Description of a new genus of primitive ants from Canadian amber, with the study of relationships between crown ants and stem ants (Hymenoptera: Formicidae)

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Abstract

A detailed study of the holotype of *Sphecomyrma canadensis* Wilson 1985 from Canadian amber led to the conclusion that the specimen belongs to a genus here named *Boltonimecia* gen.nov. not previously described. The taxonomy of stem ants is not clearly understood; thus, in order to find the taxonomic position of the new genus, it was necessary to review the classification of stem ants in a study of their relation to crown ants. Lacking morphological data for traditional taxonomic approaches, a statistical study was done based on a morphometric analysis of antennae. The elongation of the scape is believed to play an important role in the evolution of eusociality in ants. However, this hypothesis has never been confirmed statistically. Our statistical analysis lends support to the view that the morphology of antennae reliably distinguishes stem ants from crown ants to determine whether a species belongs to one or the other group. This in turn may indicate the relationship exists between eusociality and the elongation of the scape. A review of Cretaceous records of ants is made and the higher classification of Formicidae with definitions of stem and crown groups is proposed. The newly obtained data are discussed focusing particularly on the origin, evolution and diversity of ants.

Introduction

Mammals and birds immediately come to mind when thinking of groups of animals that began to flourish after the Cretaceous–Paleogene extinction event. However, ants also started to flourish at this time. Ants were rare in the Late Cretaceous but in the Cenozoic these insects underwent an impressive radiation to become one of the largest and most widespread of terrestrial animals (Hölldobler & Wilson 1990).

There are poor quality impressions of Cretaceous ants found in sedimentary rocks, and rare specimens are also preserved in amber (reviewed in LaPolla *et al.* 2013). Among only a handful of amber sites known to contain ants, Canadian amber is of a special interest: dating from a part of the Campanian, 78–79 million years (Ma) old (McKellar & Wolfe 2010), it contains traces of one of the most late Cretaceous ecosystems flourishing in North America only 10 Ma before the Cretaceous–Paleogene (K-Pg) extinction event.

It is noteworthy that both crown ants (i.e. the descendants of the most recent common ancestor of all extant ants) and stem ants (i.e. all extinct taxa outside the crown clade but most closely related to it than to other Aculeata) are found in Canadian amber. The two groups lived together for at least 10 Ma but only in Canadian amber are they found in almost equal numbers. Of these ants, four species represent recent subfamilies Dolichoderinae (*Eotapinoma macalpini*, *Chronomyrmex medicinehatensis*) (Dlussky 1999a; McKellar *et al.* 2013a), Ectatomminae (*Canapone dentata*) (Dlussky 1999a), Aneuretinae (*Cananeuretus occidentalis*) (Engel & Grimaldi 2005) and at least three species represent the extinct subfamily Sphecomyrminae: *Sphecomyrma canadensis* (Wilson 1985), *Haidoterminus cippus* (McKellar *et al.* 2013b), *Sphecomyrma* (?) *sp*. (Grimaldi *et al.* 1997).

The present paper focuses on the holotype of *Sphecomyrma canadensis* held in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC). Some authors noted that the description of *S. canadensis* is unsatisfactory, no character of *Sphecomyrma* is visible (Dlussky 1996; Grimaldi *et al.* 1997; Engel & Grimaldi 2005) and the holotype and the paratype are irrelevant to one another (Dlussky 1999a).

Examining the holotype, we found the head, mandibles and the antennae's distal parts almost invisible and so establishing a link to *Sphecomyrma* impossible. After the amber was polished, visibility improved and some details of the ants' morphology could be seen. What had seemed to be a black inclusion hiding the head, could be identified as a thick raised platform, a unique morphological structure. The head also have lateral protrusions posterior to the insertion points of the antennae. Because of these morphological characteristics, we decided to treat the specimen as belonging to a genus not previously described.

The next step was to find a taxonomic position for the new genus, which because of the unsatisfactory state of stem ant taxonomy is not an easy task. Classification of stem ants is still in its infancy because there is very limited morphological data, and molecular data are impossible to obtain. Stem ants have never been a subject of a general revision, and only twice were they included in morphological cladistic analyses (Baroni Urbani *et al*. 1992; Grimaldi *et al*. 1997). At the moment, they are assigned to two poorly supported subfamilies, Sphecomyrminae and Armaniinae (Bolton 2003), but some species, such as *Gerontoformica cretacica* Nel & Perrault, and *Myanmyrma gracilis* Engel & Grimaldi, are so bizzare that they cannot be assigned even to these subfamilies and are left as insertae sedis (Nel *et al*. 2004; Engel & Grimaldi 2005). There is also a long-standing debate regarding the taxonomic status of Armaniinae, which represent either the most basic stem ants (Dlussky 1983) or are the sexuals of Sphecomyrminae preserved only in rock impressions due to their large size (Wilson 1987). The new genera described recently (*Zigrasimecia*) are causing uncertainty as well (Barden & Grimaldi 2013). The absence of sufficient morphological data creates a need to invent new methods of taxonomic analysis based on principal differences between stem ants and crown ants.

In an attempt to fill this void, we chose Dlussky's (1983) approach suggesting that the antennal morphology can be a diagnostic tool to distinguish stem ants from crown ants, carrying out statistical analysis of antennal indexes. This idea was first expressed by Wilson, Carpenter and Brown (1967) in their diagnosis of Sphecomyrminae, and later explained in terms of evolutionary history and expanded by means of comparative analysis by Dlussky (1983). Since then, antennal characteristics have been used in diagnoses of stem-ant subfamilies, including Bolton's system (2003), the most comprehensive for the time being. That they have never been tested by means of statistics, is surprising considering the highly interesting biological background of Dlyssky's hypothesis: the elongation of the scape was necessary for the emergence of eusociality in ants (Dlussky 1983).

The final logical step of such a study was to develop the higher classification of ants including both stem and crown branches. Developing the crown group/stem group distinction, affects our thinking about ant origins; the importance of taking some definitive position has been overlooked in previous discussions on this topic (Ward 2007).

Material and methods

Study of amber inclusion. Photographs were taken with a Nikon D1X digital camera attached to the microscope Leica Z6 APO. Photographs were used to make drawings, which were then computer generated and adjusted using Adobe Photoshop. All measurements were made using an ocular micrometer and are in millimeters (mm). The following measurements were recorded: HL - head length (measured in full-face view as a straight line from the anterior-most point of median clypeal margin to the mid-point of the posterior margin of the head), HW - head width (maximum head width in full-face view), SL - scape length (maximum length without the condyle and the neck) F1L-F9L - length of flagellomeres (from 1st to 9th), AL - antenna length, ML - mandible length (maximum length of horizontal part of a mandible), WL - Weber's length (the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum), TL - total body length.

Taxon sampling and morphometry. We took all morphometric data on antennae and heads of stem ants available from the literature; also we either made measurements or took published data on antennae and heads of crown ants representing all extant subfamilies (Table S1). Only species of crown ants with a satisfactory description in the literature and high resolution images with good visibility of all antennal segments (available from AntWeb) were selected. Also, species were selected in such a way that they represent broad phylogenetic diversity. If a subfamily has high diversity, we tried to choose representatives with SL between the extremes (so that SLs are near to the SL mean for that given subfamily). For example, in our data the minimum value of SL is in *Pseudomyrmex pallidus*; SLs in representatives of Myrmicinae and

Formicinae 2-3 times higher, although the minimum values in those subfamilies may be even smaller than in *P. pallidus*. All subfamilies are represented by one species, except for the largest subfamilies (Ponerinae, Dolichoderinae, Formicinae, Myrmicinae) represented by two species. Recently, six subfamilies of the dorylomorph group have been subsumed into a single subfamily, Dorylinae (Brady *et al.* 2014), but here in order to cover larger variation we sampled all six subfamilies as valid groups.

Measurements were made on mounted specimens using a Wild M10 stereomicroscope with an accuracy ±1 µm. For all stem and crown ants we calculated nine indexes showing size of antenna's parts compared to the head length (indexes SL/HL, FL/HL, PL/HL, F1L/HL, F2L/HL) and compared to the rest of antenna (indexes SL/FL, PL/(AL-PL), F1L/(AL-F1L), F2L/(AL-F2L)) (Tables S2, S3). In those indexes, HL – head length (see definition above), SL – scape length (see definition above), FL – length of flagellum (including pedicel), PL – length of pedicel, F1L and F2L – length of 1st and 2nd flagellomeres respectively. Although F1 is in fact the second flagellar segment, the pedicel being the true first, we call it "first" throughout the paper to make a clear distinction from the pedicel; thus our nomenclature follows that of Barden and Grimaldi (2012, 2013). For indexes we always used HL, not HW, as HL is available for more fossil species; in addition, using HL, our data can be compared with Dlussky's data on antennal morphometry (Dlussky 1983, Dlussky and Fedoseeva 1988). Two additional indexes AL/HL and SL/AL (where AL – antenna length, SL – scape length) were used only to compare obtained data with Dlussky’s data on Vespoidea and Apoidea (Dlussky and Fedoseeva 1988).

For general observations on the shape of pedicels, the morphology of the middle and terminal antennal segments, we used high resolution images available from AntWeb. To study the width of the petiolar attachment of Armaniinae, we calculated the index PG/PH (where PG - the width of the petiole in the broadest point of its attachment to the gaster; PH - the maximal height of the petiole).

Statistical analysis. Two statistical tests on equality of means were performed using the SPSS 17.0 statistical package: the Student's t-test and one-way ANOVA with planned comparison. The log transformation was applied in those cases where substantial heteroscedasticity and non-normal distribution were observed. Also, a correlation and regression analysis as well as a canonical discriminant analyses were performed using the SPSS 17.0.

The power analysis was performed using the G* Power 3 program (Faul *et al*. 2007). Despite the lack of sufficient data on extinct taxa, in all cases where the t test showed statistically significant results, the statistical power was also high enough. However an unbalanced design in an ANOVA could be be a problem (McDonald 2014). Indeed, the results showed that the unbalanced design in which extinct ants are underrepresented, had low statistical power. In such a case, the only way to confirm the reliability of the obtained results is to reduce big groups to the size of the smallest group, and run the power analysis and ANOVA again. Doing this, we obtained very high values of the statistical power with the results of ANOVA almost identical to that of the unbalanced design.

The next concern about the reliability of the obtained statistical data is a measurement error. Since the measurements of extinct taxa were taken independently by different persons, with different material and calibration, those slight differences might presumably alter the obtained conclusions. To check how strongly our statistical results are sensitive to fluctuations, we added/ subtracted 10% (a considerable measurement error) to/from the indexes and to/from the measurements. To insert these modifications randomly, we used a random number generator. Then the modified data were again used in ANOVAs and t tests. In all cases no noticeable effect was observed, the statistical model proved to be robust and not sensitive to fluctuations. Caution, as always, should be taken about data on the verge of statistical significance.

Systematic palaeontology

Family Formicidae Latreille, 1809

Subfamily Sphecomyrminae Wilson & Brown, 1967
Tribe Boltonimeciini trib.n.

Type genus Boltonimecia gen.n.

Diagnosis (workers): see chapter "Higher classification of ants".

Genus *Boltonimecia* gen.n.

Type species: *Sphecomyrma canadensis* Wilson 1985

Diagnosis. As for the tribe.

Etymology. This genus is dedicated to the renowned English myrmecologist Barry Bolton.

Boltonimecia canadensis (Wilson 1985) comb.nov.
Figs 1, 2

Sphecomyrma canadensis Wilson, 1985: 206, figs. 1, 2 (w.)

Material examined. Holotype. Worker is preserved in a clear orange small (8×3×2 mm) piece of Canadian amber (chemawinite/cedarite) from Medicine Hat, Alberta (J.F.McAlpine, CAS 330), held in the CNC, Ottawa, Canada. Visibility is excellent from all directions, but for the ventral side which is clouded. Preservation of the ant is excellent, although mesosoma, left flagellum and right side of the head are somewhat distorted (flattened) due to amber compression, and junctions of both scapes with the pedicels are gone.

The specimen known as the paratype of *Sphecomyrma canadensis* (Wilson 1985) (CAS 205 held in CNC, Ottawa, Canada) represent body fragments of very poor preservation, with no taxonomic characters visible, and thus should not be considered as the paratype and left as an unidentifiable ant.

Diagnosis. As for genus.

Description. HL 0.73 mm; HW 0.8 mm; SL 0.5 mm; ML 0.48 mm; WL 1.2 mm; TL 3.4 mm.

The head is small compared to the body length (1/5 of its length), subglobular, prognathous, slightly broader than longer, seems to be triangular when seen from the top, and formed into a shield: its dorsal part thick, raised, curved in profile (Fig. 2B, C, D). Such shield-like head is likely formed by the expanded frontal lobes. Under posterolateral edges of the expanded frontal lobes, on both side of the head, there are two sticklike processes directed anterolaterally; they limit the mobility of the antenna posteriorly, so that when a scape pressed to the head and lifted, it touches a process. Eyes and ocelli absent. The wierd processes are hardly deformed eyes, since there is no trace of facets visible, plus processes are completely covered by appressed pubescence similar to that on the front of the head. The clypeus is not large, in profile strongly convex. The convex medial part of the clypeus is highest, it gradually declines towards the lateral margins. Lateral margins of the clypeus bear semitransparent semicircular projections, covering the insertions of mandibles. Clypeus posteriorly not inserted between antennal sockets. The anterior clypeal margin bears 25 peg-like setae 0.01 mm long. The width of the clypeus 0.5 mm (without the lateral semicircles), length - 0.15 mm.

Mandibles linear, two toothed, curved at almost 90°. The apical tooth is longer than preapical - 0.15

mm and 0.06 mm respectively. On the inner side of the apical tooth there is a longitudinal impression, which probably fits the other mandible when mandibles are closed. When fully closed, the mandibles overlap at half the length of their horizontal parts. The length of the horizontal part of mandibles is 0.48 mm, vertical - 0.17 mm.

Antennae 11-segmented. The scape hardly reaches the occipital margin. The measurements of antenna (mm): SL - 0.5, PL - 0.2, F1L - 0.15, F2L - 0.2, F3L-F8L - 0.17, F9L - 0.25, AL - 2.32. Insertions of antennae are not far from each other (0.17 mm), partly exposed under the anterior side of the expanded frontal lobes, touching the posterior margin of the clypeus. Toruluses not fused to the frontal lobes. Antenna moves in a special fossa bounded laterally by the expanded frontal lobes, and posteriorly by the sticklike process.

The metanotal groove visible. The propodeum located a little bit lower than the promesonotum, without teeth or spines, its basal surface slightly shorter than the declivity. Propodeal spiracles located high, in the upper half of the propodeum. The metapleural gland orifice covered by guard setae.

Petiole pedunculate, 0.4 mm long; peduncle 0,1 mm long, node 0.2 mm high. The anterior part of the peduncle is narrow (the width of its attachment to the propodeum is about half the height of the node); posterior foramen more broad.

Gaster subglobular, 1.1 mm long. Helcium projecting below the midheight of the anterior face of abdominal segment III, which has vertical and relatively high anterior face. Abdominal segment IV without presclerites. Sting present; visible length 0.05 mm.

Legs long - 3.3 mm forelegs (shortest), 5.07 mm hind legs (longest, 1.5 of body length). Measurements of leg segments shown in Table 1. Pretarsal claws with one preapical tooth (Fig.1D). Each tarsal segment has two stiff setae on both sides of its apex. Basitarsus with notch and comb for cleaning the antennae. Protibia with one pectinate and two simple spurs, while meso- and metatibia with one pectinate and one simple spur (Fig. 1E).

The dorsal surface of the head as well as antennal fossae covered with dense short appressed pubescence. Sticklike processes covered with very short and hardly visible appressed pubescence. The lateral margins of the head covered with erect and suberect hairs. Antennae covered with dense short appressed pubescence. Long standing sensory hairs project anteriorly from anterior margin of the clypeus, from its middle part, and from anterior margin of the expanded frontal lobes; some of those hairs are so long, that they go beyond the closed mandibles. The external margin of each mandible covered with suberect hairs. Short appressed pubescence completely cover mesosoma, legs and gaster. In addition, middle and hind tibia covered with sparse suberect hairs; small bundles of erect hairs project from the apex of the middle and hind femurs; ventral surfaces of coxae covered with long erect hairs; pronotum and propodeum covered with long white erect hairs tapering to sharp points (especially long on pronotum); abdomen covered with sparse suberect hairs, longer on the ventral surface.

Sculpture invisible. The entire body is transparent, colored as surrounding amber, but the ventral surfaces of coxae, abdomen, proximal halves of tibiae, lower half of propodeum are brown to black. The dorsal surface of the head and pronotum black, opaque.

Discussion. Some authors noticed that *Sphecomyrma canadensis* has no synapomorphies of *Sphecomyrma* - namely a short pedicel and 2nd flagellomere two or more times longer than other flagellomeres (Dlussky 1996; Grimaldi *et al.* 1997; Engel & Grimaldi 2005). Dlussky & Fedoseeva (1988) even suggested that this species has "formicoid" antenna (or at least antenna transitional towards formicoid type), unlike *Sphecomyrma* which has "sphecoid" antennae, so *S. canadensis* has to be assigned to its own subfamily.

After polishing the amber of the holotype, I uncovered even more differences of the specimen from all known Cretaceous ants.

B.canadensis has 11-segmented antennae, a unique character of Cretaceous ants (the statement of McKellar *et al.* (2013b) that *Haidomyrmex* and *Haidomyrmodes* have 11-segmented antennae is erroneous).

A small proximal part of both scapes of *B.canadensis* is missing because of amber destruction, but the articulation of the scape and pedicel of the left antenna is intact and thus one can confidently infer about the scape length. The visible articulation is not an articulation between pedicel and F1 because (1) pedicel's curved base (distinct character of a pedicel only and a point of its attachment to the scape) is clearly visible, (2) localization of the scape and flagellum infers that there is no room left for one more antennomer between them. In general, the relative size of the antennomeres are not diferent from the Wilson's drawings (Wilson 1985). The only exception is the distal parts of the antennae, which are curled back under the head and were almost invisible before polishing; this probably led to Wilson's assumption about 12-segmented antenna as in *Sphecomyrma*.

The most distinctive character of *B.canadensis*, which immediately sets it apart from all fossil and recent genera is a morphologically unique head: thick shield-like head, sticklike head processes, long sensory hairs. Although the left side of the head is flattened due to amber compression, the processes are clearly visible on both sides of the head.

Some Myrmicinae, *Aulacopone relicta* (Heteroponerinae) and Agroecomyrmecinae, have shield-like heads formed by the expanded frontal lobes. In Myrmicinae, the clypeus usually inserted between antennal sockets, unlike *B.canadensis.* In *A. relicta* the clypeus is shallow, but antennal insertions close together, and the fronto-clypeal part of the head is extended forwards and hangs over the mandibles (Taylor 1980), unlike *B.canadensis*. Species of enigmatic subfamily Agroecomyrmecinae have shield-like heads; in addition, in arboreal *Ankylomyrma coronacantha* the occipital margin of the head bears weird spiniform processes projecting especially strongly at the occipital corners (Bolton 1973), that resembles specialized head of *Boltonimecia*. However in Agroecomyrmecinae the clypeus is large and broadly inserted between the frontal lobes. Most Ponerini have a clypeus not inserted between antennal sockets, but their fused frontal lobes form only a small triangle or linear strip partially covering the sockets, never occupying the entire dorsal part of the head. In Proceratiinae, clypeus reduced, and antennae inserted close to the anterior margin of head. Some Proceratiinae (*Dyscothyrea*) have frontal lobes fused together and forming small raised platform behind the level of antennal sockets, the sides of which are strongly convergent anteriorly (Bolton 2003). Also in Proceratiinae as well as in *A.relicta*, and in Agroecomyrmecinae the frontal lobes take part in the formation of antennal scrobes, absent in *B.canadensis*. In any case, it is important to emphasize that such morphological similarities between crown ants and stem ant *B.canadensis* are likely acquired by a parallel evolutionary process.

Any assumption about lifestyle of *B. canadensis* reflected in its bizzare head morphology, can be very speculative. The lack of eyes and ocelli, as well as multiple sensor hairs on the anterior margin of the head may imply cryptic lifestyle. However, extant blind ants are not always exclusively subterranean (e.g. *Dorylus*). Long legs of *Boltonimecia* speak in favor of above-ground or arboreal lifestyle. I also do not reject the possibility that the eyes of *Boltonimecia* could be reduced to a single facet, and thus simply invisible in amber inclusion.

Determining the phylogenetic place of *Boltonimecia*, we cannot avoid the study of classification of stem ants and their relationship to crown ants. That is a difficult task still absolutely unexplored.

What is the difference between stem ants and crown ants?

We realized the distinction between crown group and stem group with the launch of phylogenetic approach to taxonomy (Hennig 1966). Crown group is a clade that consists of the living species together with their ancestors back to their most recent common ancestor, while a pan group or total group is the crown group and all organisms more closely related to it than to any other extant organisms. From this definition, stem group is just the total group minus the crown group. It is important to emphasize that stem group, contrary to the crown group, is not a taxa - it is an artificial assemblage, a paraphyletic group (Ax 1985).

Here I treat ant subfamilies Sphecomyrminae and Armaniinae, as well as insertae sedis genera

Gerontoformica and *Myanmyrma* as stem ants. This idea will be expanded further in details.

Extant ants (i.e. crown ants) have four commonly accepted synapomorphies: elongated scape, petiole, metapleural gland, and the non-morphological trait of eusocial behavior, which is expressed morphologically in caste differences between queens and workers (LaPolla *et al*. 2013).

Out of characters thought to be plesiomorphic for Formicidae, and helpful in distinction between stem ants and crown ants, the following ones are mentioned most often: a wide attachment of the petiole and the gaster, pretarsal claws with preapical tooth, bidentate mandibles, two spurs on meso- and metatibiae, short scape, trochantellus, anterial clypeal peg-like setae, and ocelli. It would be useful to review briefly all of them.

Petiole of non-ant Vespoidea is less pronounced and more broadly attached to the gaster than in most Formicidae, except for only one ant subfamily, Amblyoponinae. Thus a broad petiolar attachment can be viewed as a reliable plesiomorphic character. It follows from the direction of ant evolution, highlighted in an increase of the gaster mobility and as a result in an ease of mesosoma-gaster articulation. If the ancestor of all ants possessed a wide attachment of the petiole and the gaster, all presently known stem ants should be viewed as quite advanced, because they all have narrow petiole-gaster attachment, as most crown ants (the issue of petiole of Armaniinae ramains open and I will come back to it below).

Preapical tooth on pretarsal claws present in many crown ants: poneroids and primitive members of the formicoid clade (Myrmeciinae, Pseudomyrmecinae, Dorylinae) (Dlussky & Fedoseeva 1988). This character is common in other families of Vespoidea, and are present virtually in all stem ants.

Bidentate mandibles is a very common character in Vespoidea and Apoidea and universal for stem ants. It is believed that in females of crown ants this character is a result of reduction of initial triangular mandibles (Dlussky & Fedoseeva 1988). In crown ants, this character is mainly present in poneroids and primitive formicoids, being quite rare in advanced formicoids - Formicinae, Myrmicinae, Dolichoderinae (Bolton 2003, Appendix 2). In males of crown ants, this character is usual, although it is not as pronounced as in other Vespoidea, and is again most likely the result of teeth reduction. Such a reduction in males may be linked to the fact that they do not feed outside a nest. As in females, in males of the formicoid clade this character is not as usual as in males of the poneroid clade: in Formicinae and Myrmicinae it present in 1/4 of genera; rarely present in males of Dolichoderinae, ectaheteromorphs, Pseudomyrmecinae; absolutely absent in males of Myrmicinae, but usual in Dorylinae (Bolton 2003, Appendix 2).

