larger, more removed perspective helps appreciate the origination of eusociality (especially for the abilities of the author). In terms of being eusocial, WILSON & HÖLDOBLER (2005b) infer that once an anatomically distinct worker caste appears, social evolution fully reaches a point of no return. In fact, at this point, the colony is typically most accurately described as a superorganism. Working from this premise, one can surmise that all Cretaceous primitive ants have attained a eusocial status, based on the emergence of a distinct worker caste. But, did they all attain superorganism status such that they had a profound impact on the surrounding biota? As further stated by WILSON & HÖLDOBLER (2005b), ecological colony selection is the strong binding force of eusocial evolution. Assuming that pre-adaptation/predisposition exists to form colonies and behaviors to defend the colony (essentially the first and second rules outlined by WILSON & HÖLDOBLER), essentially it is the division of labor within the colony (both from reproductives to workers and within workers as well) that elevates the evolutionary state of social complexity. In other words, colony size increases as specialization within the castes and communication between them becomes more complex. At some point, the social complexity is high enough that large colonies appear and dominate the surrounding niches, truly becoming a superorganism. While not many Cretaceous ant specimens occur, it is proposed here that the extinction of Sphecomyrminae may be partially caused by their inability to evolve a more complex caste and communication system while the other primitive ants (basal to extant lineages) were evolving in this fashion, laying the ground plan to becoming true superorganisms.

With the extreme rarity of Cretaceous ant specimens, it is perhaps peculiar that two primitive ants not belonging to Sphecomyrminae, both this specimen and *Myanmyrma gracilis* ENGEL & GRIMALDI, 2005, are generally large, slender, graceful ants found contemporaneous with nest material. Furthermore, both appear to be highly modified worker forms, particularly with respect

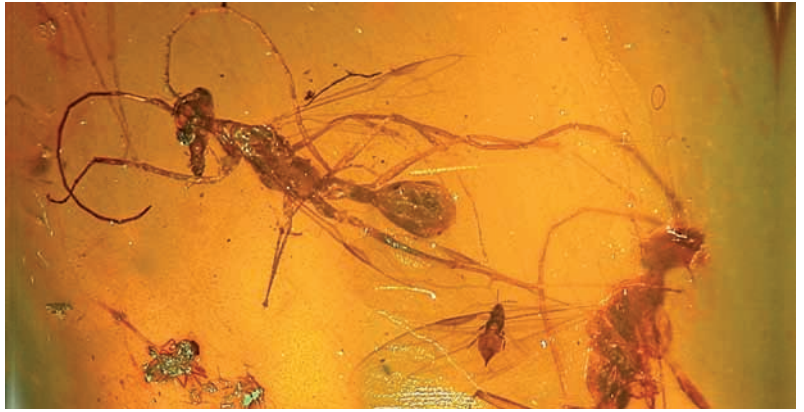


Fig. 9: Two winged male Sphecomyrminae (*Baikuris*) in Burmite, one with a thrip securely in its mandibles and the other with a thrip near its wing.

to the extremely long legs and slender body (*Myanmyrma gracilis* exhibits highly modified mouthparts and genae as well [ENGEL & GRIMALDI 2005]). From a qualitative perspective, general differences in body plans occur between these specimens and Sphecomyrminae, whereas the latter typically are more stout. This is not to imply that all (or even most) Sphecomyrminae specimens are stout, but with respect to the legs and body, these two specimens are „less stout“ than many Sphecomyrminae. The two non-Sphecomyrminae specimens also have modest sized eyes (if not relatively small) compared to Sphecomyrminae. A detailed anatomical analysis of the new specimen presented in this paper may also allow for the conclusion of further caste specialization, particularly concerning the inability to develop wings (specimen does not appear to be a wingless female) and perhaps in conjunction with this evolutionary derivation, inability to produce viable offspring (based on generally small gaster). Therefore, based on the morphological differences between the two primitive ants discussed herein compared to Sphecomyrminae, it appears that specialization for these ants is generally toward brood care within the nest (perhaps not coincidental that these ants are found with nest materials) while Sphecomyrminae focuses on foraging.

