

*In memory of G.M. Dlussky, A.A. Zakharov, and E.O. Wilson,
the giants on whose shoulders we stand*

Cretaceous-Burmese-Amber Ants: Morphological Features and Community Structure

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Abstract—We consider the phenomenon of the morphological diversity of ants from Cretaceous Burmese amber (Kachin). An ethologic-ecological hypothesis of its origin and features of Mesozoic and Cenozoic myrmecocomplexes is put forward. It seems that some morphological features of stem Formicoidea allow the assumption of the absence of effective communication and, as a result, coordinated behavior and collective hunting. Thus, the diversity of Cretaceous stem ants as predators represents food specialization according to the types of prey, under the condition of a family lifestyle, which leads to division of the ecological space into subniches between ant species. Crown groups of ants have evolved a crucial adaptation, i.e., effective communication and collective hunting (mobilization). This adaptation allowed them to move beyond the niches of specialized predators and serve large colonies, since with developed communication the type and size of the prey are not strictly limited to the size of the ants and its jaws. Due to this, the myrmecocomplexes of modern ants are arranged not so much according to the principle of division of ecological niches, as in the Mesozoic, but according to the principle of colonies dominance.

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INTRODUCTION

Burmese amber (Burmite, Kachin amber), about 99 million years old, is rich in fossil organisms of amazing preservation and taxonomic diversity, which gives an idea not only of the taxonomic diversity of oryctocenoses, but a rare opportunity to study the structure of extinct biocenoses. At the moment, 651 families, 1382 genera, and 2038 animal species have been described, of which 583 families, 1264 genera, and 1908 species are those of arthropods (Ross, 2021). Ants, according to currently accepted taxonomy, are represented in Burmite by one family of Formicidae, 31 species of three extinct subfamilies (Haidomyrmecinae, Zigrasimeciinae, and Sphecomyrminae) and, judging by some unpublished data, at least three crown subfamilies (Ponerinae, Dolichoderinae, and Formicinae) (although data on crown subfamilies may be valid only for later Burmese amber: Tilin amber, 72 million years) (Zhang et al., 2018; Zheng et al., 2018; Boudinot et al., 2020) (Table 1). Recently, two more genera (*Camelomecia* and *Camelosphecia*) have been discovered, assigned to the superfamily Formicoidea as a sister group to Formicidae, described from winged reproductive individuals (two females and a male of three species) (Barden and Grimaldi, 2016;

Boudinot et al., 2020). It is doubtful whether insects without metapleural glands, as in *Camelomecia* and *Camelosphecia*, should be classified as Formicoidea, also because of the non-Formicoidea venation of the wings of *Camelomecia*. However, addressing these issues is beyond the scope of this study. The taxonomic and morphological diversity (in particular, the unique structure and diversity of the jaw apparatus) of formicoid ants in Burmite at the moment does not have a satisfactory explanation, despite the fact that almost every publication with a description of new species of ants from Burmese amber raises questions about how and why such morphological diversity arose, because modern ants, despite their taxonomic richness (almost 14000 recent species, 17 subfamilies), have no analogues of such jaws. The structure of the mandibles of all modern ants has common features, and although there are specialized forms, the modifications of the mandibles are quite well studied and line up in morphological series with a common root (Dlussky and Fedoseeva, 1988). The purpose of this study is to analyze representatives of the myrmecofauna of Burmese amber, the causes of the specific morphological radiation of stem taxa and their extinction.

Table 1. Taxonomic composition and some morphological characteristics of Burmite ants

Taxon	Antenna index* (AI)	Individual sizes female/male/worker, mm
Haidomyrmecinae		
<i>Aquilomyrmex huangi</i> Perrichot et al., 2020	0.45	9/–/–
<i>Chonidris insolita</i> Perrichot et al., 2020	0.12	10/–/–
<i>Dhagnathos autokrator</i> Perrichot et al., 2020	0.1	14/–/–
<i>Dilobops bidentate</i> Lattke and Melo, 2020	0.12	–/–/4.1
<i>Ceratomyrmex ellenbergeri</i> Perrichot et al., 2016	0.22	–/–/5.5
<i>Ceratomyrmex planus</i> Lattke and Melo, 2020	0.25	–/–/3.5
<i>Linguamyrmex brevicornis</i> Perrichot et al., 2020	0.27	7/–/4
<i>Linguamyrmex rhinocerus</i> Miao and Wang, 2019	0.27	–/–/6.6
<i>Linguamyrmex vladi</i> Barden and Grimaldi, 2017	Incomplete antennae	–/–/5.6
<i>Protoceratomyrmex revelatus</i> Perrichot et al., 2020	0.24	–/–/4.3
<i>Haidomyrmex cerberus</i> Dlussky, 1996	0.21	–/–/5
<i>Haidomyrmex davidbowiei</i> Lattke and Melo, 2020	0.25	–/–/4.4
<i>Haidomyrmex scimitarus</i> Barden and Grimaldi, 2012	0.16	8/–/–
<i>Haidomyrmex zigراسي</i> Barden, Grimaldi, 2012	0.21	–/–/3.5
Zigrasimeciinae		
<i>Protozigrasimecia chauli</i> Cao et al., 2020	0.13	–/–/11.75
<i>Zigrasimecia ferox</i> Perrichot et al., 2014	0.16, 0.17	2.8/–/2
<i>Zigrasimecia hoelldobleri</i> Cao et al., 2020	0.11, 0.21	–/–/2.6
<i>Zigrasimecia tonsora</i> Barden and Grimaldi, 2013	0.15	2.3/–/–
<i>Zigrasimecia goldingot</i> Zhuang et al., 2021	0.23	2.4/–/–
Sphecomyrminae		
<i>Gerontoformica gracilis</i> Barden and Grimaldi, 2014	0.15	–/–/6.6
<i>Gerontoformica orientalis</i> Engel and Grimaldi, 2005	0.1	–/–/5.2
<i>Gerontoformica robusta</i> Barden and Grimaldi, 2014	0.11	–/–/5.7
<i>Gerontoformica spiralis</i> Barden and Grimaldi, 2014	0.15	–/–/5
<i>Gerontoformica subcuspis</i> Barden and Grimaldi, 2014	0.19	–/–/5.7
<i>Gerontoformica contega</i> Barden and Grimaldi, 2014	0.1	–/–/5.2
<i>Gerontoformica magna</i> Barden and Grimaldi, 2014	0.11	–/–/8.6
<i>Gerontoformica pilosa</i> Barden and Grimaldi, 2014	0.13	–/–/4.3
<i>Gerontoformica rugosa</i> Barden and Grimaldi, 2014	0.18	–/–/4.97
<i>Gerontoformica tendir</i> Barden and Grimaldi, 2014	~0.13	–/–/6.93
<i>Myanmyrma gracilis</i> Engel and Grimaldi, 2005	0.09	–/–/9.5
<i>Myanmyrma maraudera</i> Barden and Grimaldi, 2014	0.11	–/–/8.67

* Ratio of the scape length to the total length of the antenna.

MATERIALS AND METHODS

The paper analyzes published materials on studies of Cretaceous and modern ants. Images for tracing were taken from the AntWeb resource (<https://www.antweb.org/>) with the number of specimens indicated, as well as from our own archive. The morphological structures were traced and measured using the Inkscape program distributed under a free

license. Graphs are constructed using Excel2013. Structure measurements and missing information were obtained from published images, as well as from the works of various authors based on the initial descriptions of corresponding Cretaceous ants (Table 1). To measure modern ants, we took the sample used in the article comparing the morphospaces of stem and modern ants, as well as some missing measurements of Cretaceous ants (Barden et al., 2020).

RESULTS AND DISCUSSION

Diversity of Cretaceous Ants

The Cretaceous period is characterized by significant changes in the entomofauna associated with a change in the dominant groups of plants in phytocenoses, followed by a change in the structure of biocenoses. The share of modern families in the entomofauna increases from the beginning of the Cretaceous from half to three quarters, which indicates the formation of the modern appearance of the entomofauna at the family level during this period (Zherikhin, 2003). In the Cretaceous period, an increase in the diversity of phyllophagous insects, parasitoids, and other Hymenoptera is observed. Burmese amber exhibits a stunning diversity of Middle Cretaceous arthropods (Ross, 2021). Calculations of the biodiversity of arthropods in Burmite at the family level show high values for the emergence of new families and “fauna turnover” (the sum of first encountered families and the last time related to the total number of families in a given locality) in this amber (Rasnitsyn, 2016). Such facts indicate a diverse and rich resource base for terrestrial predatory insects that existed during this period.