Two spurs on the meso- and metatibia (one of which may be pectinate) are usual in poneroids and primitive formicoids (Bolton 2003, Appendix 2), as well as in other families of Vespoidea, although pectinate spur of metatibia is found only in ants and Tiphiidae (Brothers 1975). This character present in all stem ants. *Haidoterminus cippus* was reported with a single metatibial spur and two mesotibial spurs (McKellar *et al*. 2013b) that most probably is a result of poor preservation of legs, as such a condition is unknown for Formicidae.

Trochantellus absent in crown ants, except putative Cretaceous crown group species *Cananeuretus occidentalis* (Engel & Grimaldi 2005). In stem ants, trochantellus is present in one species of *Haidomyrmex* (*H. scimitarus*) (Barden & Grimaldi 2012), *Haidoterminus cippus* (McKellar *et al.* 2013b), both species of *Zigrasimecia* (Barden & Grimaldi 2013; Perrichot 2014), some species of *Sphecomyrmodes* (Barden & Grimaldi 2014), and also in males of *Baikuris* (Dlussky 1987; Grimaldi *et al*. 1997; Perrichot 2015). In Armaniinae, this character is unclear as a result of poor preservation of rock impressions: *Armania* and *Pseudarmania* have been reported either with or without a trochantellus (Dlussky 1983; Wilson 1987; Dlussky & Fedoseeva 1988). In general, trochantellus is not often present in Vespoidea (Rhopalostomatidae, some Vespidae).

Clypeal peg-like setae are thought to be an important ant plesiomorphy (Engel & Grimaldi 2005). In stem ants, this character is present in *Sphecomyrmodes*, *Boltonimecia*, *Gerontoformica*, *Myanmyrma*, *Zigrasimecia*; in crown ants - in Amblyoponinae. Peg-like setae on anterior clypeal margin present in some Vespoidea, for example in *Myzinum* (Tiphidae), and on anterolateral margins - in *Apterogyna*

(Bradynobaenidae).

Ocelli in workers are often considered as ant plesiomorphy (Engel & Grimaldi 2005). In crown ants, this character is well known in extant ants, mainly in the formicoid clade: Myrmeciinae, Pseudomyrmecinae, Dolichoderinae, Formicinae, some Dorylinae, but absent in some Cretaceous genera (*Eotapinoma*, *Chronomyrmex*, *Kyromyrma*). In stem ants, ocelli present in some Sphecomyrmini.

Therefore all mentioned characters, which can be used to separate stem and crown ants, are not universal and reliable. As noted by Dlussky (1983), the most reliable character may be an elongated scape of crown ants, compared to a short scape of stem ants. Scape elongation in crown ants follows from biological feasibility: long scape favours eusociality, since it allows brood and food manipulation (Dlussky 1983). Below I examine this character, along with other morphometric characteristics of antennae, in details.

The antennal structure as a hallmark of distinction between stem ants and crown ants

The scape length of more than 25% of the antennal length is thought to be a characteristic of extant (i.e. crown) ants (Dlussky & Fedoseeva 1988), although in the diagnosis of Sphecomyrminae Bolton (2003) stated that a "short scape" of Sphecomyrminae means “0.25 times length of flagellum”. The role of other antennal parts in distinguishing stem ants from crown ants may be no less important.

The pedicel of all insects contains Johnston's organ - a mechanosensory chordotonal organ responsible for hearing, graviception (Kamikouchi *et al*. 2009) and electric field changes which may play a role in social communication (Greggers *et al*. 2013). According to Dlussky & Fedoseeva (1988), the pedicel in crown ants is shorter than in stem ants, it is narrowed and curved at the base. This enables close contact of the pedicel and scape resulting in greater freedom and accuracy of movement of the flagellum, which together with scape elongation led to the emergence of eusociality in ants (Dlussky and Fedoseeva 1988).

The first segment is the longest flagellar segment in stem ants, males of primitive crown ants (Dlussky 1983), and the Aculeata closely related to ants (Engel & Grimaldi 2005); so it is a a symplesiomorphic character (Engel & Grimaldi 2005). Bolton (2003) listed this characters as a synapomorphy of Sphecomyrmini (while the longest flagellar segment in Haidomyrmecini is the second one). In crown ants, the first and second flagellomeres are not different from the other flagellomeres, except for the elongated terminal one (Dlussky & Fedoseeva 1988).

In stem ants, segments beyond the second flagellomere decrease in length towards the apex of the antenna, while in crown ants they often increase ending in a club-shaped expansion of the longest terminal segments (Dlussky & Fedoseeva 1988). In females of crown ants, a club is common in advanced taxa, except for formicines in which 3/4 of the genera lack it. Males of crown ants rarely have clubs too (Bolton 2003, Appendix 2). Finally, the entire flagellum in stem ants is long and flexuous (Bolton 2003).

Making his hypothesis from a comparison of ants with other Aculeata, Dlussky, however, has not provided any statistical support. This has resulted in criticism and even removal of a character "short scape" from the data matrix as it is “difficult to define” (Grimaldi *et al*. 1997). Below we check Dlussky’s hypothesis using a statistical analysis of antennal indexes as well as try to expand and generalize the aforementioned observations on antennal structure.

Comparison of antennal indexes of crown ants and stem ants.

Although indexes of Cretaceous males[1] are within the range of the indexes of crown males, in most cases they shifted from the crown males’ mean value (Table S3). The statistical tests showed that some differences between these indexes were significant (Table S15):

(1) Scape. Indexes SL/HL did not show statistically significant differences, while for SL/FL such a difference existed. The latter can be explained by a considerably longer flagellum of Cretaceous males.

(2) Flagellum. The mean of FL/HL is noticeably greater in Cretaceous males than in crown males,

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[1] Since none of Cretaceous males has yet been associated with workers or gynes, we can only assume they belong to stem ants. For this reason, we do not call them "males of stem ants" throughout the paper.

although P value is quite high.

(3) Pedicel. For PL/HL, the difference was statistically insignificant, while for PL/(AL-PL), it was on the verge of significance. The latter again resultes from a longer flagellum of Cretaceous males.

(4) The first and second segments of flagellum. The means of F1L/HL and F2L/HL are noticeably greater in Cretaceous males, although P values are quite high. The differences between F1L/(AL-F1L) as well as F2L/(AL-F2L) are not well understood due to low statistical power.

The male's regression lines look very similar for FL/HL, F1L/HL, and F2L/HL (Fig.3).

Because of low sample size of Cretaceous males, it is difficult to make broad conclusions. However preliminary results show some differences exist between lengths of flagellum, F1, and F2 in that Cretaceous males have bigger mean values than crown males.

The situation is completely different for females in which statistical analysis of indexes shows highly significant differences exist between crown ants and stem ants. ANOVA in 5 groups (extant crown, Cretaceous crown, Sphecomyrmini, Haidomyrmecini, Armaniinae) showed that the means for all indexes were significantly heterogeneous, except for the indexes of pedicel: SL/HL: $F_{4,79}$=18.38, P<0.0001; FL/HL: $F_{3,74}$=23.29, P<0.0001; PL/HL: $F_{4,78}$=1.47, P=0.22; F1L/HL: $F_{4,78}$=34.36, P<0.0001; F2L/HL: $F_{4,78}$=18.01, P<0.0001; SL/FL: $F_{3,74}$=87.78, P<0.0001; PL/(AL-PL): $F_{3,74}$=0.35, P=0.79; F1L/(AL-F1L): $F_{3,74}$=38.58, P<0.0001; F2L/(AL-F2L): $F_{3,74}$=18.07, P<0.0001. A planned comparison revealed the following picture.

All indexes of Cretaceous crown ants are very close to the mean values of the indexes of extant crown ants (Table S2); statistical analysis showed no differences between the two groups (Tables S4-S12). Relationship among other groups are more complicated.

Scape (indexes SL/FL, SL/HL):

(1) For SL/FL, all groups of stem ants differed significantly from crown ants in that they have shorter scape length compared to flagellum length. Haidomyrmecini were significantly different from both crown ants and Sphecomyrmini, with an intermediate mean value (Table S9).

(2) For SL/HL, Sphecomyrmini and Armaniinae have significantly lower mean values than crown ants. Haidomyrmecini have greater means, which are intermediate between crown ants and Sphecomyrmini, Armaniinae (Table S4); Haidomyrmecini's indexes are widely represented in crown ants (Table S2).

(3) For SL/HL, Armaniinae were not different from Sphecomyrminae and Sphecomyrmini (Table S4); for SL/FL, the only available index of Armaniinae is similar to the mean of Sphecomyrmini (Tables S2, S4).

(4) *Myanmyrma* lies close to the regression line of Sphecomyrminae (Figs 4A, 4C). *Myanmyrma*'s SL/HL is similar to the mean of Sphecomyrmini, Armaniinae, and the lowest value of crown ants obtained in this study, the index of *Pseudomyrmex pallidus*. *Myanmyrma*'s SL/FL is the lowest one, but is quite close to the minimal value of Sphecomyrmini, the index of *Sphecomyrmodes contegus* (Table S2).

(5) *Gerontoformica*'s SL/HL is much greater than that of all stem ants (i.e. *Gerontoformica* has noticeably longer scape); on the bivariate plot *Gerontoformica* lies close to the regression line of crown ants (Fig. 4). Such high SL/HL was often found in crown ants, for example in Ponerinae, Aneuretinae, Dolichoderinae, Formicinae (Table S2). *Gerontoformica*'s SL/FL is greater than the mean of Sphecomyrmini, lower than that of crown ants, and about equal to that of Haidomyrmecini (Table S2).

(6) *Boltonimecia*'s SL/HL is close to the mean of crown ants (similar indexes were found in Dorylinae, Proceratiinae, Myrmecinae, Ponerinae, Agroecomyrmecinae), but greater than that of all Sphecomyrmini and Haidomyrmecini (except for *Haidoterminus cippus*). *Boltonimecia*'s SL/FL is greater than that of most Sphecomyrmini, but lower than that of several species of Haidomyrmecini (Table S2).

Pedicel (indexes PL/(AL-PL), PL/HL):

(1) For both indexes, there was no statistical difference between the groups studied (Tables S6, S10; Fig.4D). Such stability, as already noted, may be explained by important function of a pedicel as a location of the Johnston's organ.

(2) The greatest PL/HL is in *Cananeuretus occidentalis*, followed by *Gerontoformica cretacica*,

Boltonimecia canadensis, *Sphecomyrmodes rugosus* and *Myanmyrma gracilis*; all four indexes are close to each other and the greatest value among crown ants found in *Martialis heureka* (Table S2). On bivariate plot *G. cretacica*, *M. gracilis* and *C. occidentalis* lie far away from other species (Fig. 4D).

Flagellum (index FL/HL):

(1) Stem ants were always statistically different from crown ants in having elongated flagellum (Table S5), although indexes of some of them are close to those of crown ants (e.g. some Sphecomyrminae have values similar to *Paraponera* and *Aphaenogaster*) (Table S2).

(2) The greatest FL/HL (i.e. the longest flagellum) is in *Sphecomyrmodes rubustus, S.magnus, Myanmyrma gracilis* and *Gerontoformica cretacica* (Table S2). Extremely elongated flagella of these species resemble only males' flagella (Table S3).

(3) Haidomyrmecini were not different from Sphecomyrminae (Table S5).

(4) Values of *Boltonimecia canadensis* and the only species of Armaniinae for which FL/HL can be calculated (*Pseudarmania rasnitsyni*) are about equal to the mean of Sphecomyrminae (Table S2).

The first segment of flagellum (indexes F1L/(AL-F1L), F1L/HL):

(1) Most stem ants, except for Haidomyrmecini, had significantly greater means than crown ants (Tables S7, S11). Haidomyrmecini's means are intermediate between those of Sphecomyrmini and crown ants, with weak statistical relationships (Tables S7, S11).

(2) Armaniinae were not statistically different from Sphecomyrminae and Sphecomyrmini (Table S7).

(3) *Boltonimecia*'s indexes are within the range of the indexes of Sphecomyrminae, although the former are not as great as the indexes of most Sphecomyrmini (Table S2).

(4) *Myanmyrma*'s F1L/HL is the greatest of all species reported, followed by *Sphecomyrmodes subcuspis*, and *Gerontoformica cretacica* (Table S2); on bivariate plot *Myanmyrma gracilis* lies far away from other species (Fig. 4E). *M.gracilis* and *S. subcuspis* have the greatest F1L/(AL-F1L) (Table S2).

The second segment of flagellum (indexes F2L/(AL-F2L), F2L/HL):

(1) Indexes of stem ants are usually significantly greater than those of crown ants (Tables S8, S12).

(2) Like on bivariate plots SL-HL and PL-HL, Armaniinae lie close to *Sphecomyrma mesaki* on plot F2L-HL (Figs 4A, 4D, 4F).

(3) *Boltonimecia*'s indexes are close to the mean of Sphecomyrminae (Tables S2, S8, S12).

(4) F2L/HLs of *Myanmyrma gracilis*, *Sphecomyrmodes subcuspis*, and *Gerontoformica cretacica* are close to the greatest value found in *Haidomyrmex scimitarus*. The greatest F2L/(AL-F2L) is found in *H. scimitarus* and *Sphecomyrmodes subcuspis* (Table S2).

General observations on the middle and terminal segments of the flagellum.

(1) Females of crown ants: Following F2 or F3, segment width, and often length, increase. This may be gradual along its length, or a sharp increase forming the antennal club. Very slight width increase occurs even in species with filiform antennae (which are marked "0" in Appendix 2 of Bolton 2003), for example in Paraponerinae, Formicinae, Myrmecinae. Also, in species with filiform antennae, the terminal flagellomere is very often about 1.5 times longer than the penultimate one. The exceptions are genera without an increase in width (*Eciton*) or length (*Paraponera*). In some cases the pattern resembles that of females of some stem ants: the length of segments decreases towards the apex (*Eciton*, *Nomamyrmex*, *Leptomyrmex*), but often such a decrease is combined with an elongation of the terminal segment (*Eciton, Nomamyrmex, Leptomyrmex*), and\or with a slight increase in width of last segments (*Myrmecia*).

(2) Females of stem ants: Antenna always filiform without a club; middle and terminal segments are similar in size, but in some cases segments towards the apex are slightly thicker (in *Sphecomyrmodes orientalis*, *Sphecomyrmodes contegus*, *Haidomyrmodes mammuthus*, *Haidoterminus cippus*). The terminal segment is often about 1.2-1.5 times longer than the penultimate one (except *Gerontoformica cretacica*, *Haidomyrmex scimitarus*, *Haidomyrmodes mammuthus*). In some cases antennomere length decreases towards the apex (*Gerontoformica*) or very slightly increases (*Sphecomyrmodes orientalis, S. occidentalis*). In *Sphecomyrma mesaki*, *Myanmyrma gracilis*, *Haidomyrmex zigrasi*, *Haidoterminus cippus*, and

Sphecomyrmodes subcuspis length of antennomeres decreases, then increases; in *Haidomyrmex scimitarus* - decreases, then increases, and finally decreases again. Thus *Gerontoformica* is unique in having decrease of antennomere length towards the apex, and a short terminal antennomere; this pattern resembles that of Cretaceous males and *Paraponera*, although *Paraponera'*s antennomeres are slightly widened towards the apex. *Haidomyrmex scimitarus* and *Haidomyrmodes mammuthus* also exhibit unusual antennae with short terminal antennomere.

(3) Males of crown ants: Antennae are filiform with similar segments, although in many cases the terminal antennomere is about 1.5 times longer than others. In some cases there is a slight increase in width and length of antennomeres towards the apex; in a few cases (*Leptogenys*, *Platythyrea*), segments decrease in length from F2 and F3 towards the apex (the terminal antennomere is again noticeably longer). Finally, in some genera (e.g. *Myrmica*) terminal antennomeres are very long and wide, so antenna is clavate.

(4) Cretaceous males: Length and possibly width of antennomeres decrease towards the apex; the terminal antennomere seems not to be longer than the penultimate one. Both characters are unique unique among males.

Comparison of relative length of antennal parts.

(1) When compared to flagellum, the smallest relative scape length is found in Cretaceous males, followed by males of crown ants, then females of Sphecomirmini, females of Haidomyrmecini, and finally by females of crown ants. The relative scape length of females of crown ants is more than three times greater than that of Sphecomyrmini, and two times greater than that of Haidomyrmecini. Bolton (2003) provided a SL-to-FL ratio of 25% for Sphecomyrminae, but the analysis conducted herein shows the ratio of about 20% (Table S9).

(2) Pedicels of females of crown ants are approximately 20% longer than the first two flagellomeres (Table S16), but there are exceptions when PL<F1L and PL = F1L (Table S2). Statistically F1L= F2L, but there are exceptions when F1L> F2L, F1L<F2L.

(3) In females of stem ants, except for Haidomyrmecini, and in all males (both crown and Cretaceous) statistically F1L>PL<F2L (Table S16). Moreover, the difference in length is often considerable: PL<F1L 3-7 times in Cretaceous males, up to seven times (two times on average) in males of crown ants, 2-3 times in Sphecomyrmini, *Gerontoformica*, *Myanmyrma*; PL<F2L 3-4 times in Cretaceous males, up to six times (two times on average) in males of crown ants, 1.5 times in *Gerontoformica* and *Myanmyrma*, up to almost three times in females of Sphecomyrmini. In females, there are only three exceptions to the aforementioned pattern: PL=F2L (*Boltonimecia canadensis*, *Zigrasimecia ferox* #1), PL>F2L (*Sphecomyrmodes occidentalis*). In males, exceptions are more numerous: there are species with PL>F1L, PL>F2L, PL=F2L (Table S3). Comparison of F1L and F2L shows that only in Sphecomyrmini F1L>F2L without exception (and this pattern was confirmed statistically). In all other groups, F1L is not statistically different from F2L (Table S16). The greatest difference between F1L and F2L (up to two times) is found in Sphecomyrmini, *Gerontoformica*, *Myanmyrma, Archaeopone taylori*, *Baikuris mandibularis*, and some males of crown ants.

(4) *Boltonimecia*, unlike Sphecomyrminae, but like females of crown ants, demonstrates a pattern PL>F1L . However, unlike females of crown ants, *Boltonimecia* also demonstrates patterns PL=F2L, and F1L<F2L (Table S2).

(5) Haidomyrmecini is a heterogeneous group in terms of antennal metrics. They, unlike females of crown ants and Sphecomyrmini, did not show statistical differences between PL, F1L, F2L (Table S16), but show different patterns: in *Haidomyrmex scimitarus* and *H. cerberus* PL<F1L, in *Haidoterminus cippus* and *Haidomyrmodes mammuthus* PL=F1L, in *Haidomyrmex zigrasi* PL>F1L (all differences are minor, except for *Haidomyrmex scimitarus* showing a two-fold difference), in *Haidomyrmex zigrasi* and *Haidomyrmodes mammuthus* PL=F2L; in *Haidomyrmex scimitarus* and *H. cerberus* PL<F2L (a considerable difference - 2 and 4 times respectively), in *Haidoterminus cippus* PL>F2L, in *Haidomyrmex scimitarus* and *H. cerberus* F1L<F2L (1.5- and 2-fold differences respectively), *H.zigrasi* also shows F1L<F2L but with minor difference; in *Haidomyrmodes mammuthus* F1L=F2L, in *Haidoterminus cippus* F1L only slightly longer than

F2L (Table S2).

Comparison of male's and female's indexes.

(1) Scape. The means of the two indexes (SL/HL, SL/FL) of Cretaceous males are lower than those of females of Sphecomyrminae, but the means of males of crown ants are almost equal to those of females of Sphecomyrminae. Some rare exceptions include males of crown and Cretaceous ants with large indexes - as large as those of females of crown ants (Tables S2, S3, S4, S9, S15).

(2) Flagellum. The means of FL/HL of Cretaceous males and males of crown ants are greater than those of females of stem and crown ants (Tables S5, S15).

(3) Pedicel. All pedicellar indexes of Cretaceous males and males of crown ants are not different from those of females (Tables S6, S10, S15).

(4) The first and second segment of flagellum. The patterns of these segments resemble scape patterns: indexes of males of crown ants are similar to those of females of Sphecomyrminae, and noticeably greater than those of females of crown ants. The largest indexes are found in Cretaceous males (Tables S7, S8, S11, S12, S15).

(5) Correlation between head length and length of antennal parts was weaker in males ($R^2=0.3$-0.6), than in females ($R^2=0.5$-0.8). Correlation between SL and FL was negligible in males ($R^2=0.02$).

General observations on shape of pedicel.

A long pedicel must be narrowed towards the scape and bent at its base to facilitate articulation of the scape and flagellum. Almost all females of crown ants have pedicels of such a shape, even those whose pedicels are not longer than F2 and F3. Rare exceptions include some army ants: their pedicels are very short, with almost non-existent bent; however, their pedicels are triangular (i.e. with narrowed bases) as in all other ants. Likewise, in some specimens of *Myrmecia* and *Nothomyrmecia* bent is almost non-existent, but pedicel are always narrowed at base. Males of crown ants also have pedicels narrowed towards the scape and bent at its base (triangular), but males with a short scape (SL/HL<0.2) have barrel-shaped or spherical pedicels. Cretaceous males seem to demonstrate the same pattern: the only species with the scape index below 0.2 (*Baikuris mandibularis*) has barrel-shaped pedicel, but all other Cretaceous males have triangular pedicels. All females of stem ants have the scape index equal to or greater than 0.2 and so triangular pedicels. Thus, Dlussky and Fedoseeva’s (1988) assumption about an unique shape of pedicels of Sphecomyrminae is erroneous.

Comparison of antennal indexes of female ants and female non-ant Aculeata.

(1) SL/AL of crown ants is greater than that of all Vespoidea and Apoidea listed in Dlussky and Fedoseeva (1988) (i.e. crown ants have the greatest relative scape length) (Fig. 5). The second greatest mean is found in social Vespoidea and Apoidea. Interestingly, the lowest SL/AL of crown ants (in Pseudomyrmicinae, Dorylinae, Leptanillinae, Martialinae) is almost equal to the lowest SL/AL of social non-ant Hymenoptera (Table S2). Stems ants have one of the lowest mean of this index, and the lowest absolute value. ANOVA showed the means of groups studied were significantly heterogeneous: $F_{4,109}=62.45$, $P<0.0001$. Planned comparisons showed that differences between crown ants and social Aculeata, as well as between stem ants and Vespoidea, Apoidea are negligible (Table S13). Thus crown ants and social Aculeata indeed underwent scape elongation (probably with simultaneous shortening of flagellum), as was hypothesized by Dlussky (1983). These findings are the first statistical support in favor of Dlussky's hypothesis.

(2) Stem ants have the greatest mean of AL/HL (Fig. 6), and also the two greatest absolute values of this index (Table S2). ANOVA showed the means of groups studied were significantly heterogeneous ($F_{4,109}=21.27$; $P<0.0001$) with statistically significant differences between all groups in pairwise comparison, except for the difference between crown ants and Vespoidea (Table S14).

Canonical discriminant analysis.

This analysis based on female indexes SL/HL, FL/HL, F1L/HL, and F2L/HL was performed in order to achieve separation of crown ants and stem ants. PL/HL was not used because it makes no contribution to the separation of the groups; other unused indexes are depended on aforementioned ones.

First analysis was run with all species. This approach explained 62% of the variation in the grouping variable (i.e. 62% of species were correctly classified as stem ants or crown ants); on the other hand, the cross validated classification showed 93% of species were correctly classified (100% of crown ants and 72% of stem ants). The discriminant function equation was as follows: D=(-0.73×SL/HL)+(0.63×FL/HL)+(7.40×F1L/HL)+(1.88×F2L/HL)-1.98. The mean discriminant scores (centroids): -0.90 for crown ants,1.90 for stem ants (Fig.7; Table S17). The cut-off score (weighted mean of discriminant score) separating groups was 0. A discriminant function equation can be used to predict group membership of newly discovered species comparing D, centroids and cut-off score.