If these conclusions based on the general morphological differences between the Cretaceous non-Sphecomyrminae ants and Sphecomyrminae ants (with an emphasis on this new specimen) is correct, the implication is that complexity of the social status within the colony is increasing, potentially allowing for larger, more specialized/complex and evolutionarily advanced colonies. While undoubtedly, the colonies would most likely be considered small and primitive compared to modern ant colonies, they could have been quite advanced with respect to their counterparts (Sphecomyrminae). Interestingly, a newly discovered Burmite specimen containing Sphecomyrminae *Baikuris* illustrates

that Sphecomyrminae may have been developing new social advancements focused on foraging. Figure 9 shows two large alate males where one of the males securely holds a thrip in its mandibles. The second male in the piece has a thrip located adjacent to it, suggesting that they were acting cooperatively in capturing the thrips. This is a very peculiar behavior as the role of males in modern ants is quite simple, reproduce with the queen. While many plausible scenarios may be pondered to explain their behavior, perhaps the simplest is that they were removing the thrips from a desired food source or capturing them as food for the colony (or perhaps both with a single action). In any case, this is a role typically performed by the workers, not by winged males. While both non-Sphecomyrminae and Sphecomyrminae appear to be developing new social roles, Sphecomyrminae appear to be focused on more efficient hunting strategies while non-Sphecomyrminae appears focused on increased socialization within the nest.

While the placement of the specimen presented in this paper within a subfamily was not the intent, the interpretation of Ponerinae is also interesting as it may potentially address aspects of what WILSON & HÖLDOBLER identified as „The Ponerine Paradox“ (2005b). This is better appreciated when considerations of the observations and interpretations of the piece are carefully reviewed with respect to this paradox. Essentially, the ponerine paradox is how does a socially primitive ant arrive at such a globally dominant and successful position? Primitive aspects of ponerines include minimalistic dimorphism of the castes, relatively small colony sizes, outside foraging of food by the virgin queen when establishing a new nest, solitary foraging by workers and very limited use of true oral trophallaxis (WILSON & HÖLDOBLER 2005b). At this point, dimorphism of the castes cannot be evaluated due to lack of additional fossils, but the other aspects can be contemplated.

Put simply, this specimen likely represents a basal lineage of ponerines that participated in the earliest radiations of the true ants. It is beyond the intent of this paper (and capabilities of the author) to evaluate whether or not this specimen could be a basal origin of an extant ant crown group (ponerines) or groups (including myrmicines, formicines and dolichoderines). Further studies along this avenue are warranted. Rather, the focus will remain on evaluation of this specimen with respect to the ponerine paradox, with specific reference to the initial phases of the Dynastic-Succession Hypothesis (WILSON & HÖLDOBLER 2005b). And even more specifically, the focus will be on social behaviors within the nest and possible morphological responses, implying that brood care played a crucial role in the early radiation.

Ponerines are specialized predators whose diets are typically small arthropods, usually captured fresh, but also attained through scavenging (WILSON & HÖLDOBLER 2005b). For most ponerine ants, trophallaxis is essentially absent, only occurring in a few genera. As such, with foraging as the primary food source, colonies tend to be small and social organization primitive (WILSON & HÖLDOBLER 2005b). From a nesting habit perspective, and more specifically, the food sources for the larvae, oophagy occurs within many primitive ants and to some extent, is considered to be of utmost importance (CHOE & CRESPI 1997). In *Nothomyrmecia*, pupae may be used for food for the larva when foraged food is scarce (TAYLOR 1978). Oophagy does not appear to be widespread within ponerines, generally being restricted to a few genera (CHOE & CRESPI 1997; GOBIN et al. 1998). Interestingly, however, this specimen generally resembles the genus *Amblyopone*, one of the few genera that do engage in oophagy (MASUKO 2003). Given that the specimen also shares characteristics of other primitive lineages, the occurrence of oophagy should be considered plausible, particularly in light of the observations within the piece as well (possible direct evidence of oophagy). As noted by CRESPI (1992), there seems to be an association between the evolution of social systems and utilization of trophic eggs in insects.