Today, we can say that Cretaceous ants are represented not only by the extinct subfamilies listed above, but also by several crown subfamilies. Specimens of ants of extinct genera have also been described, not yet assigned to any subfamily, although this is rather a result of a technical nature: these representatives have not yet been studied by the authors of the latest phylogenetic schemes for the presence of the characters they have distinguished (specimens from the Taimyr amber, Armaniinae). Among Cretaceous crown groups, one species has already been described: Doli-choderinae (McKellar et al., 2013), Formicinae (Grimaldi and Agosti, 2000), Aneuretinae (Engel and Grimaldi, 2005), Myrmicinae (Dlussky et al., 2004), and two species of Ponerinae (Dlussky, 1999). The Cretaceous fauna also contained transitional (intermediate) forms, Armaniinae (in the current system they are part of Formicidae) and recently described winged representatives of the sister clade to Formicidae, which includes two genera, *Camelomecia* and *Camelosphecia*. Thus, the myrmecofauna of the Cretaceous period already included representatives of the main crown subfamilies; however, extinct subfamilies demonstrated the main taxonomic and morphological diversity, in which slightly more than 50 species are currently described. On this basis, it can be expected that the Cretaceous period was the time of “formicoidization,” by analogy with the evolutionary phenomena “arthropodization,” “ornithization,” etc., i.e., the period of the emergence of individual characters of modern ants in unusual combinations in different phylogenetic branches, the entire complex of which was formed in the crown taxa of ants, which are considered a monophyletic group.

The proportion of ants in oryctocenoses has been growing throughout the entire period of the existence of the family from the end of the Lower Cretaceous to the present, but in the Cretaceous it was, as a rule, a few fractions of a percent and the number of specimens was usually a few (LaPolla et al., 2013). According to our preliminary calculations, ants make up 2.6% of all arthropod species in Burmese amber (Ross, 2021). According to studies of Hymenoptera in Burmese amber, ants make up about 9.1% of specimens of all Hymenoptera (Zhang et al., 2018). From the point of view of assessing the richness of the resource base of the biocenosis, it is important that parasitoids have a large or comparable proportion of specimens among Hymenoptera (Scelionidae, 16.1%; Chrysididae, 11.5%; and Bethyidae, 7%). Thus, the proportion of ants in the taxonomic diversity of burmite, as well as the number of individuals, were quite noticeable against the background of the general diversity of arthropods, although they are not comparable with the current state of this group of insects (for example, the proportion of ant specimens in Dominican amber is about 36%, and the biomass of ants in the modern tropical forest is 15–20% of all animals) (Hölldobler and Wilson, 1990; LaPolla et al., 2013).

Clear evidence of the significant ecological role of ants in the Burmite paleobiocenoses is the finding of *Aethiocarenum burmanicum* (Poinar and Brown, 2017), which demonstrates myrmecomorphy common among modern harmless arthropods for the purpose of self-defense (a case of Batesian mimicry) (Vršanský et al., 2018). So far, not a single representative of the crown groups of ants has been reliably described from Burmese amber, although they were found in later Tiliin Burmese amber (Zheng et al., 2018).

Hypotheses of the Origin of Modern Ants

The most well-known and widely accepted hypothesis of the conditions for the emergence of modern ants was proposed by Wilson and Hölldobler (Wilson and Hölldobler, 2005) and is known as the Dynastic-Succession Hypothesis. According to it, the main ancestral group of modern ants are forms adapted to a predatory lifestyle in ground litter, namely, Ponerinae,¹ which, having appeared in the middle of the Cretaceous, spread throughout the world in the Paleogene and gave rise to modern subfamilies, after which there was a transition to the ecological dominance of ants along with a change in diet due to the expansion of angiosperms in tropical

¹ All subfamilies of the poneromorphs were taken as Ponerinae during the time of writing the article (2005). It was subsequently recognized as polyphyletic and divided into several subfamilies: Amblyoponinae, Ectamomminae, Ponerinae, and others. Nevertheless, Wilson believed and took into account the possible polyphyletic nature of the taxon and offered as important an interpretation of the group that was ecological and not taxonomic (cladistic).

regions. There are two reasons for this conclusion: ground litter is a habitat with a very high biomass, where arthropod predators, such as Cretaceous ants and now modern primitive taxa (especially poneromorphs), can feed. The second reason, called the “ponerinae paradox” by the authors, is the contradiction (as the authors believed) between the wide geographical distribution of Ponerinae taxa with weak social organization of their families, the distinguishing features of which are low-numbered monogynous families, the absence of developed forms of polymorphism and polyethism, and solitary hunting, primitive communication in the form of an alarm signal, and practically no trophallaxis, mobilization (recruitment) of workers to a food source, or protection of the territory. Thus, the origin of ants from primitive “Ponerinae” adapted for hunting in ground litter after radiation of this group at the end of the Cretaceous and Paleocene could explain the wide geographical distribution of the primitive group of poneromorphs and the holding of positions in competition with the more progressive Myrmicinae and Dolichoderinae that spread (appeared?) later and Formicinae, which appeared due to a change in diet, accompanying the spread of honeydew insects, and could not completely replace the poneromorphs, which are well adapted and divided ecological niches in their habitat.

G.M. Dlussky did not agree with the position of the origin of modern ants from specialized predators of ground litter (Dlussky and Rasnitsyn, 2007). He pointed out that the Cretaceous ants found by that time, Sphecomyrminae, had the habitus of a terrestrial predator, successfully foraging on the surface of the ground litter and in the tree layer, i.e., are not similar to the inhabitants of the ground litter, and suggested that modern large phylogenetic branches arose as life forms adapted to hunting in different tiers of the biocenosis: in the soil (poneromorphs), on the soil surface and tree layer (Formicinae, Dolichoderinae, and Myrmicinae), and in the ground litter (Aneuretinae) (Dlussky and Fedoseeva, 1988).

It is now clear that Wilson’s assumption of an earlier origin of poneromorph taxa is not supported by paleontology. There is also no predominance of representatives of poneromorphs among Cretaceous ants, while representatives of “progressive and younger” (in the framework of the Wilson and Hölldobler hypothesis) subfamilies are found in Cretaceous oryctocenoses and have well-defined signs of belonging to crown subfamilies: Formicinae, Dolichoderinae, Myrmicinae, and Aneuretinae. It is clear that the result of the absence of forms inhabiting the ground litter in the fossil record is quite natural and cannot be the main argument. However, the assertion that adaptations to predation in the ground litter contributed to the emergence of crown subfamily ants seems rather controversial. As can be seen from modern taxa, the morphology of ants living and hunting in ground litter changes towards a decrease in the length of the antennae, a

decrease in the relative size of the eyes, thickening of the integuments, and specialization of the mandibles. This is not similar to the signs that all crown groups of ants demonstrate. At the same time, we do not deny the connection between ground litter and the ancestral taxa of ants; we only draw attention to the lack of morphological specialization in them for life in ground litter. A somewhat different pattern is presented than that described in the hypothesis of dynastic succession. The ancestors of modern crown groups must have acquired morphological features that for some reason remained fixed in all (practically without exception) modern crown groups: three-toothed (and more) mandibles, articulated antennae with a long scape, the structure of the antenna flagellum (relatively long curved pedicel, enlarged apical segments), and the presence of simple ocelli and compound eyes. In modern ants, in which one or more of these traits are changed, this is the result of specialization and modification (Dlussky and Fedoseeva, 1988). The hypothesis of the origin of ants should explain their presence. It seems that in ground litter and in primitive families, such as in some poneromorphs, this complex of characters is not needed, and therefore could not be formed.

Morphological Features of Ants and Relationship with Sociality

Recognizing the succession hypothesis of Wilson and Hölldobler as valid, some authors paradoxically contradict it. Thus, Boudinot and Perrichot et al., some of the most professional researchers of Cretaceous Formicoidea, authors of many articles analyzing their ecology and morphology, accept the hypothesis of succession, while quite rightly believing that ants within the Formicoidea formed as active terrestrial predators (Boudinot et al., 2020). Therefore, Cretaceous Formicoidea have a certain set of morphological features, including prognathism of the head (this feature was considered in the work of E.B. Fedoseeva (2001)), lateral rotation of the antennae (however, this modality is not observed in all burmite ants, see Figs. 1a, 1d, 1h), elongation of the coxae of the forelegs, and others. The authors focused on cladistic analysis (i.e., identified synapomorphies for the entire group), apparently for this reason they did not include morphological features that are also found in other Aculeata, but also characterize a complex of features of fast terrestrial predators, for example, large compound eyes and simple eyes, long antennae and legs. Indeed, 31 species of ants have been described so far from the older Burmese amber (Kachin amber) (Table 1). Three species of *Camelomecia* and *Camelosphecia* are not included in the analysis, due to the absence of metapleural glands, non-Formicoidea wing venation in *Camelomecia*, due to lack of evidence of a wingless caste, and therefore doubts about the need to include them in Formicoidea.