Better separation of crown ants and stem ants can be achieved after removal of Haidomyrmecini because their discriminant scores overlap with the scores of crown ants. This approach explained 72% of the variation and correctly classified 95% of species (98% of crown ants, 80% of stem ants) (Fig.8; Table S17). The discriminant function equation was as follows: D=(-0.63×SL/HL)+(0.37×FL/HL)+(15.24×F1L/HL)+(-5.99×F2L/HL)-1.85. Centroids: -0.98 for crown ants, 2.6 for stem ants. The cut-off score was 0.

Summing up these findings, the antennal morphometry seems to be a promising heuristic tool in taxonomy of fossil ants, because there is a strong statistical basis for separating females of stem ants and crown ants. However, the present research should be viewed as preliminary, providing a basis for future studies when more stem species are discovered. New morphological data can be used in the model developed herein to extend the conclusions obtained.

Higher classification of ants

Classification of stem ants and crown ants is an important step towards understanding of evolutionary relationships between them. They should be properly diagnosed because it affects our thinking about ant origin and evolution (Ward 2007), but it is impossible to do without classification.

On our aim to a system of the higher classification of Formicidae, it is necessary to understand how to classify such different parts of a phylogenetic tree as stem and crown groups.

First of all, let us find out whether it is possible to split stem ants into subfamilies as crown ants.

It is common practice that a group becomes a subfamily if it has so-called “strong” (stable) characters.

A gastral constriction (constriction between abdominal segments III and IV) has been long time considered as one of such characters - it is the main character of Ponerinae in old sense, or several subfamilies of poneroids in current interpretation. But a gastral constriction is also present in ectaheteromorphs, which have been assigned to the formicoid clade only on the basis of molecular analysis (Moreau *et al*. 2006; Brady *et al.* 2006; Rabeling *et al.* 2008).

One or two-segmented waist seems to be a reliable character at the subfamily level. But significant exceptions are available. In some Dorylinae, workers have two, but gynes and males only one waist segment, while in others all castes have one segment waists. In leptanilline tribe Anomalomyrmini, workers and gynes have waist of two segments, but putative males only one, while in another tribe, Leptanillini, workers have two, but gynes and males one. One genus of Myrmeciinae (*Nothomyrmecia*) has one-segmented, but another (*Myrmecia*) - two-segmented waist.

A very reduced sting present in two subfamilies, Formicidae and Dolichoderinae, but such a reduction apparently evolved independently.

Among some of few “strong” characters defining a subfamily of crown ants, are a broad attachment of petiole to gaster in Amblyoponinae, and acidopore of Formicinae, although the former is clearly plesiomorphic, as it is very usual in non-ant Aculeata.

Thus, even in extant groups it is quite difficult to find strongly-marked morphological characters to definitively characterize a subfamily. Not surprisingly, the situation in stem ants is much more complicated, because the "weight" of a character reduces the more, the farther we go back down the evolutionary scale. For example, it is very possible that in Sphecomyrminae such a character that varies within a genus, not within a subfamily as in crown ants, was a gastral constriction (will be discussed below). As Dlussky and Fedoseeva (1988) noted, the ancestors of all branches of the ant tree were probably so similar that if they existed today, we would have assigned all of them to a single genus. Also, in ancestral groups, characters which we now consider as subfamily level ones, could be combined in a very weird manner. It would not be surprising if once a fossil ant with two-segmented waist, reduced sting, and the gaster with a constriction will be discovered. Interestingly, did the common ancestor of Formicinae and Myrmicinae have waist of one or two segments? Did the ancestor of all crown ants have a gaster constriction as in poneroids, or did not - as in most formicoids? With our knowledge of ant morphology based mainly on crown ants, it would be quite unusual to accept the fact that stem ants with one and two-segmented waist might be closely related.

Hennig (1966) suggested that ranks of taxa should be coupled to taxa absolute age, and thus taxa of the same rank should originate in the same time period. As a result, we can also approach the question of what makes a group subfamily in terms of time needed to accumulate characters of a big "weight".

The youngest subfamilies of crown ants are at least 70 Ma old. For example, dorylomorph clade represented by six subclades, which until recently had the status of subfamilies, but now are subsumed into a single subfamily, Dorylinae, is 74-101 Ma old (Brady *et al.* 2014). It is very revealing that it took several decades of morphological studies to justify the split of dorylomorphs into six subfamilies (Baroni Urbani *et al.* 1992; Bolton 2003; Brady and Ward 2005), and even molecular data confirmed the split (Brady *et al.* 2006; Moreau *et al.* 2006; Rabeling *et al.* 2008). But a deeper molecular research showed that such a conclusion is eroneous (Brady *et al*. 2014).

The oldest subfamilies of crown ants (Formicinae, Dolichoderinae), as it can be judged from fossils, are at least 90 Ma old. It seems plausible that if we want to distinguish a recent subfamily with confidence, at least a similar time is required.

Sphecomyrminae had probably existed only for 20 Ma. So only if we assume that the age of this group is no less than 150 Ma, and if Sphecomyrminae had survived until the end of Cretaceous, we can say that this group is congruent with the recent taxa of a subfamily level (to say nothing of the fact that the rate of radiation of Cenozoic ants (i.e. crown ant clade) was higher than that of Mesozoic ants (comprised mainly from stem ants) and thus Sphecomyrminae probably needed more time to accumulate characters of a big "weight" than crown ants).

The same logic can be applied to lower taxa. For example, evolution of stem taxa of Dolichoderinae had lasted for 30 Ma, while of recent tribes almost two times longer - 40-60 Ma (Ward *et al.* 2010). Thus, it would be wrong to group stem dolichoderines in a taxon with the rank of a tribe.

If we cannot use the same criteria in classification of both stem and crown groups, the problem of a classification system arises.

Indeed, in the Linnean system taxa, which are not explicitly associated with ranks, cannot be formally named (Pleijel & Rouse 2003; Joyce *et al*. 2004), and as a result, this system is usually unable to classify stem taxa (Ereshevsky 2001). It means that we can name for example stem and crown ants or supra-subfamilial clades of the crown-ants (e.g. formicoids, poneroids, dolichoderomorphs), only if we assign these clades to useless intermediate ranks, what will make the system exceedingly complicated.

One more problem is that a rank system always implies comparability or comparable evolutionary history. Therefore quite paradoxically, that in the Linnean system taxa of the same rank lack equivalency (Ereshevsky 2001), they are not comparable entities in a cladistic sense (Pleijel & Rouse 2003; Dubois 2007). But if we are deciding to which ranks a given group has to be splitted, we have to compare ranks at least because we need to create ranks of the same level (for example when we split Formicidae into subfamilies). If we go outside of the crown clade, and look at the subfamily Sphecomyrminae, we cannot refrain from comparing it with the subfamilies of the crown clade. It becomes obvious to us that subfamilial rank of Sphecomyrminae is unsatisfactory, it must be higher than a subfamilial (contrary to the aforementioned fact that evidences of long evolution of Sphecomyrminae are not available), but lower than a familial one.

A long time ago Hennig (1966) noted that ranks themselves are subjective devices serving only to build classification, they are arbitrary and lack biological meaning. Exceptions could be a species (e.g. Rieseberg & Burke 2001), a genus (as ecological and morphological entity) (Bock & Farrand 1980), and a phylum as a carrier of "bauplans", body plan (e.g. Valentine 2004).

An alternative of the Linnean system is a rankless system, such as one governed by PhyloCode (Cantino & de Queiroz 2010). Phylogenetic nomenclature of PhyloCode extends the concept of “tree-thinking” (Baum & Smith 2012) to biological nomenclature. With tree-thinking, we can interpret fossil groups, which are very different from recent taxa, not as separate taxa, but as stem groups of recent taxa. It is important to emphasize that a stem taxon of a higher taxon is not merely a part of that higher taxon, it is identical to that higher taxon (Hennig 1966). That is why ant stem taxa cannot be equivalent to crown group subfamilies: each such taxon is equivalent to the crown group as a whole. Without ranks we can satisfactorily classify all organisms, not just descendants, and construct a classification that explaines ancestor-descendant relationships between stem and crown clades. In a rank-free system stem ant branches can be imagined as a gradation at the base of Formicidae, as sister groups to the crown group. For such enigmatic stem ants as *Gerontoformica* and *Myanmyrma,* one can create their own subfamilies, or try to fit them into existing subfamilies; it will be difficult to find a recent taxon for them to include into, but to create a new taxon of a high rank is even more problematic. Methodological dilemma is solved with the abandonment of ranks and classification them and other stem ants using tree-thinking approach. Similarly, a phylogeny-based system will allow us to place Cretaceous representatives of crown ants, for which placement using Linnean ranking is also problematic, in defined clades. Statistical analysis of antennal measurements shows that *Kyromyrma neffi*, *Canapone dentata*, *Eotapinoma macalpini*, *Chronomyrmex medicinehatensis*, and *Brownimecia clavata* undoubtedly belong to crown ants, but these first crown ants cannot be placed in any recent tribe; they are likely stem taxa of recent subfamilies.

Thus in the proposed phylogenetic classification I do not use ranks where they would cause the complication of the system with intermediate categories as well as imply unnecessary comparability of the taxa, distorting our view of evolutional relationships at the base of the ant tree. Also I focus mainly on clades that lay above tribal level.

The proposed classification should not be viewed as a competitor to phylogenetically-based Linnaean system. It is rather an attempt to show how clades, which are important for our understanding of ant evolution and are not explicitly associated with Linnean ranks, can be formally defined. It is a challenge for ant taxonomists in the future whether to incorporate them into Linnean classification or develop a rank-free phylogenetic classification of the ants. In either case Linnaean classification, designed to reflect phylogeny, and a clade-based system of phylogenetic nomenclature should always be viewed as mutually complementary approaches.

Crown-Formicidae

Diagnosis (workers, gynes). (1) Scape long (SL/HL no less than 0.3, often more than 0.6; SL/FL more than 0.3, often more than 0.5); (2) flagellomeres shortened (F1L/HL and F2L/HL less than 0.20, often less than 0.10) and thus whole flagellum is short (FL/HL often <1.4); (3) the terminal flagellomere usually elongated compared with other flagellomeres; (4) PL often >F1L and >F2L (on average 20%); (5) F1L=F2L, middle segments of flagellum often equal as well; (6) antenna clavate or at least its width gradual increases towards apex; (7) mandibles wide, with many teeth; (8) clypeus posteriorly inserted between antennal sockets or not; (9) two spurs of mesotibia and metatibia present or not; (10) preapical tooth on pretarsal claws present or not; (11) trochantellus absent; (12) waist of one or two segments.

Comment. Under the PhyloCode, the taxon should be named ”*Formicidae*^{P} Stephens 1829, converted clade name” and defined as “the clade originating with the most recent common ancestor of *Martialis heureka* Rabeling & Verhaagh, 2008 and *Formica rufa* Linnaeus, 1761”. The clade is congruent with the Linnean taxon Formicidae Latreile 1809 minus stem taxa.

Composition. The clade is monophyletic (Baroni Urbani *et al*. 1992; Brady *et al.* 2006), with known extant diversity of nearly 16 000 species (AntWeb). The high-level classification of Formicidae has been significantly improved by Bolton (2003) and obtained good support from molecular systematics (Brady *et al*. 2006; Moreau *et al.* 2006; Rabeling *et al.* 2008). Structure of subclades, which correspond to subfamilies in a Linnean system, is stable (Ward 2011), therefore subfamilies correspond to 15 monophyletic subclades (presumably excluding Amblyoponinae - Ward 2007) (Table S17). However, the structure above the level of subfamilies is not well understood. It is believed that the clade splits into two major subclades: formicoid clade (formicoids) and poneroid clade (poneroids) (Ward 2007). The first one is quite stable in all analyses, although its composition is different in morphological and molecular analyses; but the second one is either a sister clade to formicoids or a paraphyletic group from which formicoids arise (Ward 2011).

Discussion. In *Formicidae*^{P} flagellum has three functional parts: a long scape, shortened medial part, elongated and/or thickened terminal part. The scape comprises on average 60% of the length of flagellum, which is about 3 times greater than in stem ants; flagellum 1.3 times longer than the head (in stem ants - 1.8 times).

First representatives of *Formicidae*^{P} known from Cretaceous. The oldest one is an undescribed species of Dolichoderinae from Ethiopian amber (late Tsenoman, 93-95 Ma) (Schmidt *et al.* 2010, LaPolla *et al.* 2013), whose age is comparable to that of the oldest stem ants from Burmese amber (100 Ma). A little younger is *Kyromyrma neffi* - stem formicine (Ward 2007), and *Brownimecia clavata* - poneroid belonging to its own subfamily (Bolton 2003) from amber of New Jersey (Grimaldi & Agosti 2000) aged 92 Ma. From later Canadian amber (78-79 Ma) representatives of Dolichoderinae (*Eotapinoma macalpini, Chronomyrmex medicinehatensis*) (Dlussky 1999a; McKellar *et al.* 2013a), and Ectatomminae sensu Bolton 2003 (*Canapone dentata*) (Dlussky 1999a) are known.

Taxon that certainly belongs to *Formicidae*^{P}, but which position within the clade remains unclear: *Brownimecia clavata*.

B.clavata may be a stem taxon of poneromorphs or poneromorphs + leptanillomorphs (Bolton 2003). It is also possible that *B.clavata* is a stem taxon of a recent subfamily - Amblyoponinae or Ponerinae. In any case, the status of subfamily Brownimeciinae in the Linnean system is not comparable to other subfamilies of crown ants. This species was not included in statistical analyses, because of its uncertain taxonomic position. However, indexes of *B.clavata* are close to the mean values of the indexes of crown ants that at least confirms its affiliation with the crown clade.

Taxa which placement within or out of *Formicidae*^{P} is uncertain: *Cananeuretus occidentalis, Burmomyrma rossi,* Formiciinae.

Cananeuretus occidentalis (currently in Aneuretinae) (Engel & Grimaldi 2005) by index SL/HL is close to the mean value of the crown group, but its index PL/HL is more than twice greater than the greatest values in stem and crown ants, and more than four times greater than their mean values (see also bivariate plots - Fig. 4D). It is impossible to calculate other indexes and thus to draw a final conclusion on the taxonomic position of *C.occidentalis* due to the incomplete preservation of antennae.

Burmomyrma rossi is thought to be a stem group of Aneuretinae (Dlussky 1996), but poor preservation makes it impossible to draw a reliable conclusion.

It is not clear whether the fossil subfamily Formiciinae indeed belongs to *Formicidae*^{P}. Formiciinae known from Early Middle Eocen (app. 40 Ma) (Archibald *et al.* 2011); thus by the age it can be a "true" crown group subfamily, not a stem taxon. On a cladogram, Formiciinae placed outside crown ants (Baroni-Urbani *et al.* 1992; Grimaldi *et al.* 1997), but these data should be interpreted with caution because Formiciinae known only from poorly preserved impressions. Their antennae are not preserved, so they were not included in the statistical analysis performed here.

Pan-Formicidae

Diagnosis (workers, gynes). The characters shared by crown ants (*Formicidae*^{P}) and stem ants: (1) eusocial with perennial colonies; (2) wingless worker caste; (3) head prognathous; (4) metapleural gland present; (5) differentiated petiole present. Characters of crown ants (*Formicidae*^{P}) only: see above. Characters of stem ants only: (1) scape short (SL/HL can be less than 0.3, rarely more than 0.6; SL/FL is very often less than 0.3 and never more than 0.5); (2) flagellomeres not shortened (F1L/HL and F2L/HL > 0.10, often more than 0.20) and therefore whole flagellum is very long (FL/HL> 1.4); (3) the terminal flagellomere elongated compared to other flagellomeres or not; (4) often F1L>PL<F2L; (5) F1 can be longer, shorter, or equal to F2; (6) antenna filiform, without club; length and width of flagellomeres do not increase towards apex; rarely, hardly noticeable weak increase of the width and/or length can be observed; length of flagellomeres can decrease towards apex; (7) mandibles narrow - linear bidentate or L-, scythe-shaped monodentate; (8) clypeus posteriorly not inserted between antennal sockets; (8) trochantellus present or not; (9) mesotibia and metatibia each with two spurs; (10) preapical tooth on pretarsal claws often present; (11) waist of one segment; (12) sting often present.

Comment. Under the PhyloCode, the taxon should be named ”*Pan-Formicidae*^{P}, new clade name” and defined as “the total clade composed of the crown clade *Formicidae*^{P} and all extinct species that share a more recent common ancestor with *Formicidae*^{P} than with any extant species that are not members of *Formicidae*^{P}”. Reference phylogenies: Grimaldi *et al.* 1997 and this study.

Composition. *Formicidae*^{P}, *Sphecomyrminae*^{P} (possibly non-monophyletic clade).

Discussion. In stem ants, antenna is not divided into three functional parts, unlike crown ants. Usually there is no striking difference between the length of the scape and the segments of flagellum; club always absent. *Gerontoformica* and *Myanmyrma* demonstrate two extreme variants of modification of antennae: with a very short (*Myanmyrma*) and a very long scape (*Gerontoformica*).

It is very convenient to separate stem and crown ants using a timeline with the K-Pg extinction event: the former became extinct, the later explosively diversified.

Althought relationships among stem ants still are not fully understood, most likely, *Sphecomyrminae*^{P} should be divided into several subclades, but without a comprehensive revision of this subfamily it is preliminary to draw a final conclusion.

Taxa that definitely belong to *Pan-Formicidae*^{P}, but which position within the clade remains unclear: *Archaeopone* Dlussky 1975, *Baikuris* Dlussky 1987, *Dlusskyidris* Bolton 1994, *Poneropterus* Dlussky 1983, *Gerontoformica cretacica* Nel & Perrault, 2004, *Myanmyrma gracilis* Engel & Grimaldi, 2005. First four genera are known from males only. For Cretaceous ants, no one male has been associated with workers or gynes. For example, *Dlusskyridris* can be a male of either *Sphecomyrma* or *Cretomyrma* (Dlussky 1975), but may well be a male of *Gerontoformica* or *Myanmyrma.*

Gerontoformica occupies an intermediate position between crown and stem ants. For SL/HL, it is very similar to crown ants; its scape is the longest among all known stem ants, but its flagellum is also very elongated proportionally to the scape, and thus indexes FL/HL and AL/HL are among the largest reported in my analysis. The same applies to the pedicel, F1 and F2. Other differences of *Gerontoformica* from crown ants include: the terminal antennomere not being elongated (a unique character which is also present in two species of Haidomyrmecini), flagellum lacking a club, length of flagellomeres decrease towards the apex (a unique character for ants), bidentate mandibles, and peg-like setae on the clypeus and labrum (also present in two primitive subfamilies of crown ants). The characters of crown ants that are present in *Gerontoformica* include: simple claws, and reduced sting (the former character is widespread in the crown clade, the last one present only in two subfamilies).

Antennal indexes of *Myanmyrma* are strongly different from the indexes of the crown group. For SL/HL, *Myanmyrma* is close to Sphecomyrmini, but its index SL/AL is the lowest from all species of Aculeata studied here (i.e. *Myanmyra* has one of the shortest scape). For other parts of the antenna, *Myanmyrma* is also unique: it has the longest F1, one of the longest flagellum, pedicel, and F2. "Poneroid" habitus of *Myanmyrma* (Engel & Grimaldi 2005) is questionable. The deep gastral constriction (so deep that it suggests the differentiated postpetiole) may be an artifact. But even if a deep constriction is present, it does not indicate any relatedness of *Myanmyrma* and the crown group. Thus, it is safe to discard the assumption that *Myanmyrma* belongs to the crown group (poneroid or myrmeciine, as suggested by Engel & Grimaldi 2005), although a differentiated postpetiole is unknown for stem ants. All evidences indicate that *Myanmyrma* is a representative of stem ants, a unique species with a unique combination of characters.

Subfamily Sphecomyrminae Wilson & Brown 1967

Diagnosis (workers, gynes). (1) metapleural gland orifice not concealed by cuticular flaps or flanges; (2) pretarsal claws each with preapical tooth; (3) propodeal lobes absent; (4) sting present.

Comment. Under the PhyloCode, the taxon should be named "*Sphecomyrminae*^{P} Wilson & Brown 1967, converted clade name" and defined as ""the clade originating with the most recent common ancestor of *Sphecomyrma freyi* Wilson & Brown, 1967, *Haidomyrmex cerberus* Dlussky, 1996, and *Boltonimecia canadensis* (Wilson 1985).

Composition. Tribes Sphecomyrmini, Boltonimeciini, Haidomyrmecini.

Discussion. It has been assumed before that Sphecomyrminae is a group close to the formicoid clade of the crown group (Taylor 1978; Rabelling *et al.* 2008). Sphecomyrminae indeed resemble representatives of the formicoid clade by a habitus, the presence of ocelli, unspecialized (only in Sphecomirmini though) head capsule which resembles the head capsule of primitive formicines (*Prolasius*, *Notoncus*, *Prenolepis*) (Wilson *et al.* 1967). However, the data presented here suggest that Sphecomyrminae is a stem group, i.e. a sister groups to the crown clade as a whole.

It is difficult to find common apomorphies for all three tribes. Some characters are very variable. For example the length of the scape of Sphecomyrminae comprises on average 20% of the length of flagellum, compared with 60% in the crown group, but it varies in quite a large range (for more details see the discussion of Sphecomyrmini below). Other variable characters include clypeal peg-like setae, gastral constriction and trochantellus.

Tribe Sphecomyrmini Wilson & Brown, 1967

Taxonomic history: Sphecomyrmini as tribe of Sphecomyrminae: Bolton, 1994: 187.

Diagnosis (workers, gynes). (1) head capsule unspecialized; (2) mandibles unspecialized; (3) anterolateral margins of clypeus not expanded over the bases of mandibles; (4) clypeal peg-like setae present or not; (5) ocelli present; (6) F1L>PL<F2L, F1L>F2L; F1 often longer than the other flagellomeres; (7) neck short or long; (8) petiole subsessile or pedunculate; (9) gastral constriction present or not.

Comment. Under the PhyloCode, the taxon should be named "*Sphecomyrmini*^{P}, converted clade name" and defined as "the clade consisting of *Sphecomyrma freyi* Wilson & Brown, 1967 and all species that share a more recent common ancestor with *Sphecomyrma freyi* Wilson & Brown, 1967 than with *Haidomyrmex cerberus* Dlussky, 1996 or *Boltonimecia canadensis* (Wilson 1985)".

Composition. Genera *Sphecomyrma* Wilson & Brown, 1967, *Cretomyrma* Dlussky, 1975, *Armania* Dlussky, 1983, *Pseudarmania* Dlussky, 1983, *Orapia* Dlussky, Brothers & Rasnitsyn, 2004, *Sphecomyrmodes* Engel & Grimaldi, 2005.

Dicussion. This tribe seems to be less specialized than the other two tribes of Sphecomyrminae. Also it is quite heterogeneous; confusion is made by the genus *Sphecomyrma* and especially by the genus *Sphecomyrmodes*.

First of all, our attention is drawn to the wide range of the values of the scape index SL/HL in *Sphecomyrma*. Even in *Sphecomyrma freyi* the values range from 0.28 to 0.62 (Table S2), i.e. the second value is 120% greater than the first one. Data on the recent genera (11 genera from 6 subfamilies) show that the differences of the index SL/HL values in workers, gynes, and workers + gynes within a given species rarely exceed 10% (Radchenko 1991, 1994; Seifert 1992, 2000, 2003; MacKay 1993; Radchenko & Elmes 1998, 2003; Ward 1999; Radchenko *et al.* 2002; Baroni Urbani & De Andrade 2003; Wild 2004; Bolton 2007; Bolton & Fisher 2011), with a single absolute maximum of 20% for *Myrmica* (Radchenko 1994), 31% for *Linepithema* (Wild 2004), 31% for *Dolichoderus* (MacKay 1993). Thus the range of indexes of *Sphecomyrma freyi* is too great compared to these values. It is very probable that if the measurements of antennal segments in Engel & Grimaldi (2005) are correct, such result raise a doubt that *Sphecomyrma frey* #3 with its index SL/HL 0.28 indeed belongs to *Sphecomyrma*.