Therefore, based on the observations outlined in this new specimen, an additional component within the Dynastic-Succession Hypothesis should be considered. While the formidable hunting prowess of this primitive specimen allowed them to garner domination over other insects in the rapidly diversify Cretaceous forests, the likely feeding practice of oophagy should be considered important in their success. As such, more advanced social roles may have been attained resulting in possible further morphological derivations of the caste systems, emphasized on brood care. This would have allowed not only larger colony sizes, but also may have resulted in a „more stable“ colony, especially compared to Sphecomyrminae. Having portions of the colony deriving their energies from a specialized food source rather than relying on fresh prey is a significant advantage, both socially and evolutionarily. Given these conclusions, it would be assumed that these colonies of non-Sphecomyrminae ants were able to persist through adverse conditions more efficiently (food shortages due to disappearing prey resulting in greater reliance on oophagy) and even be able to adapt more quickly to changes in prey. This all sets the ground plan for their advancement into new areas, resulting in the wide-spread global occurrence. While it may never be known what the actual factors were that were responsible for the extinction of the Sphecomyrminae, it is certainly interesting to consider what their counterparts appear to have

been achieving within the same rapidly diversifying Cretaceous forests. Perhaps also intriguing to ponder is that several ponerines demonstrate a potential precursor to true trophallaxis, whereby they carry small liquid drops (sugary) back to nestmates (CHOE & CRESPI 1997). In short, they were poised to be able to quickly radiate in diversity (both in occurrences within niches and morphology) and dominance more efficiently than their ill-fated counterparts (Sphecomyrminae), primarily due to their more advanced social and perhaps morphological features relating to brood care.

Zusammenfassung

Aufgrund ihrer hochentwickelten Sozialstruktur (Eusozialität) zählen Ameisen zu den weltweit erfolgreichsten und ökologisch dominanten Organismen. Während zahlreiche Neuentdeckungen und Studien über ursprüngliche Ameisen gemacht wurden, liegen die Ursprünge sowohl der echten Ameisen, als auch der Evolution der Eusozialität, weitestgehend im Dunkeln. Hinweise auf Eusozialität in primitiven Ameisen basieren bislang lediglich auf morphologischen Merkmalen (Präsenz der Metapleuraldrüse sowie verschiedener Kasten) woraus die entscheidende Bedingung der Brutpflege abgeleitet wurde. Zum ersten Mal können hier unmittelbare Beweise für Brutpflege in kreidezeitlichen Ameisen vorgelegt werden. Eine primitive Ameise aus einer unbestimmten Unterfamilie der Formicidae liegt in Burmesischem Bernstein vor, die zusammen mit Nestmaterial, einem Ameisenei sowie Nahrung für den Ameisen-Brut (erbeutete Arthropoden und Ameiseneier – Hinweis auf Oophagie) überliefert ist. Während das Vorhandensein einer Ameisen-Brutkammer Antworten auf die Frage nach der Entstehung der Eusozialität in primitiven Ameisen gibt, wirft ein Vergleich mit anderen ursprünglichen Taxa (besonders der Sphecomyrminae) viele neue Fragen auf. Etwa warum, wenn doch primitive Ameisen eusozial waren, eine Abstammungslinie (eben die Sphecomyrminae) ausstarb, während andere überlebten und sich später explosionsartig in die dominanten Organismen von heute zu diversifizieren. Eine Interpretation der allgemeinen morphologischen Merkmale der Arbeiterinnen-Kaste in Zusammenhang mit deren sozialer Rolle legt nahe, dass die Brutpflege der ausschlaggebende Faktor für den Erfolg bestimmter kreidezeitlicher Abstammungslinien war. Gegenüber den Sphecomyrminae erscheinen Arbeiterinnen der anderen Taxa größer aber zierlicher, und haben kleinere Augen sowie einfache Mandibeln, was auf eine Spezialisierung hin zur Brutpflege deutet. Sphecomyrminae hingegen haben stämmigere Körper, größere Augen und möglicherweise nicht-traditionelle soziale Rollen entwickelt, die für eine bessere Anpassung an das Jagen und

die Nahrungssuche, also für Aktivitäten außerhalb des Nestes (und der Brut), sprechen. Während Oophagie in den hier beschriebenen Ameisen wahrscheinlich vorkam, ist dies ebenso aus vielen anderen ursprünglichen Abstammungslinien bekannt, was für diese nicht-Sphecomyrminae von Vorteil war und evolutionäre Veränderungen vorangetrieben haben könnte. Die höher entwickelte Sozialstruktur erlaubte den Kontrahenten der Sphecomyrminae zudem, komplexere Nester zu bauen, die größere Populationen beherbergen konnten. Mit diesen sozialen und vermutlich evolutionären Vorteilen ausgestattet, explodierten die Abstammungslinien der nicht-Sphecomyrminae in Diversität und Anzahl während der frühen Evolution der Ameisen in den zunehmend diversen kreidezeitlichen Wäldern, bis hin zu den Superorganismen, die sie heute sind.

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