At the moment, all researchers of the Burmite myrmecofauna are unanimous in assessing the ecological role of the described ants. The variety of sizes of ants and their jaws speaks of specialized predation. The sociality of Cretaceous Formicoidae has been discussed since the first descriptions (Wilson et al., 1967; Dlussky, 1983, 1987; Wilson, 1985). Barden and Grimaldi in their study (Barden and Grimaldi, 2016) summarized the morphological evidence for the eusociality of Cretaceous Formicoidae (the presence of wingless and winged castes in at least some of them, with the presence of reproductive females with traces of discarded wings), and also suggested that indirect evidence of eusociality and the presence of group behavior is the presence of syninclusions, which are quite rare in the Cretaceous oryctocenoses of ants in one piece of resin. The mentioned morphological characteristics undoubtedly point to the eusociality of the Cretaceous Formicoidae; however, the assumption of group behavior does not seem to be substantiated. Four pieces of burmite are discussed in the article: JZC Bu1814, six individuals of *Gerontofornica spiralis*; JZC Bu116, 11 *G. spiralis* and one *Haidomyrmex zigzasi* worker; JZC Bu1645, 21 specimens of *G. orientalis*, *G. contegus*, and *G. robustus*; JZC Bu1646, fight between two worker ants *G. tendir* and *G. spiralis*. The joint presence of several rare individuals (according to the authors, but in the light of the facts presented above, not quite right) for the biocenoses of ants of the same species, as well as the fight between two ants, is interpreted by researchers as the coordination of actions when obtaining food and aggressive interactions between species; however, the authors come to the conclusion that a pheromone trail was apparently not used. It should be noted that the authors believe that crown groups have ecologically replaced stem groups, but they do not describe the mechanisms of displacement, except for the observation that ants with specialized mouthparts (Zigrasimeciinae, Haidomyrmecinae) obviously depended on food sources. We will also note some points that are important in the context of the discussion of sociality. The first is the presence in the small pieces of amber under consideration of many (tens) of other animals, among them a snail, cockroach, wasp (Scolebythidae), spider, beetles, springtails and other arthropods, which makes the second version of the authors, i.e., accumulation at a food source, the most convincing. With a eusocial lifestyle, the accumulation of ants from nearby nests of two or three species does not seem to be an astronomically improbable event even in the absence of mobilization. The second feature is the presence in one piece of worker ants of different species without signs of aggression; this also reinforces this version and excludes aggressive interactions. An interesting feature concerns the curious sample Bu1814, in which all individuals have missing metasome tips (empty abdominals), i.e., the corpses of ants may have fallen into this piece of resin. In this case, this sample is the most evi-

dence in favor of sociality, and it is possible that this is the result of care for the nest. Apparently, some species of ant stem taxa could also be characterized by the initial stage of polymorphism, i.e., size differences in workers (Cao et al., 2020a).

Thus, the presence of eusociality seems to be fully proven, but guarding of the food source (as well as mobilization to the food source) is not a regular attribute of coexistence in the described ant communities and, apparently, is carried out at the level of separate individuals. Indeed, syninclusions of two ants fighting and badly injured in a fight demonstrate that the fight lasted for quite a long time, but nevertheless, the ants were left alone, while modern ants, as a rule, have help, which is also captured in Eocene amber (e.g., Radchenko and Perkovsky, 2021). The available data on modern ants made it possible to identify several morphological features and trends that characterize the crown groups of ants representing the majority of modern species and dominating in all biocenoses (Myrmicinae, Dolichoderinae, Formicinae):

(1) Lateral rotation of the antennae and geniculated antennae with a long scape ($AI > 3$) (synapomorphy: all crown groups of ants have it, while the structure of the antennae in the stem groups of ants is not uniform, often the antennae are filamentous, very long, the scape can be very short, AI from 0.1 to 0.25 (see Table 1, Fig. 1)).

(2) Morphology of funiculus : relatively long curved pedicel and enlargement of apical segments of the flagellum (synapomorphy?) (see Fig. 1).

(3) Mandibles are relatively small, having at least three teeth (synapomorphy?) (see Fig. 1).

(4) Reduced size of compound eyes, with the presence of simple ocelli (trend) (Fig. 2).

(5) Trophallaxis (trend in dominant subfamilies).

(6) When caring for the brood, larvae and pupae are licked and transferred (synapomorphy?).

(7) Replacement of poisonous sting with acid gland (trend in dominant subfamilies).

Although sociality among ants has a rather narrow range of variations, in contrast to other higher Hymenoptera, where all stages of the formation of eusociality can be traced from single to giant bee colonies, the features of a primitive social organization are still observed in a fairly large number of ant taxa. For example, the number of (primitive) poneromorph species in forest ecosystems is 22.2% (although the number of individuals is only 12.4%) (Ward, 2000). The most primitive ants are distinguished by the following features (for progressive taxa, the modalities of these traits will be different): the presence of at least two castes of females, and quite often workers in such species can pass to the status of reproductive females; they do not build a complex nest; they get food by solitary predation, there is no mobilization; they do not guard the foraging area; no trophallaxis, but recognize