If we review the variation of the scape index within a genus, for Cretaceous males, as exemplified by *Baikuris,* it is 77% (between *B.mandibularis* and *B.casei*); for workers of *Sphecomyrma,* it is 160% (between *S.mesaki* and *S.frey* #1) (if clypeal lobe of *S.mesaki* excluded, it is 106%). Let us compare these data with the data on recent genera. Males are characterized by big differences between indexes even for specimens of one species: up to 40% in *Myrmica* (Radchenko 1994), to 80% in *Dolichoderus* (MacKay 1993). Therefore a big difference between species of one genus is not suprising: 100% for *Proceratium* (Baroni Urbani & De Andrade 2003), 204% for *Dolichoderus* (MacKay 1993), 175% (Seifert 1988) and 260% (Radchenko 1994) for *Myrmica*; thus the range in *Baikuris* is consistent with these data. For workers and gynes, the situation is different. For 7 studied genera from 5 subfamilies, the maximum difference between the indexes ranges from 30% in *Pseudomyrmex* to 55% in *Proceratium* (Radchenko 1994; Seifert 1992, 2000, 2003; Baroni Urbani & De Andrade 2003; Bolton & Fisher 2011; Ward 1999); and only in Dolichoderinae we see though single, but very big extreme values causing a wide range of data: 128% in *Dolichoderus* (MacKay 1993), 121% in *Technomyrmex* (Bolton 2007). We do not know the limits of variation in Cretaceous genera, but based on the data available for comparison, we can conclude that the range of index values for species within *Sphecomyrma* is quite high. Therefore, as in the case of *Sphecomyrma freyi* #3, taking into account the unique morphology of *Sphecomyrma mesaki* (short scape, antennal scrobes), its taxonomic position would better to be reassessed.

Genus *Sphecomyrmodes* which is known from 11 species, seems to be even more heterogeneous than *Sphecomyrma*. It is even possible that it not only can be divided into several genera, but also these genera can be assigned to different tribes - Sphecomyrmini and Boltonimeciini. Indeed, the genus is very variable by the characters of generic and higher level: presence or absence of petiolar penduncle, reduction of ocelli, length of scape, palp formula, presence or absence of gastral constriction, presence or absence of trochantellus. In some species, the head seems to be as specialized as in Boltonimeciini: antennal scrobes present, frontal part thickenned; lateral clypeal projections, which cover the insertions of mandibles, present. All species have clypeal peg-like setae, again as in Boltonimeciini (although it is possible that this character has no significance for classification as it presents in distantly related *Gerontoformica* and some primitive crown ants).

In *Sphecomyrmodes,* SL/HL ranges from 0.19 (the absolute minimum value among all studied here ants) to 0.67 (one of the highest values among stem ants) (Table S2). Thus the second value 250% greater than the first one, which is a larger range than in *Sphecomyrma* and more than any within-genus range obtained in this study.

However, the problem of wide within-genus variations of the scape length of stem ants may have another solution: elongated scape, as it is present now in crown ants, had not yet stabilized under natural selection in stem ants. There is a long-lasting discussion about whether stem ant were eusocial or not, and, as it has been repeatedly pointed out, the answer to this question is probably connected to the problem of the scape elongation (Dlussky 1983; Dlussky & Fedoseeva 1988). It is reasonable to assume, however, that the transition to esociality had not occured instantly; most probably it occured via the stage of *facultative* sociality, i.e. sociality of stem ants depended on, for example, environmental conditions and varied even in closely related species. A similar pattern of social organization now observed in some bees (Halictidae) (Yanega 1997). Using this working hypothesis, we can explain both wide variations of the scape length of stem ants and facts in favour of sociality, namely discoveries of two workers (Wilson *et al.* 1967; Perrichot *et* *al.* 2008) and three males (Dlussky 1987) in one piece of amber. In this case, both opposite points of view would be correct, and stem ants should not be viewed as strictly solitary or social.

Concerning the inclusion in Sphecomyrmini genera of Armaniinae, I have compelling reasons to justify this decision.

Traditionally there are two approaches to the interpretation of the taxonomic position of Armaniinae: Dlussky's too liberal and Wilson's too conservative. Dlussky initially assigned all described by himself Cretaceous specied to Sphecomyrminae (Dlussky 1975), but then transfered them to his new family Armaniidae (Dlussky 1983). Wilson disagreed and returned them to Sphecomyrminae, synonimized almost all genera of Armaniinae (except *Cretomyrma*) with the genus *Sphecomyrma* (Wilson 1987). Bolton made an intermediate decision and reduced the status of the Dlussky's family to subfamily - Armaniinae (Bolton 1994, 2003), although he noted that the position of this taxon is debatable (Bolton 2003). Dlussky first accepted Bolton's system (Dlussky 1996), but then called the group Armaniidae again (Dlussky 1999b), and then again returned to Armaniinae (Dlussky *et al* 2004). Wilson in the publication of 2005 suddenly recognized the status of this group as a separate family Armaniidae (Wilson & Hölldobler 2005).

All Armaniinae have been described from poor quality rock impressions as winged forms, males or gynes, except for *Dolichomyrma*, which was described as a worker.

There is a lot of confusion about reliable characters of Armaniinae distinguishing them from other groups, especially from Sphecomyrminae.

Most of confusion caused by the gastral constriction. *Dolichomyrma* described either without (Dlussky 1975), or with the constriction (Wilson 1987); *Armania* - either with (Dlussky 1983), or without (Wilson 1987); *Arhaeopone* - either with (Dlussky 1975), or without (Dlussky 1983). *Petropone*, most probably, has the gastral constriction (Dlussky 1975). As it is obvious from the data accumulated at this time, in Sphecomyrminae the gastral constriction was a variable character being present in some genera and absent in others.

According to Wilson (1987), two-segmented trochanter is the only significant character distinguishing Armaniinae and Sphecomyrminae, although it is a character which is very hard to see on rock impressions. However it is clear now that in stem ants this character is unreliable too, being variable even on a generic level (e.g. in *Sphecomyrmodes*) (Barden & Grimaldi 2014).

Other characters of Armaniinae (the apically directed base of the vein 1Rs, the presence of a rudiment of 1r-rs dividing cell 1+2r) (Dlussky *et al.* 2004) found not only in Sphecomyrminae, but also in crown ants (ponerines and myrmeciines).

Also, Armaniinae are characterized by a "very short scape", compared to just a "short scape" of Sphecomyrminae (Bolton 2003). This very short scape is one of the most important diagnostic characters of Armaniinae (Dlussky 1983). However, when I expressed the scape lengths as digital indexes, it became clear that not only for these indexes, but also for other indexes of antennae, Armaniinae are not at all different from Sphecomyrminae in general and Sphecomyrmini in particular (Tables S2, S4-S8). The same conclusion can be drawn from the bivariate plots: Armaniinae always lie along the regression lines of Sphecomyrmini (Fig. 4).

To close the problem of the scape length difference of Armaniinae and Sphecomyrminae, let us answer the following question: when we split Sphecomyrmini into at least two groups according to the scape length, will it be possible to view these groups as separate subfamilies, if Armaniinae falls into one of them? The difference between the extreme values of the scape index of Sphecomyrminae (between *Sphecomyrmodes orientalis* and *Sphecomyrmodes rugosus*) is 3.5 times (differences between Armaniinae and Sphecomyrminae even less). SL/HL values of subfamilies of crown ants (workers only) are the following. For Ponerinae, the difference is 2.2 times: from index 0.53 of *Feroponera* (Bolton & Fisher 2008), to 1.16 of *Diacamma* (Shattuck & Barnett 2006). For Dolichoderinae, it is 3.4 times: from 0.65 of *Anillidris* (Shattuck 1992; Schmidt *et al.* 2013) to 2.3 of *Leptomyrmex* (Lucky & Ward 2010). For Myrmicinae it is 4.6 times: from 0.28 of *Metapone* (Alpert 2007) to 1.3 of *Aphaenogaster* (Shattuck 2008). For Formicinae it is 6.2

times: from 0.34 of *Cladomyrma* (Agosti *et al*. 1999) to 2.13 of *Euprenolepis* (La Polla 2009). Althought recent subfamilies have higher species diversity and occupy more ecological niches compared to Cretaceous taxa, Sphecomyrmini, even compared to them, can be viewed as quite a homogeneous group in terms of the variations of the index SL/HL. Moreover, it seems unlikely that the scape length can be as stable at the subfamily level as it is at the species or genus level, and therefore it cannot be considered a diagnostic character of a subfamily.

Finally, another important character listed in the diagnosis of Armaniinae is the shape of a petiole: in Armaniinae the petiole is poorly separated from the gaster, it is even more primitive than in Amblyoponinae, and resembles the petiole of non-ant Vespoidea (i.e. Sierolomorphidae), while in Sphecomyrminae the petiole is nodiform (Dlussky 1999b). This may be the only remaining serious argument to maitain a special status of Armaniidae, as such an articulation of the petiole and the gaster is unique and obviously plesiomorphic. Thus let us focus more on this character.

The first glance at drawing and photos of Armaniinae immediately convinces us that the conclusion about a unique plesiomorphic petiole of Armaniinae is premature. For example, in *Orapia*, *Pseudoarmania*, *Armania curiosa* petiole is quite rounded, not different from the petiole of Sphecomyrminae. Other impressions of Armaniinae are of too poor quality to draw a conclusion about the shape of their petioles. For example, in *Khetanaia*, *Armania pristina*, *Armania capitata* the petioles are so poorly differentiated that (if it is not a result of a poor preservation) there is a reason to doubt the assignation of these specimens to the ants.

In putative males of Armaniinae (*Archaeopone* and *Poneropterus*), the petiole also does not look different from that of putative males of Sphecomyrminae. Only in *Baikuris* (Sphecomyrminae) the petiole is nodiform and clearly separated from the gaster; but in males of *Sphecomyrma* and *Dlusskyridris* it could easily leave impressions like *Archaeopone* and *Poneropterus*. In *Sphecomyrma* and *Dlusskyridris* petioles are more broadly articulated with the gaster, and the nodes are only slightly outlined; but at the same time, their nodes are even smaller than in *Poneropterus*. It is important to emphasize that the very presence of the petiolar node in *Poneropterus* indicates that the petiole is *thickened in the middle*, thus it cannot be broadest at the point of its attachment to the gaster. Poor quality impressions of *Archaeopone* give us no useful information.

The only exception among Armaniinae is quite a clear impression of *Armania robusta* with a relatively massive petiole, which looks indeed broadly articulated with the gaster (interestingly, this particular specimen Wilson (1987) considered as a gyne of *Sphecomyrma*, explaining that the difference of its petiole from the petiole of Sphecomyrma is a sexually dimorphic feature, i.e. it is not a subfamilial or even species-level character). However, a careful examination of the holotype of *Armania robusta* allows to to conclude that the petiole is not fully visible - its ventral part is covered by the coxa, and thus it is possible that in this case, again, there are no significant differences from the petiole of Sphecomyrminae.

Furthermore, an explanation of a "broad attachment" does not exist in the literature (as it has been before no explanation of extensively used term "short scape"). Again, I tried to fill this void measuring both the petiole of the holotype of *Armania robusta* and several species of stem and crown ants, and calculating index PG/PH, which most accurately describes the width of the petiole-gaster attachment.

The value of this index in ants with the nodiform petiole is the following: in workers of *Sphecomyrmodes subcuspis* - 0.5, in *Sphecomyrma freyi* - 0.6, in *Boltonimecia* and gynes of *Leptanilla* - 0.7. The value of this index in the gyne of *Armania rubusta* is greater (i.e. petiole more broadly articulated with the gaster) - 0.8. But in workers and gynes of Amblyoponinae (as exemplified by several species of *Stigmatomma*) it varies from 0.7 to 0.9. Thus I cannot draw an unambiguous conclusion that the petiole of *Armania robusta* has a unique status in terms of the width of its articulation with the gaster.

Therefore having rejected all the "unique" characters of Armaniinae, we arrive at the only difference: Sphecomyrminae known to us from ambers, while Armaniinae - only from rock impressions (except for *Dolichomyrma*, which relationship to the ants is doubtful - see below). This fact should have drawn our attention from the very beginning, as it drew attention of Wilson (1987).

If approached from a strict taxonomic point of view, we should agree with Wilson (1987) that Armaniinae as a subfamily has to be abandoned, because this taxon does not have any difference worth of the subfamily level, to say nothing of the family one. The existence of Armaniinae needed rather from the purely heuristic point of view - because we have to have an ancestral group of ants with a short scape and poorly separated petiole as required by a modern paradigm of the origin of the ants. But the scheme of synonimization proposed by Wilson is too straightforward. It is worth recalling that Wilson was biased against a high generic diversity of stem ants, and thus almost all known genera at that time he placed in the genus *Sphecomyrma* (Wilson 1987) (this explains, by the way, his error in the interpretation of the morphology of *Boltonimecia*).

My approach to the interpretation of the taxonomic position of Armaniinae is similar to that of Grimaldi *et al.* (1997). Those genera of Armaniinae, which are relatively well preserved and which I used in the statistical analysis (*Armania*, *Pseudoarmania*, *Orapia*), I transfered to *Sphecomyrmini*^{P}. All other genera I left as genera of uncertain taxonomic position within *Formicidae*^{P} or Aculeata. *Orapia* could be also viewed as a genus of an uncertain position within *Formicidae*^{P}, because its rock impression is of a very poor quality. At least, it is obvious that *Orapia* is neither a representative of Myrmeciinae as it has been thought before (Wilson & Hölldobler 2005), nor representative of other crown ant clades. Antennal morphometry demonstrates that *Orapia* is a typical stem ant probably closely related to Sphecomyrmini.

Tribe Haidomyrmecini Bolton, 2003

Taxonomic history: Haidomyrmecini as tribe of Sphecomyrminae: Bolton 2003: 74.

Diagnosis (workers, gynes). (1) head capsule unspecialized; (2) mandibles long, scythe or L-shaped (putative apomorphy); (3) anterolateral margins of clypeus not expanded over the bases of mandibles; (4) clypeal peg-like setae absent; (5) ocelli present or absent; (6) length of antennomeres variable; (7) the terminal flagellomere sometimes not elongated; (8) neck long; (9) petiole pedunculate; (10) gastral constriction present or not.

Comment. Under the PhyloCode, the taxon should be named "*Haidomyrmecini*^{P}, converted clade name" and defined as "the clade consisting of *Haidomyrmex cerberus* Dlussky, 1996 and all species that share a more recent common ancestor with *Haidomyrmex cerberus* Dlussky, 1996 than with *Sphecomyrma freyi* Wilson & Brown, 1967 or *Boltonimecia canadensis* (Wilson 1985)".

Composition. Genera *Haidomyrmex* Dlussky, 1996, *Haidomyrmodes* Perrichot, Nel, Néraudeau, Lacau, Guyotet, 2008, *Haidoterminus* McKellar, Glasier & Engel, 2013.

Discussion. This group is very morphologically distinct, and highly specialized mandibles is its main character. In terms of antennal morphometry, the group is very heterogenous, although some important patterns can be observed.

Concerning the scape indexes, Haidomyrmecini are different from Sphecomyrmini in having greater index values, although not as great as in crown ants. Mean value of SL/HL is 1.4 times greater than that of Sphecomyrmini; SL is about 30% of the length of FL (20% in Sphecomyrmini). Index F1L/HL of Haidomyrmecini is also occupies an intermediate position between crown ants and Sphecomyrmini: it is less than in Sphecomyrmini (on average 2 times), but not as small as in crown ants. All other antennal indexes are only slightly different from those of Sphecomyrmini.

Compared to Sphecomyrmini, there is no pattern F1L>P<F2L (many exceptions). However at generic level, some patterns in the ratio of the first two flagellomeres can be noted: *Haidomyrmex* - F2L>F1L, *Haidomyrmodes* - F2L=F1L, *Haidoterminus* - F1L>F2L.

The situation with the gaster constriction is not clear. *Haidomyrmodes* has the gastral constriction, but highly likely it is an artifact of preservation. But even if the constriction is present, the situation can be viewed as the same as in Sphecomyrmini: this character is not so important in stem ants as in crown ants, and is probably a variable character even within a genus.

Tribe Boltonimeciini trib.n.

Diagnosis (workers). (1) head capsule specialized: wider than longer; frontal part rough and thickened ("shield-like head"), separated anteriorly from the clypeus by impression, and laterally limited by fossae in which scapes are moving (putative apomorphy); (2) mandibles bent almost at 90°; (3) base of mandibles concealed by large expansion of anterolateral margin of clypeus (putative apomorphy); (4) peg-like setae present; (5) ocelli absent; (6) the length of antennomeres variable; (7) neck long; (8) foreleg with three spurs: one pectinate and two simple (putative apomorphy); (9) petiole pedunculate; (10) gastral constriction absent.

Comment. Under the PhyloCode, the taxon should be named "*Boltonimeciini*^{P}, converted clade name" and defined as "the clade consisting of *Boltonimecia canadensis* (Wilson 1985) and all species that share a more recent common ancestor with *Boltonimecia canadensis* (Wilson 1985) than with *Sphecomyrma freyi* Wilson & Brown, 1967 or *Haidomyrmex cerberus* Dlussky, 1996".

Composition. Genera *Boltonimecia* gen.nov. from Canadian amber and *Zigrasimecia* Barden & Grimaldi, 2013 from Burmese amber.

Discussion. Because of a short scape, long funiculus, clypeus which is not inserted between antennal sockets, two spurs on meso- and metatibia, and pretarsal claws with a preapical tooth, *Boltonimecia* certainly belongs to stem ants, and is closest to the subfamily Sphecomyrminae. The only uncertainty of *Boltonimecia*'s morphology and the diagnosis of Sphecomyrminae given by Bolton (2003) concerns the form of metapleural gland orifice and the presence of mesoscutum and scutellum. These characters cannot be observed due to the compression of the mesosoma.

Statistical analyses also leave no doubt about the assignation of *Boltonimecia*, as well as *Zigrasimecia* to stem ants, namely to Sphecomyrminae.

In terms of antennal indexes, *Boltonimecia* and *Zigracimecia* are very similar to Sphecomyrminae, although the scape index of *Boltonimecia* is one of the greatest among Sphecomyrminae and is closer to the indexes of crown ants. Both genera have more elongated pedicels, compared to the average values of Sphecomyrminae; in *Boltonimecia* pedicel is so elongated that PL>F1L as in crown ants, not as in Sphecomyrmini which always have F1L>PL. In *Boltonimecia* and *Zigrasimecia ferox* #1 PL=F2L (in Sphecomyrmini PL<F2L, except for *Sphecomyrmodes occidentalis* which have PL slightly longer than F2L). Also in *Boltonimecia* F1L<F2L (in Sphecomyrmini F1L>F2L without exception).

I believe that *Zigracimecia* is closest to *Boltonimecia*, and they both compose a separate tribe, which, in turn, is closest to Sphecomyrmini.

The specialized head is a unique character of this clade, although it is possible that this character is also present in some newly described species of *Sphecomyrmodes* (Barden & Grimaldi 2014).

Alterolateral margins of clypeus with projections covering the bases of mandibles is also a unique character, which was recently described in two species of *Sphecomyrmodes* (S.*spiralis* and S.*tendir*) (Barden & Grimaldi 2014).

Three spurs of protibia present in *Zigrasimecia ferox* (Perrichot 2014) and in *Boltonimecia*. This character also has been recently described in four species of *Sphecomyrmodes* (S.*spiralis*, S.*subcuspis*, S.*magnus*, S.*rubustus*) (Barden & Grimaldi 2014), though in those species authors call it "two stiff setae". If these setae can be considered spurs, this is another argument for relatedness at least some species of likely polyphyletic genus *Sphecomyrmodes* to the tribe Boltonimeciini.

Characters of Boltonimeciini, which may have potential phylogenetic value, but the final conclusion on which cannot be done at the moment: elongated pedicel and clypeal peg-like setae. In Boltonimeciini pedicel is longer than in most Sphecomyrmini and Haidomyrmecini, but at least in four species of Sphecomyrmini and Haidomyrmecini (*Sphecomyrmodes rugosus*, *S. spiralis*, *Haidoterminus cippus*, *Haidomyrmodes mammuthus*) it is of the same length as in Boltonimeciini. Peg-like setae are also present in *Sphecomyrmodes and Gerontoformica*, and, as it has been already mentioned, it is very unlikely that this character is significant for classification.

Concerning a subclade composition of the crown group *Formicidae*^{P}, 16 recent subfamilies form monophyletic clades. Thus phylogeny-based classification of *Formicidae*^{P} will be congruent with the well established Linnean system (Bolton 2003; Brady *et al*. 2006, 2014). In Table S18, I give a formal phylogenetic definition of the subclades of *Formicidae*^{P} with the authors of converted clade names. It is important to emphasize that the name of the author of a phylogenetic clade is different from the name of the author of a corresponding subfamily, because according to International Code of Zoological Nomenclature, the author is one who named and diagnosed a taxon (ICZN 1999), but in Phylocode - one who just established a name in its current spelling (Cantino & de Queiroz 2010).

For clade definition in Table S18, I chose such and so many specifiers (species), which would be enough to keep a clade definition unchanged after future thorough molecular analysis. Attention was also paid to a recommendation that type species (article 11.7, PhyloCode, 2010) and species used in reference phylogenies (article 11.8, PhyloCode, 2010) should be preferably used as specifiers. Thus, phylogenetic definition of most subfamilies is straightforward, as they based on genera, which are already included in the available phylogenies (Brady *et al.* 2006; Moreau *et al.* 2006, Schmidt 2013, Ward *et al.* 2010, 2014, 2016). For most clades in Table S18, I gave a node-based definition. For clades consisting of one extant species (*Martialinae*^{P}, *Paraponerinae*^{P}, *Agroecomyrmecinae*^{P}, *Aneuretinae*^{P}), a node-based definition is not possible, thus a branch-based definition is given.

Now an important question arises: what fossil ants can be placed in these subclades of *Formicidae*^{P}? The vast majority of presently known fossil ants (Cenozoic only) either fall into clades that would correspond to Linnean tribes or genera. Some Cretaceous species (*Brownimecia* is a good example) probably are stem taxons of a clade of higher (supra-subfamilial) level, and only a few Cretaceous species are closely related to recent subfamilies (or clades for which a formal definitions given in Table S18), but do not fall into any recent tribe; i.e. from the point of view of phylogenetic systematics, they are equivalent to that Linnean subfamilies with which they have the closest relatedness (they are stem taxa of corresponding subfamilies). In my opinion, only five such taxa (genera) are known at the moment. They are sister taxa to three recent subfamilies, thus forming with them pan-clades.

Pan-Formicinae

Diagnosis (workers, gynes). (1) acidopore present (apomorphy); (2) sting absent; (3) helcium attached low on anterior face of abdominal segment III.

Comment. Under the PhyloCode, the taxon should be named "*Pan-Formicinae*^{P}, new clade name" and defined as "the total clade composed of the crown clade *Formicinae*^{P} and all extinct species that share a more recent common ancestor with *Formicinae*^{P} than with any extant species that are not members of *Formicinae*^{P}".

Composition. *Formicinae*^{P} and *Kyromyrma* Grimaldi & Agosti, 2000.

Discussion. *Kyromyrma* possess generalised morphology (Grimaldi & Agosti 2000) and thus cannot be a member of any recent tribe of Formicinae. There is no doubt that *Kyromyrma* is a representative of stem formicines (Ward 2007), i.e. it belongs to a clade *Pan-Formicinae*^{P}. Given that the crown group *Formicinae*^{P} arose around 80 Ma (Brady *et al.* 2006), the age of *Kyromyrma* (92 Ma) is consistent with this assumption.

Pan-Dolichoderinae

Diagnosis (workers, gynes). (1) junction of pygidium and hypopygium slit-like (apomorphy); (2) sting reduced; (3) helcium attached low on anterior face of abdominal segment III.

Comment. Under the PhyloCode, the taxon should be named "*Pan-Dolichoderinae*^{P}, new clade name" and defined as "the total clade composed of the crown clade *Dolichoderinae*^{P} and all extinct species that share a more recent common ancestor with *Dolichoderinae*^{P} than with any extant species that are not members of *Dolichoderinae*^{P}".

Composition. *Dolichoderinae*^{P}, *Eotapinoma* Dlussky, 1988, *Zherichinius* Dlussky, 1988, *Chronomyrmex* McKellar, Glasier & Engel, 2013.

Discussion. As Dlussky (1988, 1999a) has noted, such stem dolichoderines as *Eotapinoma* (Sakhalin and Canadian amber) and *Zherichinius* (Sakhalin amber) have similarities with both Dolichoderinae, and Formicinae. This is not surprising, given that they are not far from the common ancestor of both subfamilies, who lived around 100 Ma (based on assessment of Dolichoderinae+Aneuretinae emergence time by Ward *et al.* 2010 and assuming that separation of Formicinae occured very close to that point). Therefore, doubts about assigning these genera to Dolichoderinae arise, as they could be members of Formicinae (Dlussky 1999a). However, the idea that Dolichoderinae and Formicinae are closely related was based only on morphological data. According to molecular studies, Dolichoderinae is not closely related to Formicinae, but more closely related (along with Aneuretinae) to Pseudomyrmicinae+Myrmicinae (Brady *et al.* 2006; Moreau *et al.* 2006; Rabeling *et al.* 2008), i.e. to subfamilies with two-segmented waist, a distinct character which must be clearly seen in fossil ants. Therefore, we should have little doubt about the assignation of *Eotapinoma* and *Zherichinius* to the clade *Pan-Dolichoderinae*^{P}. Most likely, these genera are stem dolichoderines (Ward *et al.* 2010). Because of a poor preservation of *Zherichinius*, we cannot also reject its possible inclusion in the crown dolichoderines (*Dolichoderinae*^{P}), since they originated around 60-67 Ma (Ward *et al*. 2010), and therefore hypothetically can be presented in Sakhalin amber which is 56-59 Ma.

Eotapinoma is similar to recent representatives of the tribe Tapinomini, but preservation of specimens from Sakhalin amber (Dlussky 1988) is quite poor, so it is difficult to make a final conclusion. Another specimen of this genus known from Canadian amber (Dlussky 1999a), described briefly, and is now lost[2]. Therefore an unambiguous conclusion that the two specimens represent the same genus is not possible. According to Dlussky (1988), one more specimen of this genus is known from Baltic amber (Wheeler 1915). However, new genus has been established for this specimen (Heterick & Shattuck 2011). It is likely that a similar destiny would occur for the Canadian amber species. It looks like *Eotapinoma* is a collective group name for all ant-like entities with reduced petiole. The only conclusion that can be drawn is that, at least in terms of the age, the specimen from Canadian amber is a stem dolichoderine (Ward *et al.* 2010).

McKellar *et al.* (2013a) included *Chronomyrmex* (Canadian amber) in Leptomyrmecini based on the observation that it possesses all the characters of Leptomyrmecini as listed by Ward *et al.* (2010). But in light of the fact that the tribe Leptomyrmecini diagnosed as morphologically heterogenous assemblage recorded primary by disagreement with the three other tribes (Ward *et al.* 2010), it is clear that *Chronomyrmex* simply has no characters of other tribes; and, given time of its emergence, it simply cannot belong to the crown dolichoderines (and as a result to any recent dolichoderine tribe). This genus is a stem taxon of Dolichoderinae, or (less probably though) a stem taxon of all dolichoderomorphs (Dolichoderinae+Aneuretinae).

Pan-Ectatomminae

Diagnosis (workers, gynes). (1) clypeus broadly incerted between frontal lobes; (2) outer margins of frontal lobes not pinched in posteriorly; (3) abdominal segment III with a girdling constriction; (3) helcium projects from about the midheight of the anterior face of abdominal segment III; no high vertical aterior face to abdominal segment III above the helcium.

Comment. Under the PhyloCode, the taxon should be named "*Pan-Ectatomminae*^{P}, new clade name" and defined as "the total clade composed of the crown clade *Ectatomminae*^{P} and all extinct species that share a more recent common ancestor with *Ectatomminae*^{P} than with any extant species that are not members of *Ectatomminae*^{P}".

Composition. *Ectatomminae*^{P}, *Canapone* Dlussky, 1999.

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[2] Despite a statement that the holotypes of *Eotapinoma macalpini* and *Canapone dentata* (see below) have been deposited in CNC (formerly Biosystematic Research Center) (Dlussky 1999a), they in fact have never been deposited there after the description. All my attempts to find them were in vain, so at the moment both holotypes have to be declared as lost.

Discussion. The characters are from Bolton (2003), but the first and second character should be viewed as putative, as the morphology of the anterodorsal head of *Canapone* is invisible. *Canapone* (Canadian amber) was originally placed in Ponerinae (Dlussky 1999a), then transfered to Ectatomminae incertae sedis (Bolton 2003). It is very likely that *Canapone* is a member of Ectatomminae (see Bolton 2003, p.46 for justification), but it cannot be placed in any recent ectatommine tribe as it is unique in having plesiomorphies lost by recent species (Bolton 2003).

Aculeata incertae sedis

Genera: *Cretopone* Dlussky, 1975, *Dolichomyrma* Dlussky, 1975, *Khetania* Dlussky, 1999, *Petropone* Dlussky, 1975.

Discussion. These four Cretaceous genera cannot be placed in any clade or Linnean taxon. Preservation of three of them is so poor that there is even a doubt that they belong to the ants. I agree with Grimaldi *et al.* (1997) that *Cretopone* and *Petropone* are Aculeata insertae sedis, as they have no one ant synapomorphy visible. *Khetania* also has no ant synapomorphy, its petiole is poorly defined, antennae are not preserved. *Dolichomyrma* draws attention by its small size (3-5 mm) and the absence of wings like that of worker ants. Its petiole has no node, which is why Dlussky initially believed it is a dolichoderine or specialized sphecomyrmine (Dlyssky 1975), but then placed it in Armaniidae (Dlussky 1983). I believe *Dolichomyrma* must be placed in Aculeata incertae sedis, because it has no ant synapomorphies, and its petiole very similar to the petiole of some Bethylidae.

Conclusion: origin and evolution of the ants

Almost half a century ago Wilson *et al.* (1967) discovered Cretaceous *Sphecomyrma,* a primitive ant with plesiomorphic characters, claimed to be the ancestor either of one of two branches of the ant lineage (Wilson *et al*. 1967) or all living ants (Taylor 1978). In the past fifty years other ants, 10 Ma older than *Sphecomyrma* have been discovered. There is now general agreement that Cretaceous stem ants are not only very diverse but also very specialized. If primitive stem lineages existed alongside representatives of the crown group such as *Kyromyrma*, *Canapone*, *Eotapinoma*, and *Brownimecia* then the former can not be the direct ancestors of the latter. Stem groups like Sphecomyrminae are the result of a primary radiation at the base of Formicidae; the true ancestor of both stem ants and crown ants has to have existed before them.

There is no consensus of opinion about the true ancestor of ants. Wheeler (1926) proposed the *Myzine* genus of Tiphiidae as the taxa closest to ants; Wilson et al (1967) concurred about Tiphiidae but chose the genus *Methocha*. Dlussky & Fedoseeva (1988) argued that ancestor claims for groups in which the females are wingless leaves unexplained the secondary emergence of wings in ants.

With the emergence of cladistics there was a hope it would be possible to delineate the origins of ants. However, the issue became even more complicated. The first morphological cladistic study by Brothers (1999) showed that ant's sister-group to be Vespidae + Scoliidae. DNA analysis of Hymenoptera (Heraty *et al*. 2011) showed ants' sister groups range from a clade of Mutillidae + Sapygidae + Tiphiidae + Bradynobaenidae + Pompilidae + Scoliidae to Sphecidae + Scoliidae. Similarly another study (Peters *et al*. 2011) showed ants' sister groups to be either Vespidae + Mutillidae + Bradynobaenidae + Bethylidae + Pompilidae or Tiphidae with close close links to Mutilidae and Plumaridae. A study combining molecular and morphological data of Vespoidea (Pilgrim *et al*. 2008) showed that ants' sister groups range from Sapygidae + Bradynobaenidae to Vespidae + Rhopalostomatidae with very close links to Scoliidae + Bradobaenidae. A phylogenomic study (Johnson *et al*. 2013) based on an analysis of the genomes and transcriptomes of 11 species of Aculeata unexpectedly concluded that ants are a sister group not of Vespoidea but of Apoidea.

Although there is no consensus in the research data it is possible to conclude that none of the now living species is the ant ancestor. Also an ancestor of several groups of Aculeata rather than an ancestor of a single group is closest to the ants. What did the ant ancestor look like? Many stem ants have long legs suggesting an arboreal lifestyle; the fact they are preserved in amber is secondary evidence of this. Nevertheless we now have a good reason to think that the ant ancestor did not have *Sphecomyrma*-like morphology and was neither arboreal nor above-ground but rather cryptic.

Extant primitive ants (Martialinae, Leptanillinae, poneroids) are small cryptic subterranean species. These groups, of course, could have evolved from above ground ancestors but the general trend of ants' morphological evolution suggests otherwise and so there is some reason to believe the ant ancestor was cryptic too. Increased mobility of the gaster with the resulting separation of a petiole is likely indication of an adaptation to underground lifestyle. This type of adaptation is also recognizable in the emergence of the metapleural gland that performs a sanitation function in underground colonies (Yek & Mueller 2011). Therefore the first ants probably enjoyed an underground lifestyle (Lucky *et al.* 2013); Martialinae and other primitive forms may be viewed as examples of an early diversification, relics changed little during the evolution because of very stable habitats (Rabeling *et al*. 2008).

Unfortunately, finding preserved specimens of such ancestral ants is unlikely. The reasons are in their (1) number (for example Late Cretaceous ants comprise only 0.001 - 0.05% of all insects preserved in amber (Grimaldi & Agosti 2000), so one might hazard that the number of ants in amber of an earlier period would be even lower); (2) cryptic lifestyle (the fact that ants are not found in the Early Cretaceaous deposits, for example in ambers from Spain and Lebanon, as well as in the Santana Formation of Brazil and the Yixian Formation of China may show that 145-110 Ma ago ants did not exist (LaPolla *et al*. 2013); an alternative hypothesis to explain this lack of evidence is that the first ants were subterranean and/or litter-dwellers); (3) small size that precludes finding impressions in rocks. However ichnofossils such as those of putative report from the Upper Jurassic Morrison Formation dated 156-146 Ma (Hasiotis & Demko 1996) may be traces of these ants.

Phenotypic plasticity and the construction of ecological niches are the two most probable major factors in ants' evolutionary success. Phenotypic plasticity is the capacity of a single genotype to exhibit variable phenotypes (behavioral, biochemical, physiological, developmental) in response to different environmental conditions (West-Eberhard 2003; Pigliucci *et al.* 2006). Ants are a good example of animals exhibiting phenotypic plasticity, a widespread phenomenon that can facilitate evolutionary change and specialization (Price *et al.* 2003). One example is polyphenism, which is a discrete case of phenotypic plasticity. Under strong environmental or genetic disturbances, cryptic genetic variation becomes expressed that leads to emergence of intercastes, which are protected and isolated in colonies from individual selection outside the nest. The evolution of complex caste systems in ants is likely to be the result of multiple episodes of mosaic intercastes being integrated in the genome. Thus intercastes are a basis for evolutionary innovation in ants leading to a high rate of evolution of new phenotypes (Molet *et al.* 2012).

Niche construction signifies a modification of the environment that results in modification of the pressures of natural selection. Odling-Smee *et al.* (2003) claim that niche construction "should be regarded, after natural selection, as a second major participant in evolution". In the time after the Mesozoic extinction, crown ants not only occupied vacant niches of stem ants, the niches of active above-ground and arboreal predators, but also actively constructed their own niches. The importance of niche construction by ants is difficult to overestimate because of the fact that ants are among the most active ecosystem engineers (Folgarait 1998).

In conclusion the following is a history of the evolution of ants. Ants originated in the Upper Jurassic in litter and soil (Wilson & Hölldobler 2005), or exclusively in soil (Lucky *et al.* 2013). Those first underground ants just started to switch between a solitary and social lifestyle. They had a primitive broad articulation of petiole and abdomen as found in Amblyoponinae; other features expected to be present are reduced eyes and the trochantellus.

In the late Cretaceous, about 100 Ma ago, stem ants were already diversified, mainly arboreal, having nuptial flight, eusociality or at least were at a stage of facultative sociality. From the earliest evidence of ants in Albian amber as well as of imprints in stone dated 100 Ma ago, and the latest evidence of Canadian amber (Campanian) dated 79 Ma ago, it seems stem ants existed for about 20 Ma. Without hard evidence it appears stem ants existed until the Mesozoic extinction event 66 Ma ago.

The common ancestor of crown ants lived about 123 Ma (from 141 to 116 Ma) ago (Brady *et al*. 2006; Schmidt 2013). Moreau et al. (2006) extend the upper limit of the range to 168 Ma. Accepting the arguments against this extended limit (Brady *et al*. 2006), the date of origin of the crown clade may be set at a maximum of 140 Ma, near the time line between the Jurassic and Cretaceous, 40 Ma before all known stem ants.

Throughout the Cretaceous period stem ants and crown ants existed alongside one another. In forests where Angiosperms came to dominate (Moreau *et al.* 2006) both stem ants and crown ants underwent some diversification and specialization. There was a transformation of the terrestrial ecosystems after the major biotic extinction at the end of the Mesozoic, during which about 47% of genera and 76% of species of plants and animals became extinct (Jablonski and Chaloner 1994); Wilf & Johnson (2004) put the number of extinct plant species in North America at 57%. Stem ant groups specialized for arboreal life were doomed. The crown ants were able to survive the extinction event and occupied the stem ants' former arboreal niches. Crown ants then enjoyed a dynamic radiation, occupied various niches and began to construct their own ecological niches.

The evolutionary destiny of ants is thus similar to mammals. In having the opportunity to find or create niches after the big reptiles disappeared, mammals had the same luck as ants after their competitors were removed from the ecosystems. After the Mesozoic extinction event both ants and mammals enjoyed remarkable adaptive radiations; in the invertebrate microworld and vertebrate macroworld respectively they became successful terrestrial predators due to phenotypic plasticity, brood support systems and eusociality.

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References

Agosti, D., Moog, J., & Maschwitz, U. (1999) Revision of the Oriental plant-ant genus *Cladomyrma*. *American Museum Novitates*, 3283, 1-24.

Alpert, G. D. (2007) A review of the ant genus *Metapone* Forel from Madagascar. *Memoirs of the American Entomological Institute*, 80, 8-18.

AntWeb [online]. Available from http://www.antweb.org [accessed 1 September 2015].

Archibald, S.B., Johnson, K.R., Mathewes, R.W., & Greenwood, D.R. (2011) Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. *Proceedings of the Royal Society. Series B, Biological Sciences*, 278, 3679-3686.

Ax, P. (1985) Stem species and the stem lineage concept. *Cladistics*, 1, 279-287.

Baroni Urbani, C., Bolton, B., & Ward, P.S. (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). *Systematic Entomology*, 17, 301-329.

Baroni Urbani, C., & De Andrade, M.L. (2003) The ant genus *Proceratium* in the extant and fossil record (Hymenoptera: Formicidae). *Regionale di Scienze Naturali Monografie (Turin)*, 36, 1-492.

Barden, P. & Grimaldi, D.A. (2012) Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *American Museum Novitates*, 3755, 1-16.

Barden, P. & Grimaldi, D. (2013) A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa*, 3681, 405-412.

Barden, P. & Grimaldi, D. (2014) A Diverse ant fauna from the Mid-Cretaceous of Myanmar (Hymenoptera: Formicidae). *PloS One*, 9, e93627.

Baum, D.A. & Smith, S.D. (2012) Tree thinking: an Introduction to phylogenetic biology. Roberts and Company, Greenwood Village, Colorado.

Bock, W. J., & Farrand, J. (1980) The number of species and genera of recent birds: a contribution to comparative systematics. *American Museum novitates*, 2703.

Bolton, B. (1973) A remarkable new arboreal ant genus (Hym. Formicidae) from West Africa. *Entomologist's Monthly Magazine*, 108, 234-237.

Bolton, B. (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge.

Bolton, B. (2003). Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1-370.

Bolton, B. (2007) Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute*, 35, 1-150.

Bolton, B., & Fisher, B. L. (2008) Afrotropical ants of the ponerine genera *Centromyrmex* Mayr, *Promyopias* Santschi gen. rev. and *Feroponera* gen. n., with a revised key to genera of African Ponerinae (Hymenoptera: Formicidae). *Zootaxa*, 1929, 1-37.

Bolton, B., & Fisher, B.L. (2011) Taxonomy of Afrotropical and West Palaearctic ants of the ponerine genus *Hypoponera* Santschi (Hymenoptera: Formicidae). *Zootaxa*, 2843, 1-118.

Brady, S.G., Fisher, B. L., Schultz, T.R., & Ward, P.S. (2014) The rise of army ants and their relatives: diversification of specialized predatory doryline ants. *BMC Evolutionary Biology*, 14, 93.

Brady, S.G, Schultz, T.R., Fisher, B.L., & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences*, 103, 18172-18177.

Brady, S.G., & Ward, P.S. (2005) Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae). *Systematic Entomology*, 30, 593-618.

Brothers, S.O. (1975) Phylogeny and classification of the Aculeate Hymenoptera, with special reference to Mutillidae. *University of Kansas Science Bulleti*n, 50, 483-648.

Brothers, D.J. (1999) Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysidoidea, Vespoidea and Apoidea). *Zoologica Scripta*, 28, 233-250.

Cantino, P.D., & Queiroz de, K. (2010) International code of phylogenetic nomenclature, ver. 4c [online]. Available from http://www. ohiou.edu/phylocode/ (accessed 1 September 2015).

Dlussky, G.M. (1975) Superfamily Formicoidea Latreille, 1802. Family Formicidae Latreille, 1802. *In*. A.P. Rasnitsyn (Ed.) *Hymenoptera Apocrita of Mesozoic*. Transactions of the Paleontological Institute, Academy of Sciences of the Union of Soviet Socialist Republics, Nauka Publishing House, Moscow, 147, pp. 114–122. [In Russian].

Dlussky, G.M. (1983) A new family of Upper Cretaceous Hymenoptera: an ‘‘intermediate link’’ between the ants and the scolioids. *Paleontologicheskii Zhurnal*, 3, 65-78. [In Russian].

Dlussky, G.M. (1987) New Formicoidea (Hymenoptera) of the Upper Cretaceous. *Paleontologicheskii Zhurnal*, 1, 131-135. [In Russian.]

Dlussky, G.M. (1988) Ants of Sakhalin amber (Paleocene?). *Paleontologicheskii Zhurnal*, 1**,** 50-61. [In Russian.]

Dlussky, G.M. (1996) Ants (Hymenoptera: Formicidae) from Burmese amber. *Paleontological Journal*, 30, 449-454.

Dlussky, G.M. (1999a) New ants (Hymenoptera, Formicidae) from Canadian amber. *Paleontologicheskii Zhurnal*, 4, 73-76. [In Russian.]

Dlussky, G.M. (1999b). The first find of the Formicoidea (Hymenoptera) in the lower Cretaceous of the northern hemisphere. *Paleontologicheskii Zhurnal*, 3, 62-66. [In Russian.]

Dlussky, G.M., & Fedoseeva, E.B. (1988) Origin and early stages of evolution in ants. *In* A.G.Ponomarenko (Ed.) *Cretaceous biocenotic crisis and insect evolution*. Nauka, Moskva. pp. 70-144. [In Russian.]

Dlussky, G.M., Brother, D.J., & Rasnitsyn, A.P. (2004) The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. *Insect Systematics and Evolution*, 35, 1-13.

Dubois, A. (2007) Phylogeny, taxonomy and nomenclature: the problem of taxonomic categories and of nomenclatural ranks. *Zootaxa*, 1519, 27-68.

Engel, M.S., & Grimaldi, D.A. (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). *American Museum Novitates*, 3485, 1-23.

Ereshefsky, M. (2001) *The poverty of the Linnaean hierarchy: a philosophical study of biological taxonomy*. Cambridge University Press, Cambridge, UK.

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007) G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39, 175-191.

Folgarait, P. J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, 7.9, 1221-1244.

Greggers, U., Koch G., Schmidt, V., Dürr A., Floriou-Servou, A., Piepenbrock, D., Göpfert, M.C., & Menzel R. (2013) Reception and learning of electric fields in bees [online]. *Proceedings of the Royal Society B*, 280: doi:10.1098/rspb.2013.0528.

Grimaldi, D., Agosti, D., & Carpenter, J.M. (1997) New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. *American Museum Novitates*, 3208, 1-43.

Grimaldi, D., & Agosti, D. (2000) A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. *Proceedings of the National Academy of Sciences of the United States of America*, 97, 13678-13683.

Hasiotis S.T., & Demko T.M. (1996) Terrestrial and freshwater trace fossils, upper Jurassic Morrison formation, Colorado Plateau. *In* M.Morales (Ed.) *The Continental Jurrasic*. Mus. Nothern Arizona Bull. pp. 355-370.

Hennig, W. (1966) *Phylogenetic systematics*. University of Chicago, Chicago, USA.

Heraty, J., Ronquist, F., Carpenter, J.M., Hawks, D., Schulmeister, S., Dowling, A.P., *et al.* (2011) Evolution of the hymenopteran megaradiation. *Molecular phylogenetics and evolution*, 60, 73-88.

Heterick, B.E., & Shattuck, S. (2011) Revision of the ant genus *Iridomyrmex* (Hymenoptera: Formicidae). *Zootaxa*, 2845, 1-174.

Hölldobler, B., & Wilson, E. O. (1990) *The ants*. Harvard University Press, Cambridge, USA.

ICZN. (1999) *International Code of Zoological Nomenclature*. Fourth Edition. The International Trust for Zoological Nomenclature, London, UK.

Jablonski, D., & Chaloner, W.G. (1994) Extinctions in the fossil record (and discussion). *Philosophical Transactions of the Royal Society of London, Series B*., 344, 11-17.

Johnson, B.R., Borowiec, M.L., Chiu, J.C., Lee, E.K., Atallah, J., & Ward, P.S. (2013) Phylogenomics resolves evolutionary relationships among ants, bees, and wasps. *Current Biology*, 23, 2058-2062.

Joyce, W. G., Parham J.F., & Gauthier J.A. (2004) Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology*, 78, 989–1013.

Kamikouchi, A., Inagaki, H.K., Effertz, T., Hendrich, O., Fiala, A., Göpfert, M.C., & Ito, K. (2009) The neural basis of *Drosophila* gravity-sensing and hearing. *Nature*, 458, 165-71.

LaPolla, J. S. (2009) Taxonomic revision of the Southeast Asian ant genus *Euprenolepis*. *Zootaxa*, 2046, 1-25.

LaPolla, J.S., Dlussky, G.M., & Perrichot, V. (2013) Ants and the Fossil Record. *Annual review of entomology*, 58, 609-630.

Linnaeus, C. (1761) *Fauna suecica sistens animalia Sueciae regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes*. Editio altera, auctior. L. Salvii, Stockholm.