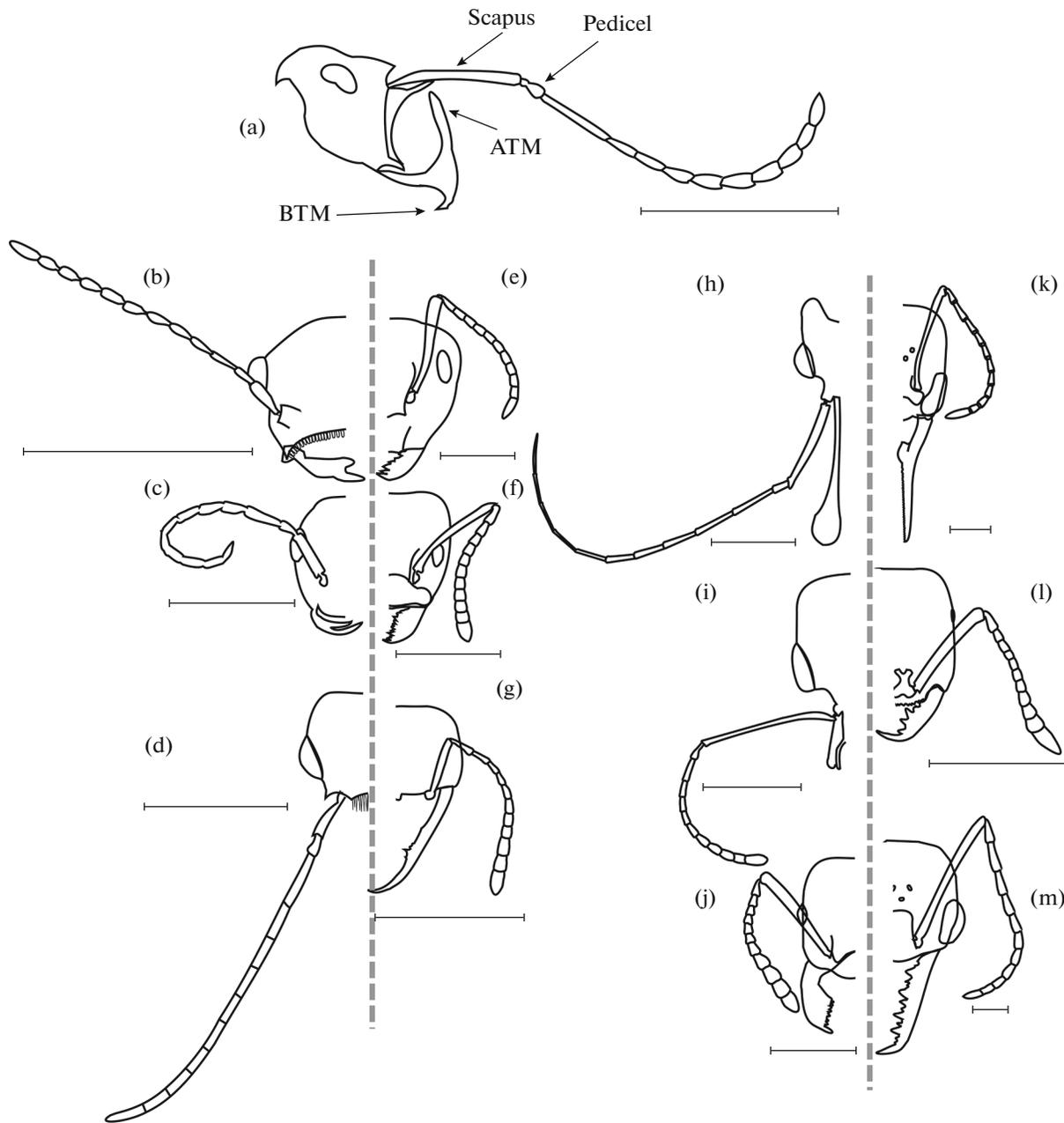


Fig. 1. Drawings from photographic images of the head from the dorsal side (b–m) and the profile (a) of Cretaceous (b–d, h, i) and modern (e–g, j–m) ants. The structure of the antennae, mandibles, clypeus, shape and size of the eyes and ocelli are shown (in parentheses are the numbers of specimens in the AntWeb database): (a) *Linguamyrmex brevicornis* (FANTWEB00035); (b) *Zigrasimecia tonsora* (ANTWEB1008098); (c) *Gerontoformica orientalis* (JWJ-BU19); (d) *Dilobops bidentata* (FANTWEB00039); (e) *Camponotus abrahami* (CASENT0910439); (f) *Azteca adrepens* (CASENT0173823); (g) *Martialis heureka* (CASENT0106181); (h) *Ceratomyrmex ellenbergeri* (NIGP164022); (i) *Aquilomyrmex huangi* (FANTWEB00024); (j) *Manica bradleyi* (CASENT0106022); (k) *Harpegnathos saltator* (CASENT0101783); (l) *Onychomyrmex* sp. (CASENT0069959); (m) *Myrmecia* sp. (CASENT0006136). ATM and BTM are the apical and basal tooth of mandibles. Scale bar: 1 mm.

a common alarm signal; care for the brood, carry larvae and pupae; contact each other when they meet, and groom. And, as a rule, these species are indeed associated with ground litter, which together seems to confirm the hypothesis of succession. However, all this does not explain the presence of common mor-

phological features of ants and the tendencies listed above.

The concept proposed here boils down to the idea of the emergence of crown ants as fast efficient terrestrial wingless predators with more developed social communication compared to stem taxa. G.M. Dlussky

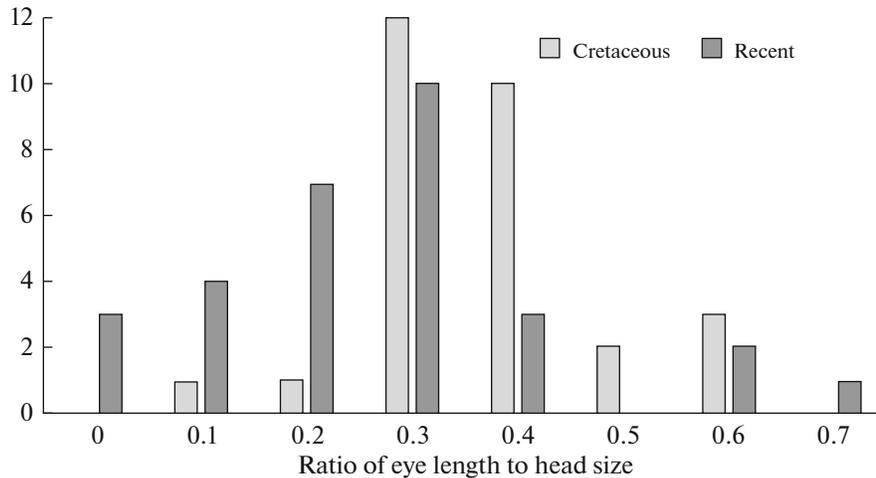


Fig. 2. Distribution of eye length relative to head size in recent and Cretaceous ants.

suggested that antenna geniculation is associated with eusociality due to the possibility of manipulating small objects, which is hard to disagree with (Dlussky, 1983; Dlussky and Fedoseeva, 1988). G.M. Dlussky and E.B. Fedoseeva showed that social wasps and bees caring for brood have a relatively elongated scape (AI \sim 0.3), and later these conclusions were confirmed statistically (Borysenko, 2017). However, within the framework of this concept, it is difficult to explain why the scape length continued to increase in ants (AI \geq 0.3), and in the most advanced dominant subfamilies Formicinae, Myrmicinae, and Dolichoderinae AI \geq 0.4) and why lateral rotation of the antennae was required, if bees and wasps coped very well with the tasks of manipulating small objects, and on the other hand, geniculated antennae are also found in non-social ichneumon wasps, for example, *Anastatus* sp. (Eupelmidae) live parasitically on the eggs of insects. In addition, termites, which are eusocial non-Hymenopteran insects, do not tend to have geniculate antennae. Therefore, apparently, some explanation is needed for the geniculation and lateral rotation of the antennae in the crown taxa of ants. We believe that a further increase in the relative length of the scape and the rotation of the antennae were required to improve the efficiency of orientation for a fast, wingless terrestrial predator. It is possible that one of the reasons for this could be the Johnston's organ located in pedicel, which is a multisensory organizer, partially taking away the functions of orientation from the visual organ. Johnston's organ in ants performs the functions of a wind compass, gravity perception, and a step integrator (estimating the distance traveled) (Grob et al., 2021). From an engineering point of view, it is more convenient to analyze the data from such receptors, the farther they are from each other. The compromise between the need to place the analyzers as far apart as possible, but at the same time to completely control the space directly near the mouth opening and the

mandibles, led to: (i) lateral rotation of the antennae, (ii) elongation of the scape, and (iii) a change in the shape of the pedicel (an elongated segment curved at the base flagellum as close as possible to the scape and, consequently, to the mandibles and mouth opening).

The third feature of ant antennae is that the apical flagellum segments increase in relative size, so that the apical segment is the largest (thickness, length), and sometimes the last flagellum segments can form a club (see Fig. 1). In our opinion, this structure is explained by the same reasons, i.e., an increase in the efficiency of spatial orientation, in this case, due to an increase in the role of olfactory analyzers with a smaller contribution of vision compared to flying Hymenoptera, care for offspring, and subsequently communication through smell. These two selection vectors (increase in the efficiency of orientation and control of the perioral space) lead to an increase in the number and concentration of olfactory receptors on the apical segments of the flagellum. The fact is that olfactory receptors can be distributed in the flagellum of Hymenoptera almost evenly along its entire length (although this rule is not strict), but in ants they are concentrated on the apical and preapical segments of the antennae, this tendency is especially pronounced in Myrmicinae, in which the segments of the base flagellum are practically devoid of olfactory sensilla (Hashimoto, 1990; Nakanishi, 2009; Euzébio et al., 2013; Tribble et al., 2017). The decisive importance of olfactory receptors in the phylogenetic lineage of ants in comparison with other insects, including Hymenoptera, is evidenced by the results of studies of the brain and genomes of ants (Guo and Kim, 2007; Gronenberg, 2008; Zhou et al., 2012). The number of genes responsible for odor receptors in ants is several times greater, sometimes by an order of magnitude, than in other insects. The presence of 340–400 such genes was shown in studied ant species with different social organization and from different subfamilies (Dolichoderinae: *Linepithema*

humile, Formicinae: *Camponotus floridanus*, Ponerinae: *Harpegnathos saltator*, Myrmicinae: *Pogonomyrmex barbatus*), while the fruit fly *Drosophila melanogaster* only has 61 such genes, the honey bee *Apis mellifera* has about 170, and the parasitoid wasp *Nasonia vitripennis* has about 300. It has also been shown that odor-receptor genes are a rapidly evolving and variable group of genes in ants. Such results, especially in comparison with other eusocial Hymenoptera, according to experts, indicate a more complex communication system in ants, based specifically on chemical reception. Experiments on turning off olfactory receptor genes confirmed that workers without smell have a sharply reduced or lack of ability to navigate by smell, communicate with relatives, follow the pheromone trail, and care for larvae, although they can feed on their own (Yan et al., 2017). Therefore, evolution aimed at optimizing the organ that carries olfactory receptors raises no questions. The intensification of spatial-orientation functions in ant antennae is indirectly confirmed by a relative reduction, a decrease in the size of optical analyzers, i.e., compound eyes, as well as by the structure of the brain of modern ants, in which the processing zones of olfactory signals are developed to a greater extent than the visual ones (Gronenberg and Hölldobler, 1999; Gronenberg, 2008). Indeed, the closest relatives of ants that can fly have huge eyes; many ants of stem taxa from Burmese amber also have relatively large eyes in comparison with modern ants, while retaining not the ant structure of the antennae; large bulging anteriorly displaced eyes in modern ants are associated with a life form of solitary predators (*Myrmoteras*, *Gigantiops*, *Myrmecia*, and *Harpegnathos*). It should also be noted that some representatives of Dolichoderinae and Formicinae have simple eyes in worker individuals and are practically absent in Myrmicinae and Ponerinae, which tend to live in ground litter, indicating a tendency to the loss of simple eyes in specialized inhabitants of ground litter. In this regard, it is important to note that, in order to leave a pheromone trail, ants of different phylogenetic lines use completely different organs and substances: secretion of the poison gland, Dufour's glands, secretions of the mandibular glands, secretion of the hindgut, secretion of special glands on the legs, Pavan's gland, etc. (Morgan, 2009). This diversity indicates the independent and repeated appearance of "following" behavior in the crown lines of ants, which, according to the hypothesis put forward here, is based on the mechanisms of perfect orientation and odor differentiation. Thus, the improvement of antennae for orientation purposes served as an impetus for the intensification of chemical communication, i.e., was a morphological pre-adaptation for the further development of sociality.