Lucky, A., & Ward, P. S. (2010) Taxonomic revision of the ant genus *Leptomyrmex* Mayr (Hymenoptera: Formicidae). *Zootaxa*, 2688, 1-67.

Lucky, A., Trautwein, M.D., Guenard, B.S., Weiser, M.D., & Dunn, R.R. (2013) Tracing the rise of ants-out of the ground. *PloS One*, 8, e84012.

MacKay, W.P. (1993) A review of the new world ant of the genus *Dolichoderus*. *Sociobiology*, 22, 1-148.

McDonald, J.H. (2014) Handbook of Biological Statistics (3rd ed.). Sparky House Publishing, Baltimore, Maryland.

McKellar, R.C. & Wolfe, A.P. (2010) Canadian amber. *In*: D. Penney (Ed.) Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press. pp. 96-113.

McKellar, R.C., Glasier, J.R.N., & Engel, M.S. (2013a) New ants (Hymenoptera: Formicidae: Dolichoderinae) from Canadian Late Cretaceous amber. *Bulletin of Geosciences*, 88, 583-594.

McKellar, R.C., Glasier, J.R.N., & Engel M.S. (2013b) A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. *The Canadian Entomologist*, 145, 454-465.

Molet, M., Wheeler, D.E., & Peeters, C. (2012) Evolution of novel mosaic castes in ants: modularity, phenotypic plasticity, and colonial buffering. *The American Naturalist*, 180, 328-341.

Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., & Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of Angiosperms. *Science*, 312, 101-104.

Nel, A., Perrault, G., Perrichot, V., & Néraudeau, D. (2004) The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geologica Acta*, 2, 23-29.

Odling-Smee, F. J., Laland, K.N., & Feldman, M.W. (2003) *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton.

Perrichot, V. (2014) A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecological News*, 19, 165-169.

Perrichot, V. (2015) A new species of *Baikuris* (Hymenoptera: Formicidae: Sphecomyrminae) in mid-Cretaceous amber from France. *Cretaceous Research*, 52B, 585-590.

Perrichot, V., Nel, A., Neraudeau, D., Lacau, S., & Guyot, T. (2008) New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften*, 95, 91-97.

Peters, R.S., Meyer, B., Krogmann, L., Borner, J., Meusemann, K., Schütte, K., *et al*. (2011) The taming of an impossible child: a standardized all-in approach to the phylogeny of Hymenoptera using public database sequences. *BMC biology*, 9, 55.

Pigliucci, M., Murren, C.J., & Schlichting, C.D. (2006) Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, 209, 2362-2367.

Pilgrim, E.M., Von Dohlen, C.D., & Pitts, J.P. (2008) Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families and subfamilies. *Zoologica Scripta*, 37, 539-560.

Pleijel, F., & Rouse, G.W. (2003) Ceci n'est pas une pipe: names, clades and phylogenetic nomenclature. *Journal of Zoological Systematics and Evolutionary Research*, 41, 162-174.

Price, T. D., Qvarnström, A., & Irwin, D.E. (2003) The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 1433-1440.

Rabeling, C., Brown, J.M., & Verhaagh, M. (2008) Newly discovered sister lineage sheds light on early ant evolution. *Proceedings of the National Academy of Sciences*, 105, 14913-14917.

Radchenko, A.G. (1991) Ants of the genus *Strongylognathus* (Hymenoptera, Formicidae) of the fauna of the USSR. *Zoologicheskii Zhurnal*, 70, 84-90. [in Russian]

Radchenko, A.G. (1994) Identification table for ants of the genus *Myrmica* (Hymenoptera, Formicidae) from central and eastern Palearctic. *Zoologicheskii Zhurnal*, 73, 130-145. [In Russian]

Radchenko, A.G., & Elmes G.W. (1998) Taxonomic revision of the ritae species-group of the genus *Myrmica* (Hymenoptera, Formicidae). *Vestnik zoologii*, 32, 3-27.

Radchenko, A., Elmes, G.W., & Woyciechowski M. (2002) An appraisal of *Myrmica bergi* Ruzsky, 1902 and related species (Hymenoptera: Formicidae). *Annales Zoologici (Warsawa)*, 52, 409-421.

Radchenko, A., & Elmes G.W. (2003) A taxonomic revision of the socially parasitic *Myrmica* ants (Hymenoptera: Formicidae) of the Palaearctic region. *Annales Zoologici*, 53, 217-243.

Rieseberg, L. H., & Burke, J. M. (2001) The biological reality of species: gene flow, selection, and collective evolution. *Taxon*, 50, 47-67.

Schmidt, C. (2013) Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). *Zootaxa*, 3647, 201-250.

Schmidt, F. A., Feitosa, R. M., de Moraes Rezende, F., & Silva de Jesus, R. (2013) News on the enigmatic ant genus *Anillidris* (Hymenoptera: Formicidae: Dolichoderinae: Leptomyrmecini). *Myrmecological News*, 19, 25-30.

Schmidt, A.R., Perrichot, V., Svojtkad, M., Anderson, K.B., Belete, K.H., Bussert, R., *et al.* (2010) Cretaceous African life captured in amber. *Proceedings of the National Academy of Sciences*, 107, 7329–7334.

Seifert, B. (1988) A taxonomic revision of the *Myrmica* species of Europe, Asia Minor, and Caucasus (Hymenoptera, Formicidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, 62, 1-75.

Seifert, B. (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str.(Hymenoptera, Formicidae). *Abhandlungen und Berichte des naturkundemuseums Görlitz*, 66, 1-67.

Seifert, B. (2000) A taxonomic revision of the ant subgenus *Coptoformica* Mueller, 1923 (Hymenoptera, Formicidae). *Zoosystema-Paris*, 22, 517-568.

Seifert, B. (2003) The ant genus *Cardiocondyla* (Insecta: Hymenoptera: Formicidae) - a taxonomic revision of the *C. elegans, C. bulgarica, C. batesii, C. nuda, C. shuckardi, C. stambuloffii, C. wroughtonii, C. emeryi* and *C. minutior* species groups. *Annalen des Naturhistorischen Museums in Wien. B, Botanik, Zoologie*, 104, 203-338.

Shattuck, S. O. (2008) Australian ants of the genus *Aphaenogaster* (Hymenoptera: Formicidae). *Zootaxa,* 1677, 25-45.

Shattuck, S. O. (1992) Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). *Sociobiology*, 21, 1-181.

Shattuck, S. O., & Barnett, N. J. (2006) Australian species of the ant genus *Diacamma* (Hymenoptera: Formicidae). *Myrmecologische Nachrichten*, 8, 13-19.

Stephens, J. F. (1829) A systematic catalogue of British insects: being an attempt to arrange all the hitherto discovered indigenous insects in accordance with their natural affinities. Baldwin & Cradock, London.

Taylor, R. W. (1978) *Nothomyrmecia macrops*: a living-fossil ant rediscovered. *Science*, 201, 979-985.

Taylor, R.W. (1980) Notes on the Russian endemic ant genus *Aulacopone* Arnoldi (Hymenoptera: Formicidae). *Psyche (Cambridge)*, 86, 53-361.

Valentine, J. W. (2004) On the origin of phyla. University of Chicago Press, Chicago.

Ward, P.S. (1999) Systematics, biogeography and host plant associations of the *Pseudomyrmex viduus* group (Hymenoptera: Formicidae), Triplaris-and Tachigali-inhabiting ants. *Zoological Journal of the Linnean Society*, 126, 451-540.

Ward, P. S. (2007) Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). *Zootaxa*, 1668, 549-563.

Ward, P.S., Brady, S.G., Fisher, B.L., and Schultz, T.R. (2010) Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Systematic Biology*, 59, 342-362.

Ward, P.S. (2011) Integrating molecular phylogenetic results into ant taxonomy (Hymenoptera: Formicidae). *Myrmecological News*, 15, 21-29.

Ward, P.S., Brady, S.G., Fisher, B.L., and Schultz, T.R. (2014) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*. doi: 10.1111/syen.12090

Ward, P. S., Blaimer, B. B., and Fisher, B. L. (2016). A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. Zootaxa, 4072(3), 343-357.

West-Eberhard, M.J. (2003) *Developmental plasticity and evolution*. Oxford University Press, New York.

Wheeler, W.M. (1915) The ants of the Baltic Amber. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, 55, 1-142.

Wheeler, W. M. (1926) Les sociétés d'insectes: leur origine, leur évolution. Gaston Doin & Co., Paris, France.

Wild, A. L. (2004) Taxonomy and distribution of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, 97, 1204-1215.

Wilf, P., & Johnson, K. R. (2004) Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafloral record. *Paleobiology*, 30, 347-368.

Wilson, E.O., Carpenter, F.M., & Brown Jr, W.L. (1967) The first Mesozoic ants, with the description of a new subfamily. *Psyche*, 74, 1-19.

Wilson, E.O. (1985) Ants from the Cretaceous and Eocene amber of North America. *Psyche*, 92, 205-216.

Wilson, E.O. (1987) The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology*, 13, 44-53.

Wilson, E.O., & Hölldobler, B. (2005) The rise of the ants: a phylogenetic and ecological explanation. *Proceedings of the National Academy of Sciences*, 102, 7411-7414.

Yanega, D. (1997) Demography and sociality in halictine bees (Hymenoptera: Halictidae). *In* The evolution of social behavior in insects and arachnids. *Edited by* J. Choe and B. Crespi. Cambridge University Press, England. Pp. 293-315.

Yek, S.H., & Mueller, U.G. (2011) The metapleural gland of ants. *Biological Reviews*, 86, 774-791.

Table 1
Measurements (in mm) of leg segments for *Boltonimecia canadensis*

Segment	Foreleg	Middle leg	Hind leg
coxa	0.4	0.34	0.5
femur	0.75	0.85	1.25
tibia	0.75	0.75	1.2
tarsomer I	0.5	0.6	0.9
tarsomer II	0.15	0.25	0.25
tarsomer III	0.2	0.2	0.25
tarsomer IV	0.1	0.15	0.17
tarsomer V	0.15	0.15	0.25
pretarsal claws	0.15	0.15	0.15
total length	***3.3***	***3.6***	***5.07***

Fig.1. Photomicrographs of *Boltonimecia canadensis*

A General habitus, lateral view; **B** Part of the head, anterodorsal view; **C** Clypeus and mandibles; **D** Pretarsal claws; **E** Spurs of metatibia. Scale bar 0.1 mm.

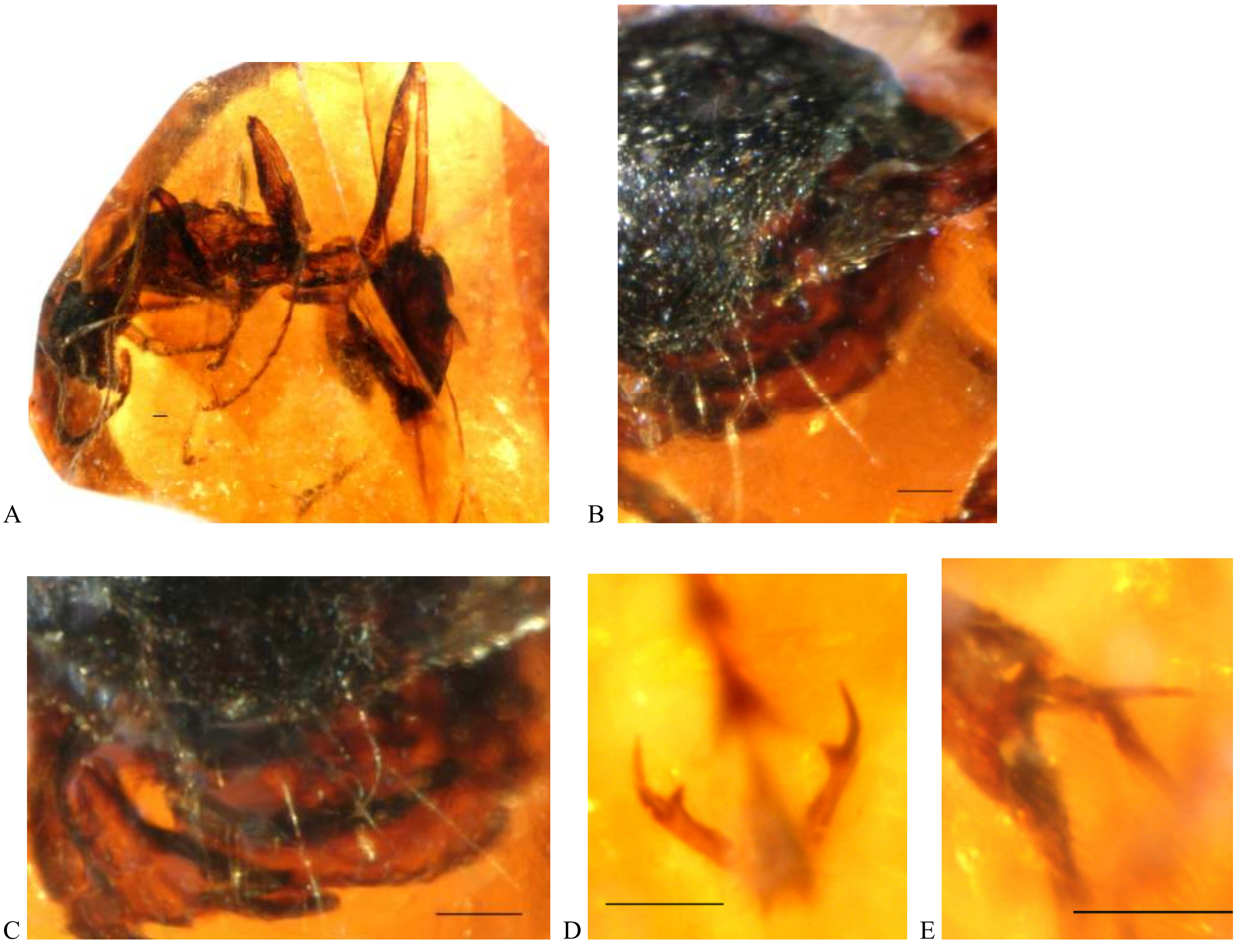


Fig.2. Line drawings of *Boltonimecia canadensis*

A General habitus, lateral view (pubescence covering mesosoma, legs and gaster omitted); **B** Head, anterodorsal view (reconstruction); **C** Head, anterolateral view; **D** Head, dorsal view (reconstruction); **E** Propodeum, lateral view. Scale bar 0.1 mm.

Note that junctions of scapes and pedicels are gone; first two flagellomers of left antenna distorted due to amber compression; right side of head flattened and distorted due to amber compression and thus reconstruction is shown here.

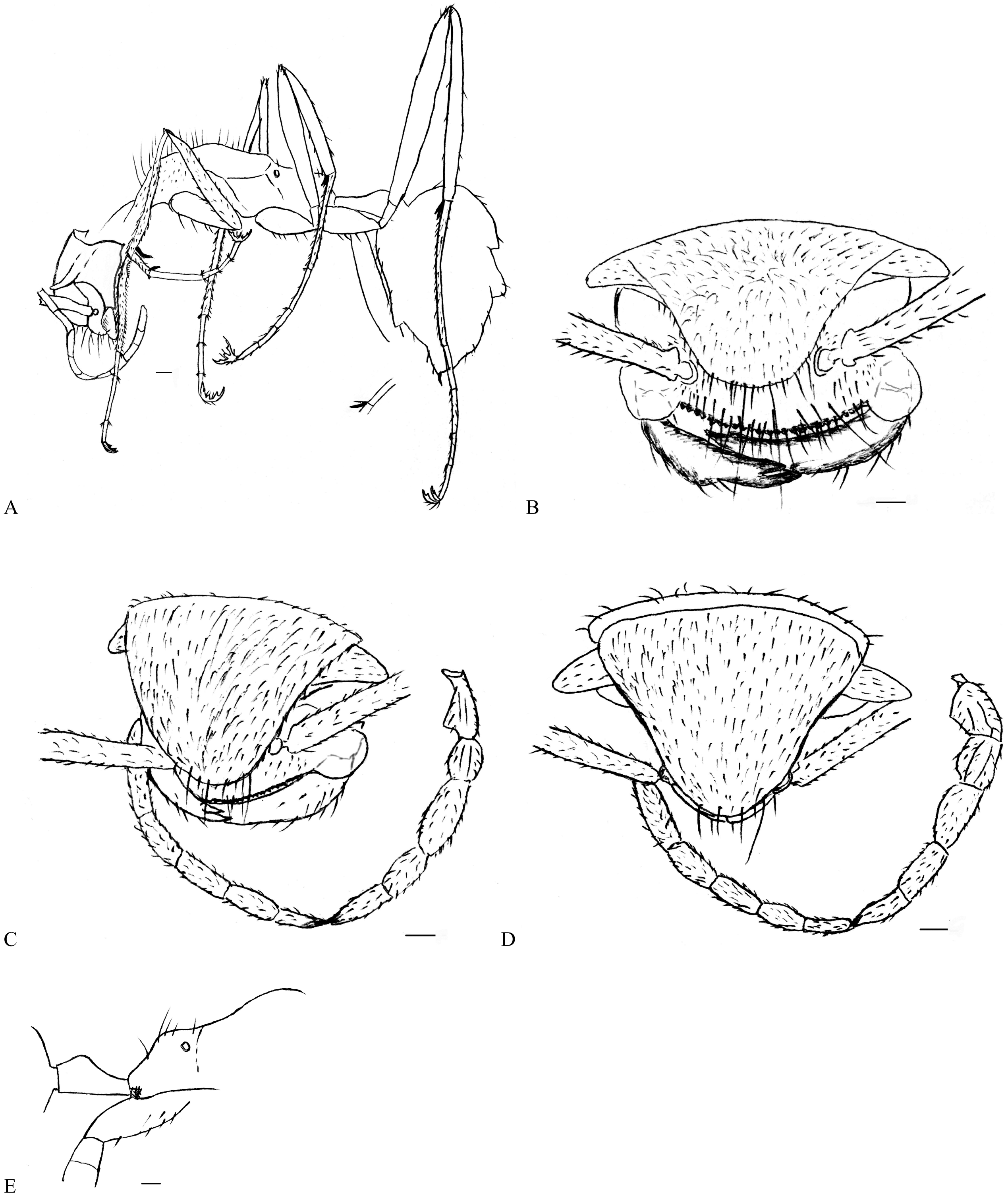
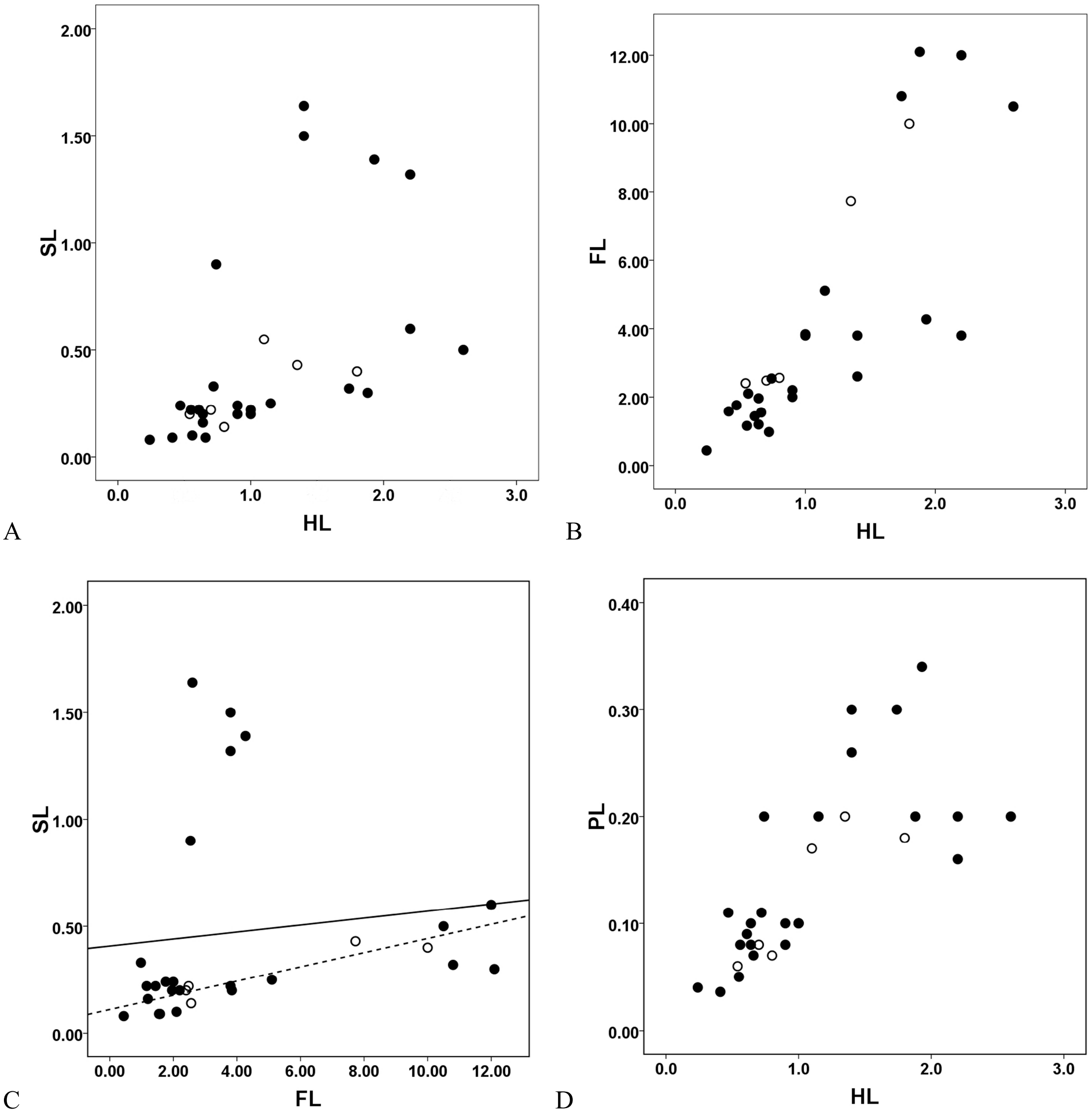


Fig.3. Bivariate plots of scape length and head length (**A**), flagellum length and head length (**B**), scape length and flagellum length (**C**), pedicel length and head length (**D**), flagellomer 1 length and head length (**E**), flagellomer 2 length and head lengh (**F**) in ant males.

Filled circles are crown ants; open circles are stem ants. Regression lines for both groups are shown in cases where statistical difference between them exists.



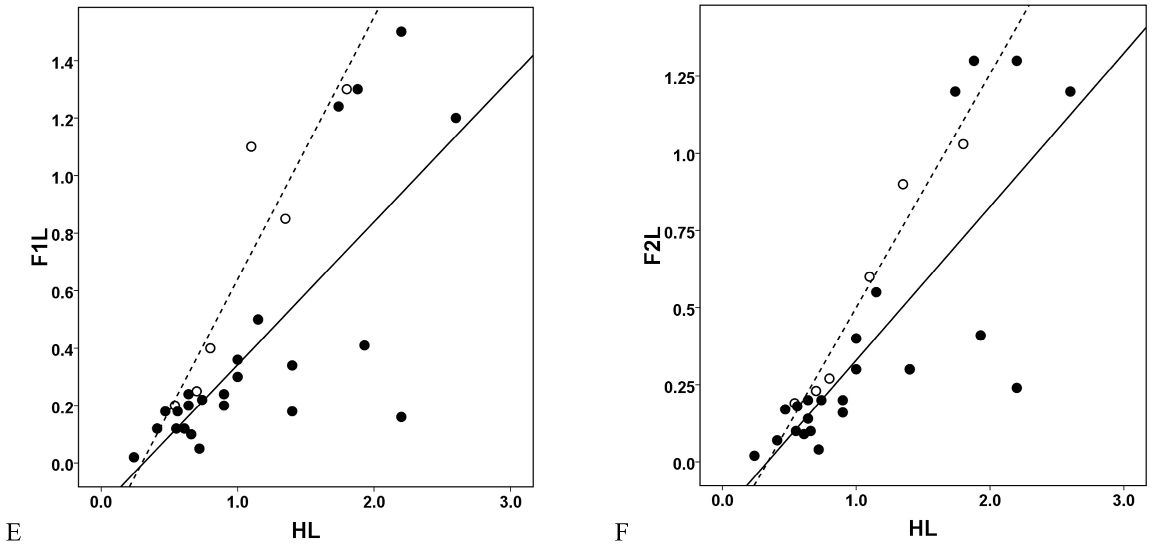
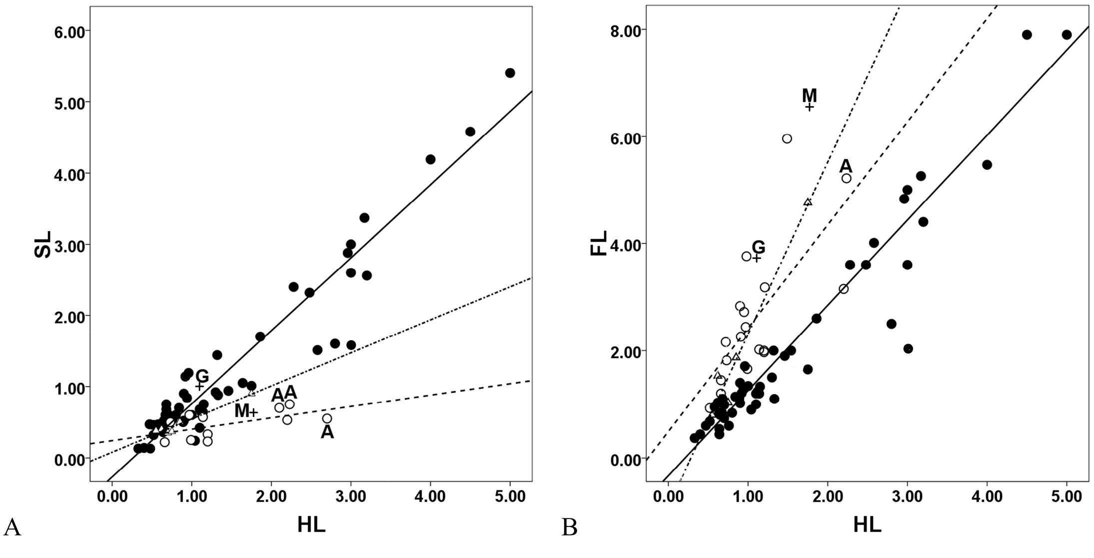


Fig.4. Bivariate plots of scape length and head length (**A**), flagellum length and head length (**B**), scape length and flagellum length (**C**), pedicel length and head length (**D**), flagellomer 1 length and head length (**E**), flagellomer 2 length and head length (**F**) in ant females.

Filled circles are crown-group ants; open circles are Sphecomyrmini; open triangles are Haidomyrmecini; A - Armaniinae (sensu Dlussky 1983); C - *Cananeuretus occidentalis*; G - *Gerontoformica cretacica*; M - *Myanmyrma gracilis*. Regression lines for crown ants (solid line), Sphecomyrmini (dash line) and Haidomyrmecini (dash dotted line) are shown in cases where statistical difference between two or all these groups exists. Note that *Cananeuretus occidentalis* is tentatively included in crown ants; *Brownimecia clavata*, *Kyromyrma neffi*, *Canapone dentata*, *Eotapinoma macalpini*, *Chronomyrmex medicinehatensis* are indicated as crown ants; Armaniinae, *Boltonimecia canadensis*, *Zigrasimecia tonsora* are indicated as Shecomyrminae.



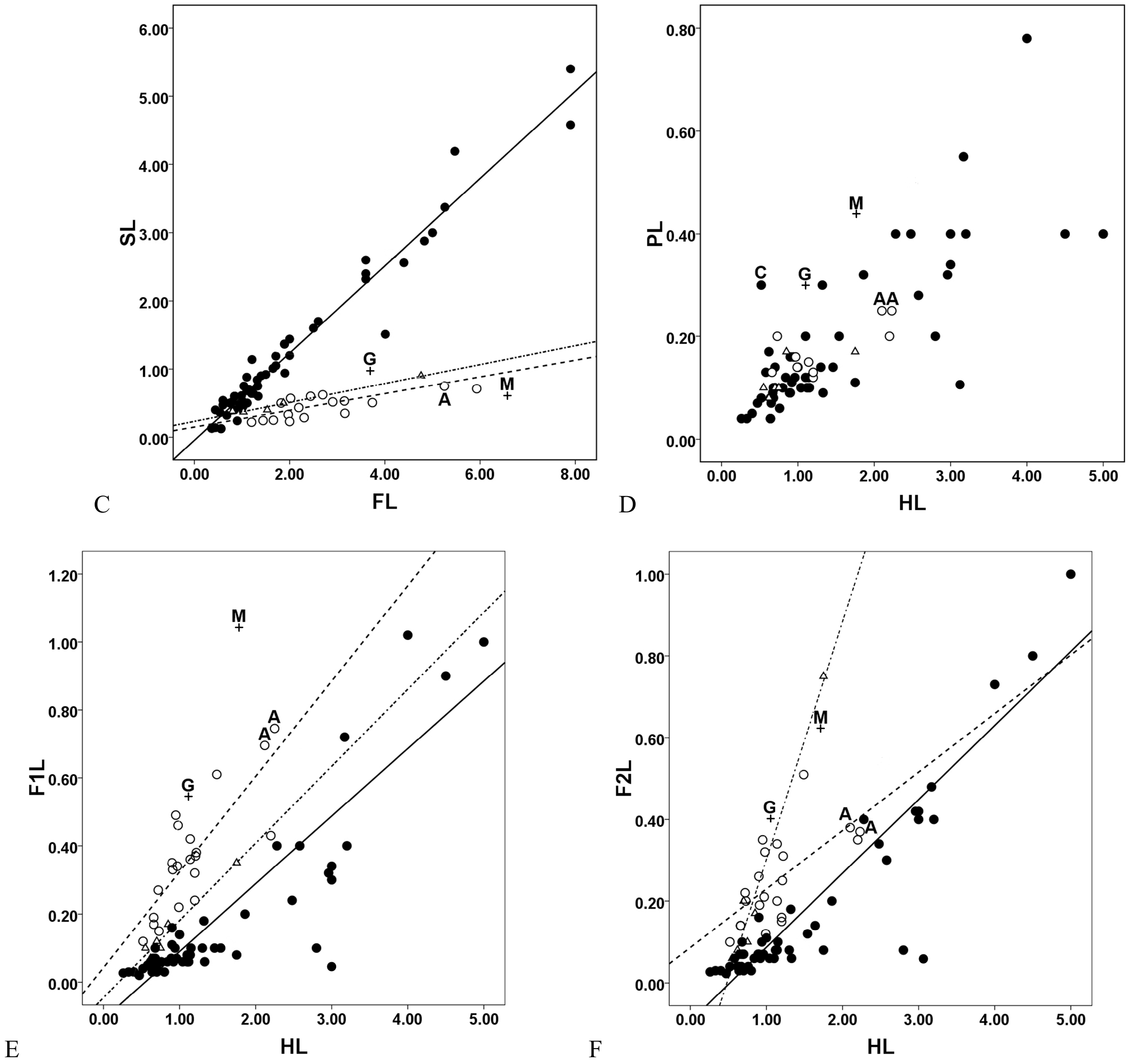

SL
6.00
5.00
4.00
3.00
2.00
1.00
0.00
0.00
2.00
4.00
6.00
8.00
FL
G
A
M
C
PL
0.80
0.60
0.40
0.20
0.00
0.00
1.00
2.00
3.00
4.00
5.00
HL
M
C
G
AA
D
F1L
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
1.00
2.00
3.00
4.00
5.00
HL
M
A
A
G
E
F2L
1.00
0.80
0.60
0.40
0.20
0.00
0.00
1.00
2.00
3.00
4.00
5.00
HL
M
G
A
A
F

Fig.5 The range of a data for index SL/AL for females of Vespoidea and Apoidea.

Diamond is arithmetic mean. Data on non-ant species are from Dlussky and Fedoseeva (1988), assigned to families in accordance with the current classification. Vespoidea: Sapygidae, Scoliidae, Tiphiidae, Mutillidae, Bradynobaenidae,Vespidae. Apoidea: Sphecidae, Crabronidae, Andrenidae, Melittidae, Megachilidae, Apidae. Social Hymenoptera: *Vespa sp., Vespula sp., Polistes sp., Apis sp.* (1 species each), *Bombus sp.* (4 species). Solitary Hymenoptera: all other species of Vespoidea and Apoidea as listed in Dlussky and Fedoseeva (1988). Stem ants: all Cretaceous stem taxa as in Table S1. Crown ants: all crown ants studied here as in Table S1.

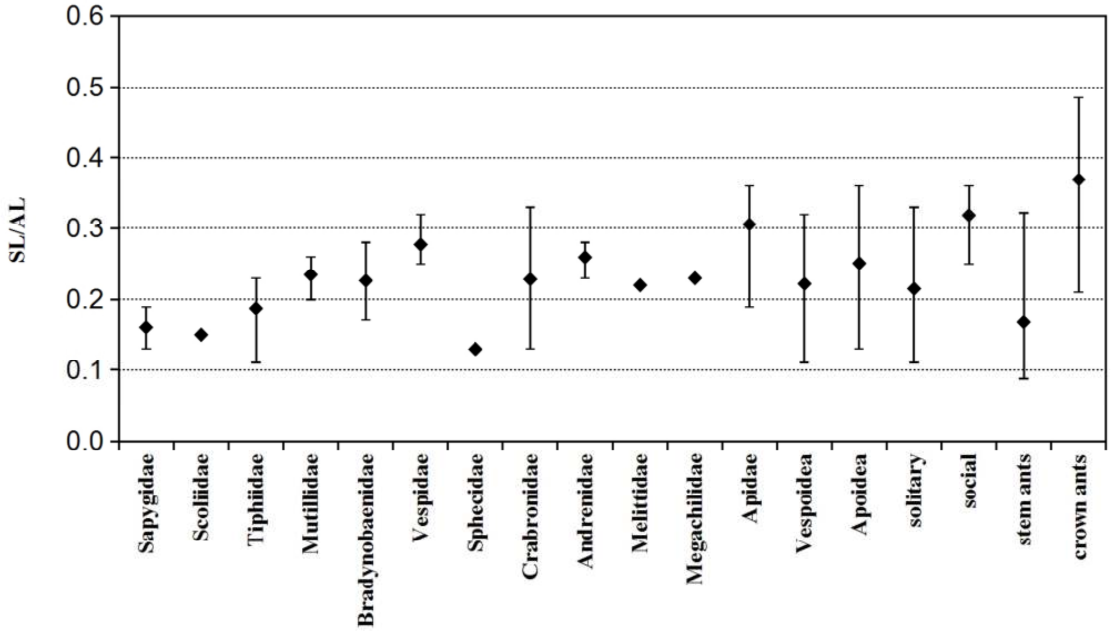


Fig.6. The range of a data for index AL/HL for females of Vespoidea and Apoidea.

See Fig.5 for details

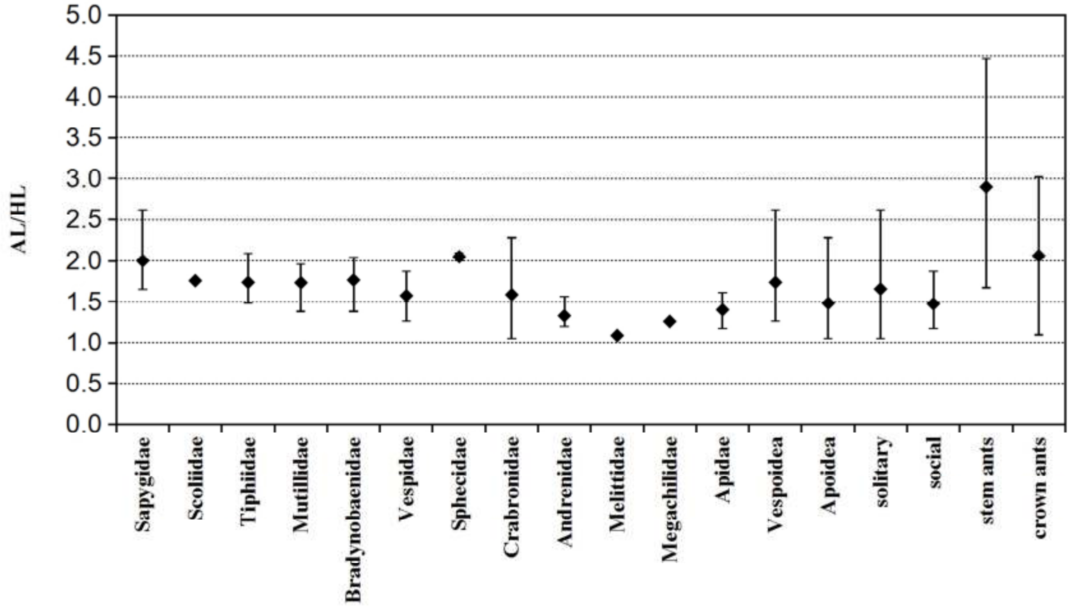


Fig.7. Separation of crown ants and stem ants in a canonical discriminant analysis (all species).

Deep red bars - crown ants; yellow bars - stem ants; purple bars - area of overlap. For comparison, Gaussian curves having the same mean and SD as actual distributions are also shown (line).

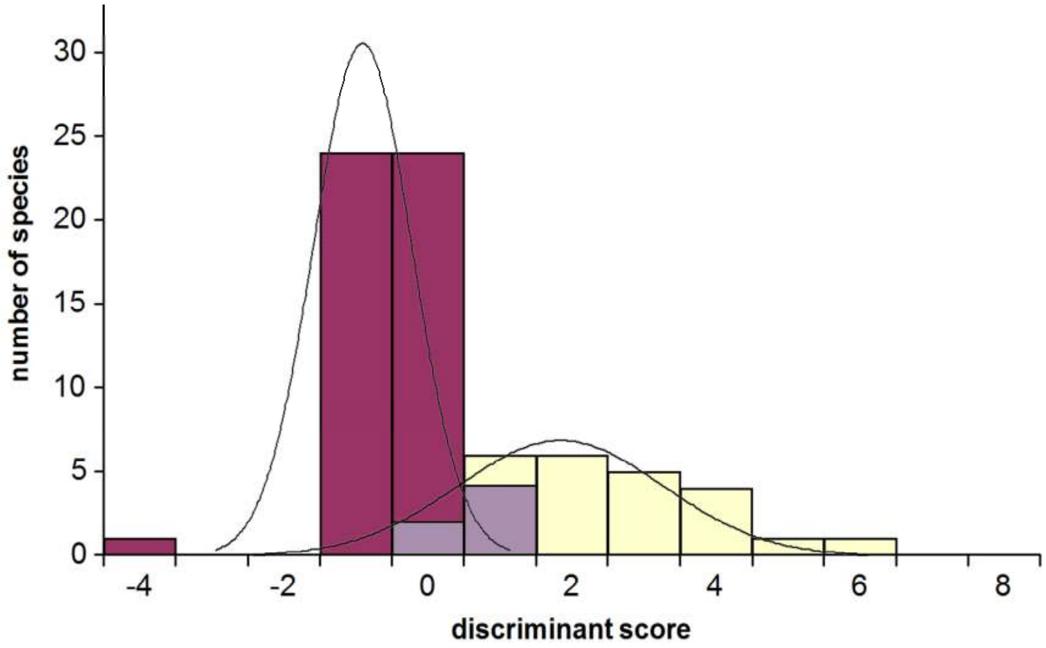
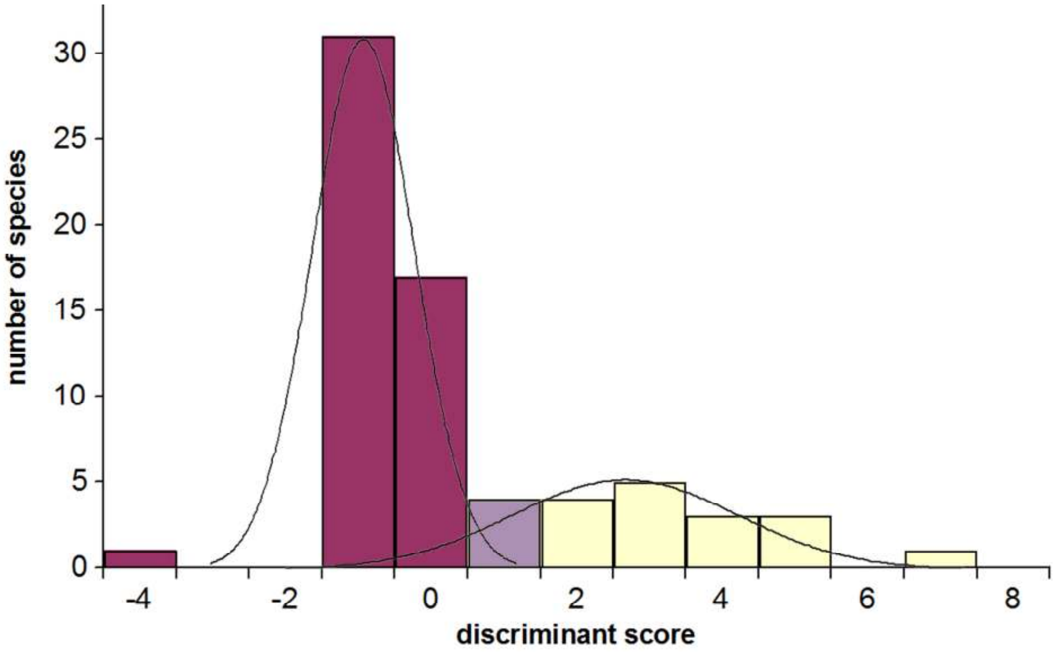


Fig.8. Separation of crown ants and stem ants in a canonical discriminant analysis (Haidomyrmecini removed).

See Fig.7 for details.



Supplemental Material:

Borysenko L. DESCRIPTION OF A NEW GENUS OF PRIMITIVE ANTS FROM CANADIAN AMBER WITH THE STUDY OF RELATIONSHIPS BETWEEN CROWN ANTS AND STEM ANTS (HYMENOPTERA: FORMICIDAE)

Table 1. List of taxa sampled, and reference for measurements of antennae

† extinct; w - worker, g - gyne, m - male; CNC - Canadian National Collection of Insects, Arachnids and Nematodes

Taxon	Reference
†Stem-clades	
Sphecomyrminae	
Sphecomyrma freyi Wilson & Brown, 1967 (w)	Wilson *et al.* 1967 (holotype) (referred to as *Sphecomyrma freyi* #1 in this study) Grimaldi *et al.* 1997 (neotype) (reffered to as *Sphecomyrma freyi* #2 in this study) Engel and Grimaldi 2005 (specimen B) (reffered to as *Sphecomyrma freyi* #3 in this study)
Sphecomyrma mesaki Engel & Grimaldi, 2005 (w)	Engel and Grimaldi 2005
Sphecomyrma sp. (m)	Grimaldi *et al.* 1997
Sphecomyrmodes orientalis Engel & Grimaldi, 2005 (w)	Engel and Grimaldi 2005
Sphecomyrmodes occidentalis Perrichot, et al., 2008 (w)	Perrichot *et al.* 2008
Sphecomyrmodes contegus Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes gracilis Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes magnus Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes pilosus Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes rubustus Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes rugosus Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes spiralis Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes subcuspis Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Sphecomyrmodes tendir Barden & Grimaldi, 2014 (w)	Barden and Grimaldi 2014
Haidomyrmodes mammuthus Perrichot, et al., 2008 (w, g)	Perrichot *et al.* 2008 (gyne reffered to as *Haidomyrmodes*

	mammuthus #1 (g) in this study; worker reffered to as *Haidomyrmodes mammuthus* #2 in this study)
Haidomyrmex cerberus Dlussky, 1996 (w)	Dlussky 1996
Haidomyrmex scimitarus Barden & Grimaldi, 2012 (g)	Barden and Grimaldi 2012
Haidomyrmex zigrasi Barden & Grimaldi, 2012 (w)	Barden and Grimaldi 2012
Haidoterminus cippus McKellar, Glasier & Engel, 2013 (w)	McKellar *et al.* 2013
Zigrasimecia tonsora Barden & Grimaldi, 2013 (g)	Barden and Grimaldi 2013
Zigrasimecia ferox Perrichot, 2014 (w)	Perrichot 2014 (paratype reffered to as *Zigrasimecia ferox* #1 in this study; holotype reffered to as *Zigrasimecia ferox* #2 in this study)
Baikuris mandibularis Dlussky, 1987 (m)	Dlussky, 1987
Baikuris casei Grimaldi, Agosti & Carpenter, 1997 (m)	Grimaldi *et al.* 1997
Baikuris maximus Perrichot, 2014 (m)	Perrichot 2014
Dlusskyidris zherichini (Dlussky, 1975) (m)	Dlussky 1975
Boltonimecia canadensis (Wilson, 1985) (w)	CNC
Armaniinae	
Armania robusta Dlussky, 1983 (g)	Dlussky 1983
Pseudarmania rasnitsyni Dlussky, 1983 (g)	Dlussky 1983
Archaeopone taylori Dlussky, 1983 (m)	Dlussky 1983
Orapia rayneri Dlussky, Brothers & Rasnitsyn, 2004 (g)	Dlussky *et al.* 2004
Incertae sedis	
Myanmyrma gracilis Engel & Grimaldi, 2005 (w)	Engel and Grimaldi 2005
Gerontoformica cretacica Nel & Perrault, 2004 (w)	Nel *et al.* 2004
Crown-clade	
Martialinae	

Martialis heureka Rabeling & Verhaagh, 2008 (w)	Rabeling *et al*. 2008
Leptanillinae	
Leptanilla taiwanensis Ogata, Terayama & Masuko, 1995 (w, g)	Ogata *et al*. 1995
Leptanilla sp. (m)	CNC
Proceratiinae	
Discothyrea sp. (w, g, m)	CNC
Amblyoponinae	
Stigmatomma pallipes (Haldeman, 1844) (w, g, m)	CNC
Ponerinae	
Ponera pennsylvanica Buckley, 1866 (w, g, m)	CNC
Neoponera villosa (Fabricius, 1804) (w, g, m)	CNC
Paraponerinae	
Paraponera clavata (Fabricius, 1775) (w, g, m)	CNC
Agroecomyrmecinae	
Tatuidris tatusia Brown & Kempf, 1968 (w, g, m)	Donoso 2012
Dorylinae	
(Leptanilloidinae sensu Bolton 2003)	
Leptanilloides erinys Borowiec & Longino, 2011 (w, g)	Borowiec and Longino 2011
Leptanilloides mckennae Longino, 2003 (m)	Longino 2003
(Cerapachyinae sensu Bolton 2003)	
Cerapachys sp. (w, g, m)	CNC
(Aenictogitoninae sensu Bolton 2003)	
Aenictogiton fossiceps Emery, 1901 (m)	Emery 1901
(Aenictinae sensu Bolton 2003)	
Aenictus sp. (w, m)	CNC
Aenictus pachycerus (Smith, F., 1858) (g)	Bharti 2003
(Ecitoninae sensu Bolton 2003)	
Eciton hamatum (Fabricius, 1782) (w, m)	CNC
Eciton hamatum (Fabricius, 1782) (g)	Wheeler 1925
(Dorylinae sensu Bolton 2003)	
Dorylus sp. (w, m)	CNC
Dorylus rufescens Santschi, 1915 (g)	Santschi 1915

Myrmeciinae	
Myrmecia gulosa (Fabricius, 1775) (w, g)	CNC
Myrmecia sp. (m)	CNC
Pseudomyrmecinae	
Pseudomyrmex pallidus (Smith, F., 1855) (w, g, m)	CNC
Ectatomminae	
Ectatomma tuberculatum (Olivier, 1792) (w, g, m)	CNC
†*Canapone dentata* Dlussky, 1999 (w)	Dlussky 1999
Heteroponerinae	
Acanthoponera mucronata (Roger, 1860) (w, g, m)	CNC (w, g); Ketterl and Verhaagh 2004 (m)
Aneuretinae	
Aneuretus simoni Emery, 1893 (w, g, m)	Wilson *et al.* 1956
†*Cananeuretus occidentalis* Engel & Grimaldi, 2005 (w)	Engel and Grimaldi 2005
Dolichoderinae	
Dolichoderus taschenbergi (Mayr, 1866) (w, g, m)	CNC
Linepithema humile (Mayr, 1868) (w, g, m)	CNC
†*Eotapinoma macalpini* Dlussky, 1999 (w)	Dlussky 1999
†*Chronomyrmex medicinehatensis* McKellar, Glasier & Engel, 2013 (w)	McKellar *et al.* 2013 (holotype reffered to as *Chronomyrmex medicinehatensis* #1 in this study; paratype reffered to as *Chronomyrmex medicinehatensis* #2 in this study)
Formicinae	
Camponotus pennsylvanicus (De Geer, 1773) (w, g, m)	CNC
Formica glacialis Wheeler, W.M., 1908 (w, g, m)	CNC
†*Kyromyrma neffi* Grimaldi & Agosti, 2000 (w)	Grimaldi and Agosti 2000
Myrmicinae	
Aphaenogaster honduriana Mann, 1922 (w, g, m)	CNC
Manica invidia Bolton, 1995 (w, g, m)	CNC
†Brownimeciinae	
Brownimecia clavata Grimaldi, Agosti & Carpenter, 1997 (w)	Grimaldi *et al.* 1997

Table S2. Female's antennal indexes sorted in acsending order

w – worker, g – gyne. Stem species are in bold. Families of Vespoidea and Apoidea for indexes AL/HL and SL/AL (data from Dlussky and Fedoseeva 1988 with current classification): Sa - Sapygidae, Sc - Scoliidae, T - Tiphiidae, Mu - Mutillidae, B - Bradynobaenidae, V - Vespidae, Sp - Sphecidae, C - Crabronidae, An - Andrenidae, Me - Melittidae, Mg - Megachilidae, Ap - Apidae.