As shown by G.M. Dlussky and E.B. Fedoseeva (1988) in the study of the craniomandibular systems (CMS) of ants, the presence of at least three teeth, the triangular shape of the mandibles, and well-developed

mandibular muscles also belong to the features that unite the crown groups of ants and, apparently, are the initial modality of mandibles in modern ants. The authors believed that three-toothed jaws were more effective in holding prey, as well as in manipulating objects, which is necessary for ants, since ants, unlike other Hymenoptera, during the care of larvae transport them. These arguments seem well founded. In this regard, we suggest that the presence and morphology of the basal teeth in ants with the most gigantic jaws (Haidomyrmecinae) indicates that workers could carry their larvae with them (Figs. 1a, 3b, 3c). Similarly, modern ants with primitive sociality *Harpegnathos* sp. use the basal tooth on the giant holding jaws to carry larvae (Fig. 3). At the same time, it is important that winged reproductive females apparently have the same jaws (Barden and Grimaldi, 2016) (i.e., there is no worker-caste polymorphism), which indicates a primitive social organization. Thus, this function (the transfer of larvae) could have arisen somewhat earlier than the effective structure that performs it, which corresponds to ideas about the course of morphological evolution.

Additional teeth on the mandibles appear in different lineages of Hymenoptera. For example, solitary *Megachile* leaf-cutting bees, stonemason bees *Chalicodoma* (Megachilidae), *Vespa*, and *Vespula* (Vespidae) have mandibles with several small teeth, which is apparently associated with complex nest-building behavior, and can also successfully hold and dismember prey. The leptanilloid CMS (mandibles with three to five teeth) of ants look somewhat different and are more suitable for holding prey rather than building a nest, so the question of the origin of multitoothed jaws in ant ancestors requires additional research. However, it seems that the appearance of three-toothed (or more) mandibles with developed musculature and jaw mobility, which is special compared to other insects (Richter et al., 2020), was one of the key adaptations that allowed crown ants to occupy dominant positions in communities. G.M. Dlussky and E.B. Fedoseeva (1988) showed that the types and possible ways of evolution of the shape of the jaws in ants can be associated with the lifestyle of the species and the presence of pronounced polyethism and polymorphism, while the mechanism of the jaws can be significantly modified. Thus, species with a primitive social organization are predators with specialized jaws (holding CMS, a trap-type system), and in nomadic ants, specialized individuals (soldiers) have smooth mandibles in the form of hooks, while simple workers have leptanilloid mandibles, etc. It is the combination of the new shape of the mandibles and the increase in the jaw muscles that indicates better, more effective control over movements, which fits well into the pattern of the evolution of the improvement of manipulations against the background of rearrangements in the anatomy and morphology of the antennae described above (leading to the mandibles; the concentration of olfactory

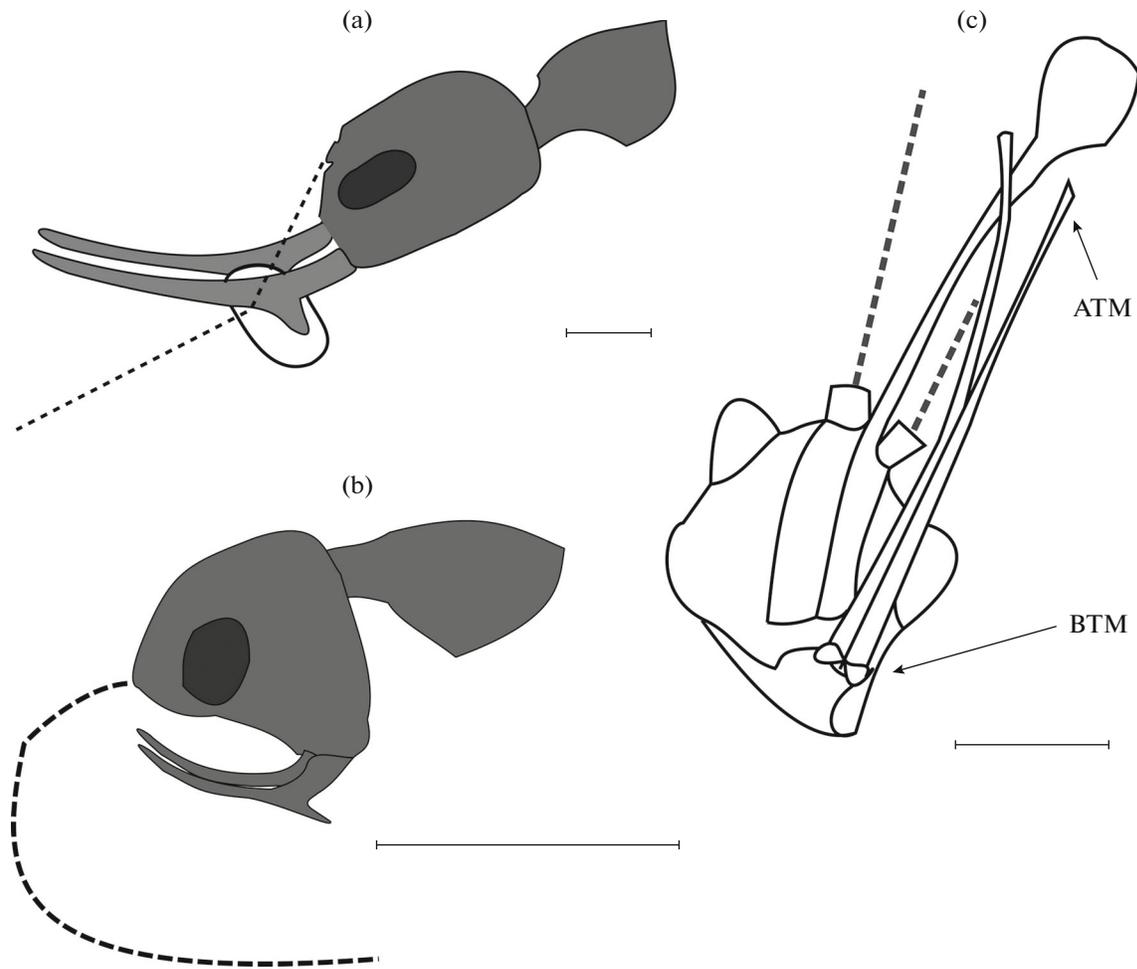


Fig. 3. Features of the mandibles of recent and extinct Cretaceous ants: (a) the use of basal teeth for the transfer of eggs and larvae by long-jawed ants *Harpegnathos* sp.; (b) drawing of the jaw in profile with characteristic arrangement of the basal tooth of the Cretaceous ant *Haidomyrmex zigrasi*; (c) head of *Ceratomyrmex ellenbergeri* (AntWeb: IGRBU002) from the ventral-lateral view. ATM, BTM are the apical and basal tooth of mandibles. Scale bar: 1 mm.

receptors in the apical segments). Ants are capable of precise movements even with very large trap-jaws. For example, the long jaws of *Odontomachus* sp. make one of the fastest movements in the animal world: they collapse shut, catching and killing prey; however, with the same jaws, workers are capable of very accurate manipulations: carefully transferring and shifting eggs and young larvae in their nest (Just and Gronenberg, 1999). The exceptional importance and pronounced vector of evolution aimed at improving the manipulatory abilities of mandibles in crown ants is confirmed by the results of Gronenberg's studies (Gronenberg, 1996; Gronenberg et al., 1997; Just and Gronenberg, 1999; Paul and Gronenberg, 2002; etc.). In a series of works, he showed how complex the craniomandibular muscular system of ants is: changes in the length of muscles and the ratio of different types of muscle fibers cause modifications of the mandibles and fine-tune the functioning of these structures. He also showed that in order to enhance control over the

movements of the mandibles, ants have a significantly developed subpharyngeal ganglion, unlike other Hymenoptera. Therefore, the structure of the mandibles (serration) and the presence (and development) of various mandibular muscles should be considered as one of the important conditions for the formation of sociality in ants. Muscles change the shape of the head, enhancing the work of the jaws, while the jaws can be small (Fig. 4b, 4c). A different pattern is observed in stem ants (Figs. 4d, 4e).

The unique diversity of mandibles of ants from Burmese amber, as has been repeatedly shown, goes beyond the existing morphospace of recent ants and is of interest not only in terms of morphology, but also from the point of view of ecological (ethological and biocenotic) prerequisites for their occurrence (Barden and Grimaldi, 2016; Barden et al., 2020; Cao et al., 2020b; Latke and Melo, 2020; etc.). The structure of the head capsule and amazing recurved jaws of representatives of *Haidomyrmecinae* indicates a different

mechanism of operation of their craniomandibular system than in modern ants (Figs. 1a, 3c, 4d, 4e). Based on the external morphology and the unique finding of *Ceratomyrmex ellenbergeri* with captured prey, the nymph *Caputoraptor elegans*, Barden and colleagues concluded that the mandibles of these representatives moved in the vertical plane (Barden et al., 2020). The recently discovered and not yet described *Colotrechninae* sp., a representative of Chalcidoidea, shows a striking external resemblance to Cretaceous Haidomyrmecinae in terms of the head structures (frontal outgrowths and the presence of elongated setae near the outgrowths), the structure of the mandibles (elongated upwardly curved) and their relative position (Kamp et al., 2022). The study of a single specimen showed the presence of only one, namely the anterior, condyle of the mandibles, which allows the jaws to move in different planes: vertical (holding objects between the head capsule and mandibles), as well as horizontal (manipulations between the mandibles). All studied members of the superfamily also have unicondylar articulation. The authors of the study attribute this articulation of the mandibles to the evolutionary mobility and amazing species diversity of the Chalcidoidea group. The structure of the jaws themselves, i.e., the presence of an additional tooth at the top of the mandibles, a developed chewing surface at the basal part of the mandibles, as well as the way of life of the chalcids indicate only a superficial resemblance to the Cretaceous Haidomyrmecinae. However, the study of the biology of this new insect, the nature of mandible movements, combined with a comparative analysis of the articulation of mandibles and the work of the CMS in extinct and recent ants, promise excellent prospects for elucidating the features of the biology of Haidomyrmecinae. Lattke and Melo (Lattke and Melo, 2020) also drew attention to the similarity of the head shape of Haidomyrmecinae with some parasitoid stalked Hymenoptera (*Tyrannoscelio*, *Stentoriceps*, and *Nanoctulhu*). Newly discovered Neotropical *Tyrannoscelio* also have strong, long mandibles with several teeth, which can move in a vertical and somewhat inclined plane, as expected for the purpose of excavating soil (Masner et al., 2007).

The above facts of the existence of modern representatives of Hymenoptera with a modified CMS, similar (at least externally) to those observed in Haidomyrmex ants, indicate the possibility of such rearrangements of the CMS in different Hymenoptera, and, therefore, are not a unique phenomenon for extinct groups of ants. It is most likely that the movement of the jaws of Haidomyrmecinae was not strictly in the vertical or horizontal planes, but ventral lateral, since it is necessary to open the jaws to the sides in order to work with the basal teeth. This may also be evidenced by divergence of the tips of the apical teeth in species with the longest jaws (see Fig. 3c), i.e., so that the tops of the mandibles do not impede each other's movement when opening the jaws. Moreover,

some features of the jaws of stem taxa of ants testify in favor of the fact that these movements are characteristic not only of Haidomyrmecinae, but also of representatives of Zigrasimeciinae and Sphecomyrminae, at least *Gerontiformica*. It is worth mentioning that the morphological commonality that can be traced in the structure of these stem groups of ants makes relevant the system of phylogenetic relationships, where all three extinct subfamilies are assumed to be a monophyletic branch, proposed at one time by Dlussky (Dlussky and Fedoseeva, 1988; Dlussky, 1996) and later supported in Borysenko's work (Borysenko, 2017). The predisposition to a similar direction of CMS evolution in representatives of these stem taxa seems to be based on several morphological features of stem ants, namely, two-toothed mandibles and weak, imperfect CMS. The two-toothed mandibles of Hymenoptera fix prey and do not allow it to rotate around the axis at the moment of stinging. This is enough for flying predators, even those hunting large prey: the prey is motionless after being stung and fixed during transportation through the air (such behavior can be observed in *Amophila*, for example). But a flightless social predator needs to carry prey to the nest along the substrate, which competitors can still take away on the way. The solution implemented by Sphecomyrminae and other stem taxa is to press the prey against the head capsule (forehead, clypeus), in contrast to recent ants, which clamp objects between the mandibles. It is for this reason that in some Cretaceous Formicoidae, with an increase in the size of the prey, the apical tooth lengthens, the frontal space increases and is reinforced, and the prey is now placed not between the jaws, but between the head and jaws. Thus, an analysis of the diversity of the oral appendages of a dozen species of Haidomyrmecinae revealed the parallel and independent occurrence of recurved elongated mandibles and clypeal outgrowths, "horns," in different genera in this subfamily, and also established a strict correlation between the development of mandibles and the size of the clypeus, which is absent in modern ants (Barden et al., 2020). The apical tooth of the mandibles increases in size, while the basal one remains closer to the base of the mandibles and the mouth opening. In some cases, the basal tooth undergoes some modifications. It is obvious that the basal tooth was used for more precise manipulations, possibly, manipulations with brood, butchering prey in the nest, or when caring for the nest (see Figs. 1a, 3b, 3c, 4e). Thus, large jaws are needed more not as a murder weapon, but as a means of fixing the victim for stinging and then bringing the prey to the nest. Modern ants have powerful jaws and powerful muscles, which is reflected in the size and shape of the head capsule (Fig. 4b, 4c); the second advantage of modern ants is collective hunting, when both protection of prey and its transportation can be carried out by very small individuals with small jaws, independent of the size of the prey (Fig. 5). The jaws of Haidomyrmex ants, despite

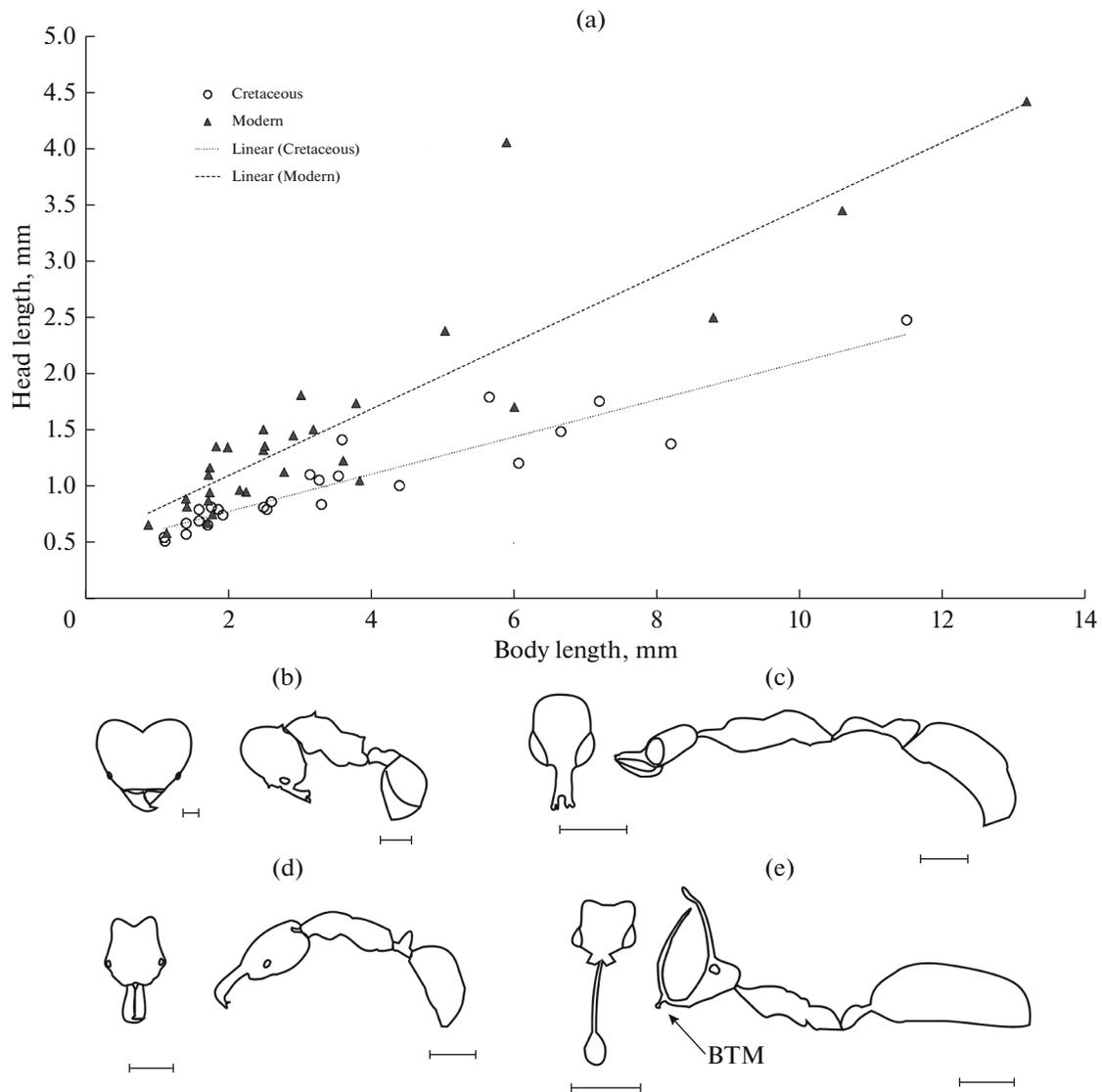


Fig. 4. Size ratios and features of the habitus of recent and Cretaceous extinct ants: (a) the relationship between the length of the head and the length of the body in stem and recent ants; (b–d) contours of the head from the dorsal side and body in profile: (b) *Atta laevigata* (CASENT0922055), (c) *Anochetus* sp. (CASENT0010781), (d) *Aquilomyrmex huangi* (NIGP171999), (e) *Ceratomyrmex ellenbergeri* (NIGP164022, NIGP164022). BTM is the basal tooth of the mandibles. Scale bar: 1 mm, besides (b)—for body 2 mm.

their length, as a rule do not look powerful, and the shape of the head capsule does not reflect an increase in muscle volume (as in modern ants, in contrast to the head outgrowths, “horns,” the size of the head capsule remains relatively small (Fig. 4). The fragility of the jaws of Haidomyrmex ants was also noted by Latke and Melo (Latke and Melo, 2020), in contrast to the thick, rigid mandibles of *Tyrannoscelio*. The jaw concept proposed here suggests that the serrated edge, bristles, and hairs on the head projections are required for prey fixation and control. At the same time, setae and teeth are present both in long-horned and long-jawed Haidomyrmecinae (*Ceratomyrmex*), and in representatives of medium-sized Sphecomyrminae with

small mandibles (*Gerontiformica*), and in the smallest representatives of stem groups with tiny mandibles (*Zigrasimecia*) (Figs. 1b, 1d). Unlike stem ants, in which the jaw remains two-toothed and an increase in the size of the jaw occurs due to lengthening of only the apical tooth, the jaws of modern ants increase along the entire length and the teeth are also distributed along the entire length, due to which they become more powerful (Figs. 1a, 1g, 1l, 1m, 3c, 4e).

Based on the above arguments, we assume that the version of trap-jaws, expressed even when describing the first representative of Haidomyrmecinae (*H. cerberus*) (Dlussky, 1996), is not ideal, since powerful muscles are needed for their implementation, espe-

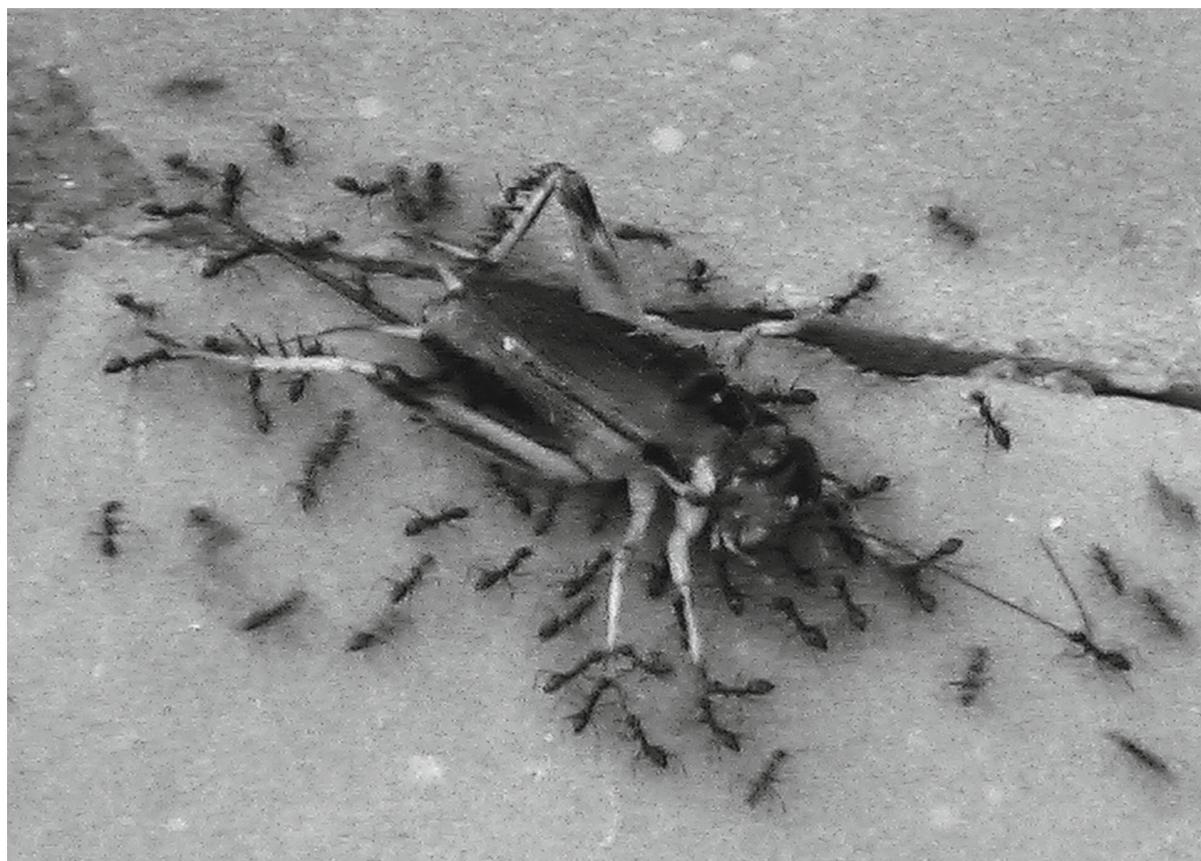


Fig. 5. Collective transportation of large prey by small recent ants includes several stages: detection of prey, mobilization of ants from the nest to prey (killing prey), protection of prey, direct joint transportation, and cutting of prey.

cially if the victim is supposed to be pierced. The hemolymph-feeding hypothesis (Barden et al., 2017) seems poorly substantiated. Firstly, to feed on hemolymph, long and especially curved jaws are not needed (see Figs. 1a, 3b): it is enough to pierce or bite through the victim with a sharp short “tool” (and modern ants perfectly use mandibles of any shape for this purpose (*Mystrium camillae*, *Adetomyrma venatrix*, *Amblyopone silvestrii*, etc.); secondly, it is rather difficult to imagine the process of removing the victim from these “sabers” and their subsequent cleaning; the third argument is that feeding on liquid food implies its transfer to other family members, which is quite difficult with such jaws, and in the concept presented here could not be characteristic of the socially primitive stem taxa of ants. It should also be taken into account that feeding on liquid food involves the transfer of significant amounts of it in the abdomen, which should be stretchable, so it would be interesting to evaluate this characteristic in inclusions. More plausible, in our opinion, is the use of relatively short and strong mandibles for fixation and killing prey (including its piercing), as well as butchering and feeding it like modern representatives of *Myrmoteras* (repeated piercing and consumption of ground substance) (Moffett, 1986).

Nourishment by liquid food in the form of plant exudates and honeydew, apparently, could also be common among stem taxa as additional feeding, as is done by some poneromorphs that do not use oral trophallaxis, but feed “for themselves on the road” or use the (weakly effective) technique of fluid transfer between the mandibles (Paul and Roces, 2003).

In the same vein, the structure of the unique mouth armament of *Zigrasimecia* can be considered: bristles or chitinous brushes are not evidence of the unique way of hunting (or prey) of these ants, but only a way to hold the soft bodies of small invertebrates, which, apparently, could make up the diet of the smallest ants with body lengths of about 2 mm, as well as other soft invertebrates in the case of larger ant species. The authors of the description of *Zigrasimecia hoelldobleri* and *Protozigrasimecia chauli* also consider small invertebrates to be their most likely prey (Cao et al., 2020b). The presence of a stinger and a powerful relief of the head capsule in such a small insect are more likely evidence of predation than feeding on liquid food, as some authors suggest. In the case of *Zigrasimecia*, it is very successful to compare the mechanism of operation of the oral appendages with the operation of the upper and lower jaws of fish, since the

flat mandibles on different sides of the body are complementary in shape and can fit tightly to each other, forming a single plane.

Crown taxa took a different path, manipulating objects only between the mandibles without involving the head capsule, and achieved success by varying the size, shape, and number of teeth of the mandibles, on the one hand, and the volume and muscle groups of the craniomandibular system, on the other.

The appearance of an acidic gland with the ability to spray acid in some crown groups was also associated by Wilson and Hölldobler with a change in diet (types of prey?), but the relationship between diet (change in type of prey) and this ability has not been characterized (Wilson and Hölldobler, 2005). It seems that the ability to spray acid can be required only with coordinated collective actions; it is more effective for a single hunter to have a sting. Although the excellent work of Smith (Smith, 2019) has demonstrated the benefits of *Formica archboldi* acid attack against the powerful and strong solitary hunter *Odontomachus brunneus* with trapping jaws, acid attack is still a good defensive strategy to protect food resources and nests in highly social ants: as both a poisonous agent and alarm signal (Yakovlev, 2010). It is possible that the appearance of the acid gland and the ability to disperse the secretion is associated with sociality to a greater extent than with diet. This is evidenced by the fact that not only Dolichoderinae and Formicinae subfamilies have this ability, but it is the highly social members of the Myrmicinae, such as *Crematogaster*, that have also acquired it.

*Oryctocenosis of Burmese Amber as a Model
of the Process of the Origin of Modern
Myrmecocomplexes. Gibson's Principle. Ethologic-
Ecological Hypothesis of the Emergence of Ant Crown
Groups and Their Evolutionary Success*

There is no doubt that the biodiversity of Burmite paleobiocenoses is very high. It can be said that the modern biocenoses of this territory are direct “descendants” of the Cretaceous. Nevertheless, the taxonomic composition of ants from burmite and in similar modern ecosystems of this region at the subfamily and generic levels is different. What are the reasons for the change in taxonomic composition? The change in the flora of gymnosperms is undoubtedly an important factor, but in itself it does not explain the cardinal change of stem taxa to crown taxa, as glacial cycles and thermal optima (and with them a change in the floristic composition of biocenoses) in the Cenozoic led only to a change in the prevailing groups, but not to a change in the morphological “construction” of Formicidae. To explain the hypothesis expressed here, we resort to the introduction of Gibson’s principle, **as a short formulation known in morphological evolution, the evolution of biocenoses, and the evolution of sociality** (Treanore et al., 2021) (and, most likely, a common feature of evolution at all its levels of organization:

molecular evolution, evolution of ontogeny, and macroevolution) **of a tendency for the formation of something new not “immediately” and not “gradually,” but mosaically, in the course of sorting through combinations of elementary units of “construction.”** In the evolutionary history of the biota, examples of parallel morphological evolution in different (sister) phylogenetic branches are well known: for example, “ornithization” traits characteristic of birds, “mammalization” of mammals, and “arthropodization” of arthropods. The effect of the influence of certain conditions of biotic relationships and the common genetic (ontogenetic) environment in phylogenetically (and, consequently, structurally) close organisms leads to the emergence of a similar direction of evolution. In turn, new adaptations change biotic interactions, i.e., the very environment in which evolution takes place, making it more acceptable for taxa that accumulate the whole complex of adaptations. The famous quote by American-Canadian science fiction writer William Gibson: “The future is already here. It’s just not evenly distributed yet,” characterizes these evolutionary phenomena in the best possible way. According to Gibson’s principle, we propose a hypothesis of the origin and formation of the modern biocenotic role of ants under the conditions of food (ecological) specialization of ant stem taxa and the emergence of a complex of key adaptations of ant crown taxa using the example of Myanmar paleocenoses. Being an active, diverse group, ant stem taxa “created” an adaptive space divided between themselves into ecological subniches, keeping out other active arthropod predators. It can be assumed, in accordance with Gibson’s principle, that ant stem taxa during the Cretaceous demonstrated the process of “formicoidization”: various characteristics of the morphological structure and social organization in different combinations. However, a set of key adaptations, i.e., the possibility of collective behavior (mobilisation), effective communication, coordination of actions at the colony level, and the construction of the craniomandibular system and antennas, as a result of interrelated morphological changes and behavioral patterns, was fully manifested namely in crown groups of ants, which made it possible for the latter to become generalists, but at the same time more effective predators than ants of stem taxa. All this gave competitive advantages over stem-group specialist ants. Indeed, food specialization in modern ants is: (a) in some taxa with a primitive social structure, with small families (where tendencies to increase the relative size of the jaws often persist, often the same inhabitants of the ground litter and upper layers of the soil: Myrmicinae and Ponerinae); (b) in specific environmental conditions with the strict limitation of layering and resources, for example, deserts (differentiation in absolute sizes of working individuals between species); (c) formed much later in tropical forests with a predominance of mortmass, namely, among fungus-growing specialized ants. The taxa of

ants that dominate modern ecosystems are species with large colonies (developed social organization, a communication system, and protected territory) with a wide food spectrum, which includes the maintenance of honeydew insects (developed forms of trophallaxis) and collective predation that is not specialized in prey. Most likely, none of the listed items can be afforded to ants with primitive social organization. The habitus of an effective terrestrial fast flightless herpetobiont predator (dendrobiont) and the social structure contributed to the autocatalytic process of perfecting a new life form. At this moment, apparently, there occurs the radiation of crown taxa according to G.M. Dlussky, i.e., adaptation of the new form to different biocenotic layers with the displacement of stem taxa. Despite specialization, ants of stem taxa cannot hold their positions, because it has been shown that improved social skills contribute to more efficient retention of food resources (i.e., their monopolization) both in the community of modern ants and in Hymenoptera in general (Putyatina, 2011; Zakharov, 2015; I'Anson Price et al., 2021). Thus, for example, "the ability of a family to eat from a large food source is affected by: the efficiency of searching for food; mobilization efficiency; the number of individuals mobilized for food and the aggressiveness of the species in the fight for the resource" (Putyatina, 2011), and these characteristics, in turn, reflect the level of social (communicative) intrafamily skills, but not the size of the jaws. Thus, poneromorphs were not pushed aside from the main positions, as the hypothesis of succession suggests, but always occupied the same place (where they originated) as now, where the resource base allows the existence of small families of social predators (sometimes specialized) with a single type of foraging with a small proportion of carbohydrates in the diet: geobionts, stratobionts, and herpetobionts in the rich (forest) biocenosis of a warm climate.

Based on the stated logical premises and morphological analysis, the ethologic-ecological hypothesis is as follows. Representatives of ant stem taxa had less perfect communication ability, less effective CMS, and more visual-spatial orientation than olfactory, which blocked the development of sociality based on odor stimuli (development of communication skills, increase in family size, polyethism and polymorphism). Due to their weaker communicative organization, their ecological role as predators among insects (arthropods) in conditions of abundance and diversity of resources leads to adaptive radiation through food specialization, which is a common trend in evolution among insects (including solitary Hymenoptera), and, in particular, in modern ants with primitive social organization. Food specialization, in turn, against the background of a running, not flying, life form with poorly developed communicative ability and a specific two-toothed craniomandibular system, the absence of a developed caste structure of the family determines

the adaptive morphological evolution of species: diversity and relative sizes of jaws; sizes of individuals. A complex of key adaptations of crown groups, i.e., the possibility of complex communication and coordination of actions and morphological features of the craniomandibular system and antennae, arises with strengthening of the role of olfactory analyzers based on a running, well-oriented in three-dimensional space, social herpetobiont insect and leads its owners to create effective nonspecialized predators, which gained the ability to control the resource base and, thanks to trophallaxis, use and redistribute a new resource in the family, i.e., liquid food rich in carbohydrates (Hemiptera honeydew and nectar).

In the adaptive space created by the stem taxa of ants, the ecological niches divided by experts in terms of size and type of prey are "formatted" in a new way by representatives of crown groups: a system of subordination arises, understood for modern ants as dominance (dominant species, subdominant species, and influents), where the type and size of prey at the species level is determined not by the size of the jaws, but by the size of the colony (Kaczmarek, 1953; Reznikova, 1980; Zakharov, 1991, 1994, 2015). However, thanks to a perfect CMS and polyethism (polymorphism), under conditions of efficient distribution of food and division of functions within the family, the jaws of ants can be modified for specific tasks even within the colony (colony polymorphism: workers and soldiers).

Thus, it seems that the change in the myrmeco-fauna of stem taxa to the modern one did not occur due to a change in diet (due to the consequences of the replacement of gymnosperms by angiosperms), as suggested in the dynastic-succession hypothesis, but due to the formation of a new progressive group of ants. The change in diet (in particular, the use of liquid food), in turn, was a consequence of the morphological and ethological evolution of crown taxa. Since, according to Gibson's principle, the environment was "prepared" by the mosaic distribution of traits and characteristics among specialized ant stem taxa for the appearance of the trait complex implemented in crown ants, stem taxa, less perfect in this space, could not withstand the competition.

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COMPLIANCE WITH ETHICAL STANDARDS

I declare I have no conflict of interest.

This article does not contain any studies using warm-blooded animals as subjects.

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