SL/HL	FL/HL	PL/HL	F1L/HL
0.19 Sphecomyrmodes orientalis (w)	0.63 Dorylus rufescens (g)	0.04 Dorylus rufescens (g)	0.04 Aneuretus simoni (w)
0.20 Orapia rayneri (g)	0.69 Discothyrea sp. (w)	0.06 Acanthoponera mucronata (w)	0.04 Dorylus rufescens (g)
0.24 Sphecomyrma mesaki (w)	0.79 Discothyrea sp. (g)	0.06 Discothyrea sp. (w)	0.04 Dorylus sp. (w)
0.25 Sphecomyrmodes occidentalis (w)	0.83 Canapone dentata (w)	0.06 Tatuidris tatusia (w)	0.04 Ponera pennsylvanica (g)
0.28 Sphecomyrma freyi #3 (w)	0.84 Tatuidris tatusia (w)	0.07 Canapone dentata (w)	0.04 Ponera pennsylvanica (w)
0.28 Sphecomyrmodes contegus (w)	0.87 Pseudomyrmex pallidus (g)	0.07 Dorylus sp. (w)	0.05 Acanthoponera mucronata (w)
0.33 Armania robusta (g)	0.89 Dorylus sp. (w)	0.08 Discothyrea sp. (g)	0.05 Canapone dentata (w)
0.33 Zigrasimecia tonsora (g)	0.91 Pseudomyrmex pallidus (w)	0.08 Paraponera clavata (g)	0.05 Pseudomyrmex pallidus (w)
0.33 Pseudomyrmex pallidus (g)	0.94 Acanthoponera mucronata (w)	0.09 Aenictus pachycerus (g)	0.05 Stigmatomma pallipes (w)
0.34 Pseudarmania rasnitsyni (g)	0.95 Tatuidris tatusia (g)	0.09 Paraponera clavata (w)	0.05 Tatuidris tatusia (w)
0.34 Sphecomyrmodes tendir (w)	1.03 Leptanilloides erinys (w)	**0.09 Sphecomyrma mesaki (w)**	0.06 Leptanilla taiwanensis (w)
0.36 Myanmyrma gracilis (w)	1.05 Ponera pennsylvanica (g)	0.09 Stigmatomma pallipes (w)	0.06 Cerapachys sp. (w)
0.37 Zigrasimecia ferox #1 (w)	1.05 Stigmatomma pallipes (g)	0.10 Cerapachys sp. (g)	0.06 Manica invidia (g)
0.38 Sphecomyrmodes pilosus (w)	1.06 Ponera pennsylvanica (w)	**0.10 Haidomyrmex scimitarus (g)**	0.06 Pseudomyrmex pallidus (g)
0.38 Pseudomyrmex pallidus (w)	1.09 Acanthoponera mucronata (g)	**0.10 Sphecomyrma freyi #3 (w)**	0.07 Acanthoponera mucronata (g)
0.41 Leptanilla taiwanensis (g)	1.11 Stigmatomma pallipes (w)	0.10 Brownimecia clavata (w)	0.07 Aneuretus simoni (g)
0.41 Zigrasimecia ferox #2 (w)	1.13 Brownimecia clavata (w)	0.10 Pseudomyrmex pallidus (g)	0.07 Aphaenogaster honduriana (g)
0.42 Sphecomyrmodes gracilis (w)	1.15 Manica invidia (w)	0.11 Acanthoponera mucronata (g)	0.07 Aphaenogaster honduriana (w)
0.43 Leptanilloides erinys (g)	1.16 Aenictus pachycerus (g)	0.11 Eciton hamatum (g)	0.07 Cerapachys sp. (g)
0.47 Leptanilla taiwanensis (w)	1.20 Camponotus pennsylvanicus (g)	0.11 Eotapinoma macalpini (w)	0.07 Chronomyrmex medicinehatensis #2 (w)
0.47 Sphecomyrmodes rubustus (w)	1.23 Eotapinoma macalpini (w)	0.11 **Sphecomyrmodes orientalis (w)**	0.07 Dolichoderus taschenbergi (w)
0.47 Sphecomyrmodes magnus (w)	1.24 Leptanilloides erinys (g)	0.11 Manica invidia (w)	0.07 Leptanilloides erinys (w)
0.49 Haidomyrmodes mammuthus #2 (w)	1.24 Leptanilla taiwanensis (w)	0.11 Neoponera villosa (g)	0.07 Stigmatomma pallipes (g)
0.49 Leptanilloides erinys (w)	1.27 Aneuretus simoni (g)	0.11 Neoponera villosa (w)	0.08 Aenictus sp. (w)
0.50 Sphecomyrma freyi #2 (w)	1.28 Aneuretus simoni (w)	0.11 Pseudarmania rasnitsyni (g)	0.08 Discothyrea sp. (g)
0.50 Haidomyrmex cerberus (w)	1.30 Cerapachys sp. (g)	0.11 Stigmatomma pallipes (g)	0.08 Manica invidia (w)
0.51 Haidomyrmex scimitarus (g)	1.30 Manica invidia (g)	0.12 Kyromyrma neffi (w)	0.09 Aenictus pachycerus (g)
0.53 Sphecomyrmodes spiralis (w)	1.31 Aenictus sp. (w)	**0.12 Armania robusta (g)**	0.09 Tatuidris tatusia (g)
0.56 Stigmatomma pallipes (g)	1.31 Cerapachys sp. (w)	**0.12 Sphecomyrmodes magnus (w)**	0.09 Leptanilloides erinys (g)
0.56 Tatuidris tatusia (w)	1.32 Aphaenogaster honduriana (g)	**0.12 Sphecomyrmodes contegus (w)**	0.09 Leptanilla taiwanensis (g)
0.57 Dorylus sp. (w)	1.34 Eciton hamatum (w)	0.12 Aphaenogaster honduriana (g)	0.09 Chronomyrmex medicinehatensis #1 (w)
0.57 Stigmatomma pallipes (w)	1.35 Leptanilla taiwanensis (g)	0.12 Leptanilloides erinys (w)	0.09 Discothyrea sp. (w)
0.58 Acanthoponera mucronata (w)	1.36 Dolichoderus taschenbergi (w)	0.12 Leptanilla taiwanensis (g)	0.10 Camponotus pennsylvanicus (g)
0.58 Brownimecia clavata (w)	**1.37 Haidomyrmodes mammuthus #2 (w)**	0.13 Leptanilloides erinys (g)	0.10 Camponotus pennsylvanicus (w)
0.59 Eciton hamatum (g)	1.37 Myrmecia gulosa (g)	0.13 Leptanilla taiwanensis (w)	0.10 Kyromyrma neffi (w)
0.59 Haidomyrmodes mammuthus #1 (g)	1.38 Ectatomma tuberculatum (g)	0.13 Aneuretus simoni (g)	0.10 Martialis heureka (w)
0.60 Eciton hamatum (w)	1.40 Dolichoderus taschenbergi (g)	0.13 Aphaenogaster honduriana (w)	0.11 Eotapinoma macalpini (w)
0.62 Acanthoponera mucronata (g)	1.40 Formica glacialis (g)	0.13 Camponotus pennsylvanicus (g)	**0.11 Haidomyrmex zigrasi (w)**
0.62 Aenictus sp. (w)	1.41 Chronomyrmex medicinehatensis #2 (w)	0.13 Cerapachys sp. (w)	0.11 Dolichoderus taschenbergi (g)
0.62 Sphecomyrma freyi #1 (w)	**1.43 Sphecomyrma mesaki (w)**	0.13 Ectatomma tuberculatum (g)	0.11 Formica glacialis (g)
0.63 Cerapachys sp. (w)	1.45 Camponotus pennsylvanicus (w)	**0.13 Sphecomyrmodes tendir (w)**	0.11 Neoponera villosa (g)
0.63 Discothyrea sp. (w)	**1.45 Haidoterminus cippus (w)**	**0.13 Haidomyrmex zigrasi (w)**	0.11 Neoponera villosa (w)
0.64 Cerapachys sp. (g)	1.52 Formica glacialis (w)	**0.13 Haidomyrmodes mammuthus #2 (w)**	0.12 Brownimecia clavata (w)
0.65 Aenictus pachycerus (g)	1.53 Kyromyrma neffi (w)	**0.13 Sphecomyrma freyi #2 (w)**	0.13 Ectatomma tuberculatum (g)
0.65 Haidomyrmex zigrasi (w)	1.55 Eciton hamatum (g)	0.13 Manica invidia (g)	**0.13 Haidomyrmodes mammuthus #2 (w)**
0.65 Sphecomyrmodes subcuspis (w)	1.56 Linepithema humile (g)	0.13 Ponera pennsylvanica (g)	0.14 Eciton hamatum (w)
0.66 Canapone dentata (w)	1.58 Ectatomma tuberculatum (w)	**0.14 Haidomyrmex cerberus (w)**	0.14 Formica glacialis (w)
0.67 Sphecomyrmodes rugosus (w)	1.58 Paraponera clavata (g)	0.14 Tatuidris tatusia (g)	0.15 Linepithema humile (w)
0.68 Boltonimecia canadensis (w)	1.62 Linepithema humile (w)	0.14 Dolichoderus taschenbergi (w)	0.16 Eciton hamatum (g)
0.69 Haidoterminus cippus (w)	1.63 Neoponera villosa (w)	0.14 Eciton hamatum (w)	**0.17 Haidomyrmex cerberus (w)**
0.70 Tatuidris tatusia (g)	1.64 Chronomyrmex medicinehatensis #1 (w)	0.14 Ponera pennsylvanica (w)	0.18 Ectatomma tuberculatum (w)
0.71 Discothyrea sp. (g)	**1.64 Sphecomyrma freyi #3 (w)**	**0.14 Sphecomyrmodes occidentalis (w)**	0.18 Linepithema humile (g)
0.71 Manica invidia (w)	1.66 Martialis heureka (w)	**0.15 Sphecomyrmodes rubustus (w)**	**0.18 Haidoterminus cippus (w)**
0.71 Ponera pennsylvanica (w)	1.66 Myrmecia gulosa (w)	0.15 Aenictus sp. (w)	0.20 Paraponera clavata (g)
0.74 Martialis heureka (w)	1.67 Neoponera villosa (g)	0.15 Aneuretus simoni (w)	0.20 Paraponera clavata (w)
0.75 Ponera pennsylvanica (g)	**1.67 Sphecomyrmodes orientalis (w)**	0.15 Linepithema humile (w)	**0.20 Haidomyrmex scimitarus (g)**
0.78 Manica invidia (g)	**1.68 Sphecomyrmodes occidentalis (w)**	0.16 Camponotus pennsylvanicus (w)	**0.20 Haidomyrmodes mammuthus #1 (g)**
0.80 Ectatomma tuberculatum (g)	1.76 Paraponera clavata (w)	**0.16 Sphecomyrma freyi #1 (w)**	**0.20 Sphecomyrma freyi #3 (w)**
0.80 Eotapinoma macalpini (w)	**1.77 Sphecomyrma freyi #2 (w)**	**0.16 Sphecomyrmodes gracilis (w)**	**0.20 Sphecomyrma mesaki (w)**
0.81 Chronomyrmex medicinehatensis #1 (w)	1.78 Aphaenogaster honduriana (w)	**0.16 Sphecomyrmodes subcuspis (w)**	**0.21 Boltonimecia canadensis (w)**
0.83Dolichoderus taschenbergi (w)	**1.79 Zigrasimecia ferox #1 (w)**	**0.16 Sphecomyrmodes pilosus (w)**	**0.22 Sphecomyrmodes occidentalis (w)**
0.87 Camponotus pennsylvanicus (g)	**1.82 Zigrasimecia tonsora (g)**	0.17 Dolichoderus taschenbergi (g)	**0.23 Zigrasimecia ferox #1 (w)**
0.87 Chronomyrmex medicinehatensis #2 (w)	**2.20 Haidomyrmodes mammuthus #1 (w)**	0.17 Formica glacialis (g)	0.23 Myrmecia gulosa (w)
0.88 Cananeuretus occidentalis (w)	**2.20 Zigrasimecia ferox #2**	0.17 Myrmecia gulosa (w)	0.26 Myrmecia gulosa (g)
	2.35 Pseudarmania rasnitsyni (g)	0.18 Ectatomma tuberculatum (w)	**0.26 Zigrasimecia tonsora (g)**
		0.18 Zigrasimecia ferox #2 (w)	
		0.18 Haidoterminus cippus (w)	
		0.18 Linepithema humile (g)	

0.89 Dolichoderus taschenbergi (g) 0.90 Aneuretus simoni (g) 0.91 Formica glacialis (g) **0.91 Gerontoformica cretacica (w)** 0.94 Camponotus pennsylvanicus (w) 0.97 Neoponera villosa (w) 1.00 Aneuretus simoni (w) 1.00 Linepithema humile (g) 1.00 Linepithema humile (w) 1.00 Neoponera villosa (g) 1.02 Paraponera clavata (w) 1.05 Ectatomma tuberculatum (w) 1.05 Myrmecia gulosa (g) 1.06 Myrmecia gulosa (w) 1.08 Paraponera clavata (g) 1.09 Formica glacialis (w) 1.10 Kyromyrma neffi (w) 1.24 Aphaenogaster honduriana (g) 1.24 Aphaenogaster honduriana (w) 4.48 Dorylus rufescens (g)	**2.47 Haidomyrmex zigrasi (w)** **2.48 Sphecomyrmodes pilosus (w)** **2.49 Boltonimecia canadensis (w)** **2.52 Sphecomyrma freyi #1 (w)** **2.63 Sphecomyrmodes contegus (w)** **2.72 Haidomyrmex scimitarus (g)** **2.86 Sphecomyrmodes subcuspis (w)** **3.00 Sphecomyrmodes rugosus (w)** **3.14 Sphecomyrmodes spiralis (w)** **3.36 Gerontoformica cretacica (w)** **3.73 Myanmyrma gracilis (w)** **3.84 Sphecomyrmodes rubustus (w)** **4.00 Sphecomyrmodes magnus (w)**	0.18 Pseudomyrmex pallidus (w) **0.19 Sphecomyrmodes spiralis (w)** **0.19 Zigrasimecia ferox #1 (w)** 0.20 Chronomyrmex medicinehatensis #2 (w) **0.20 Haidomyrmodes mammuthus #1 (g)** **0.20 Zigrasimecia tonsora (g)** 0.20 Myrmecia gulosa (g) 0.22 Chronomyrmex medicinehatensis #1 (w) 0.23 Formica glacialis (w) **0.25 Myanmyrma gracilis (w)** **0.26 Sphecomyrmodes rugosus (w)** **0.27 Boltonimecia canadensis (w)** **0.27 Gerontoformica cretacica (w)** 0.27 Martialis heureka (w) 0.58 Cananeuretus occidentalis (w)	**0.27 Sphecomyrmodes orientalis (w)** **0.29 Zigrasimecia ferox #2 (w)** **0.31 Sphecomyrmodes contegus (w)** **0.31 Sphecomyrmodes tendir (w)** **0.32 Sphecomyrma freyi #2 (w)** **0.33 Armania robusta (g)** **0.34 Pseudarmania rasnitsyni (g)** **0.35 Sphecomyrma freyi #1 (w)** **0.36 Sphecomyrmodes pilosus (w)** **0.37 Sphecomyrmodes gracilis (w)** **0.38 Sphecomyrmodes rugosus (w)** **0.39 Sphecomyrmodes spiralis (w)** **0.41 Sphecomyrmodes magnus (w)** **0.47 Sphecomyrmodes rubustus (w)** **0.50 Gerontoformica cretacica (w)** **0.52 Sphecomyrmodes subcuspis (w)** **0.60 Myanmyrma gracilis (w)**

Table S2 (continued)

F2L/HL	PL/(AL-PL)	F1L/(AL-F1L)	F2L/(AL-F2L)
0.03 Dorylus sp. (w) 0.04 Dorylus rufescens (g) 0.04 Ponera pennsylvanica (g) 0.04 Ponera pennsylvanica (w) 0.05 Acanthoponera mucronata (g) 0.05 Acanthoponera mucronata (w) 0.05 Aneuretus simoni (w) 0.05 Canapone dentata (w) 0.05 Discothyrea sp. (g) 0.05 Pseudomyrmex pallidus (w) 0.05 Tatuidris tatusia (w) 0.06 Leptanilla taiwanensis (w) 0.06 Aneuretus simoni (g) 0.06 Cerapachys sp. (w) 0.06 Discothyrea sp. (w) 0.06 Manica invidia (w) 0.06 Martialis heureka (w) 0.06 Pseudomyrmex pallidus (g) 0.07 Leptanilloides erinys (w) 0.07 Aphaenogaster honduriana (g) 0.07 Aphaenogaster honduriana (w) 0.07 Cerapachys sp. (g) 0.07 Dolichoderus taschenbergi (w) 0.07 Stigmatomma pallipes (g) 0.07 Stigmatomma pallipes (w) 0.08 Brownimecia clavata (w) 0.08 Aenictus sp. (w) 0.08 Manica invidia (g) 0.09 Tatuidris tatusia (g) 0.09 Leptanilla taiwanensis (g) 0.09 Leptanilloides erinys (g) 0.09 Aenictus pachycerus (g) 0.10 Chronomyrmex medicinehatensis #1 (w) 0.10 Chronomyrmex medicinehatensis #2 (w) 0.10 Kyromyrma neffi (w) 0.11 Dolichoderus taschenbergi (g) 0.11 Eciton hamatum (w) 0.11 Eotapinoma macalpini (w) **0.11 Haidoterminus cippus (w)** 0.11 Formica glacialis (g) 0.12 Eciton hamatum (g) **0.12 Sphecomyrmodes occidentalis (w)** 0.13 Camponotus pennsylvanicus (g) 0.13 Ectatomma tuberculatum (g) **0.13 Haidomyrmex zigrasi (w)** **0.13 Haidomyrmodes mammuthus #2 (w)** **0.13 Sphecomyrma freyi #3 (w)** **0.13 Sphecomyrmodes orientalis (w)** 0.14 Camponotus pennsylvanicus (w)	**0.03 Sphecomyrmodes magnus (w)** **0.03 Haidomyrmex scimitarus (g)** 0.03 Dorylus rufescens (g) 0.03 Paraponera clavata (g) 0.03 Paraponera clavata (w) **0.04 Sphecomyrmodes rubustus (w)** 0.04 Acanthoponera mucronata (w) 0.04 Aphaenogaster honduriana (w) **0.04 Haidomyrmex zigrasi (w)** 0.04 Neoponera villosa (w) **0.04 Pseudarmania rasnitsyni (g)** 0.04 Neoponera villosa (g) **0.04 Sphecomyrmodes contegus (w)** 0.05 Tatuidris tatusia (w) 0.05 Kyromyrma neffi (w) **0.05 Sphecomyrmodes subcuspis (w)** 0.05 Canapone dentata (w) 0.05 Aphaenogaster honduriana (g) 0.05 Dyscothyrea sp. (w) 0.05 Aenictus pachycerus (g) 0.05 Dorylus sp. (w) 0.05 Cerapachys sp. (g) 0.05 Eciton hammatum (g) **0.05 Sphecomyrmodes spiralis (w)** **0.06 Sphecomyrma freyi #3 (w)** **0.06 Sphecomyrma freyi #1 (w)** 0.06 Dyscothyrea sp. (g) 0.06 Eotapinoma macalpini 0.06 Stigmatomma pallipes (w) **0.06 Sphecomyrma mesaki (w)** 0.06 Linepithema humile (w) **0.06 Sphecomyrmodes pilosus (w)** 0.06 Ectatomma tuberculatum (g) 0.06 Manica muttica (w) **0.06 Sphecomyrma freyi #2 (w)** **0.06 Sphecomyrmodes orientalis (w)** 0.06 Brownimecia clavata (w) **0.07 Myanmyrma gracilis (w)** 0.07 Aneuretus simoni (g) 0.07 Manica muttica (g) 0.07 Myrmecia gulosa (w) **0.07 Gerontoformica cretacica (w)** 0.07 Acanthoponera mucronata (g) 0.07 Cerapachys sp. (w) 0.07 Camponotus pennsylvanicus (g) 0.07 Stigmatomma pallipes (g) 0.07 Dolichoderus traschenbergi (w) 0.07 Aneuretus simoni (w) 0.07 Ectatomma tuberculatum (w) 0.07 Camponotus pennsylvanicus (w) 0.07 Ponera pennsylvanica (g) 0.07 Linepithema humile (g)	0.02 Aneuretus simoni (w) 0.02 Ponera pennsylvanica (g) 0.02 Aphaenogaster honduriana (w) 0.02 Ponera pennsylvanica (w) 0.03 Dorylus sp. (w) 0.03 Dorylus rufescens (g) 0.03 Aphaenogaster honduriana (g) 0.03 Acanthoponera mucronata (w) 0.03 Canapone dentata (w) 0.03 Chronomyrmex medicinehatensis #2 (w) 0.03 Manica muttica (g) 0.03 Stigmatomma pallipes (w) 0.03 Cerapachys sp. (w) 0.03 Dolichoderus traschenbergi (w) 0.03 Tatuidris tatusia (w) 0.04 Aneuretus simoni (g) 0.04 Leptanilloides erinys (w) 0.04 Leptanilla taiwanensis (w) 0.04 Chronomyrmex medicinehatensis #1 (w) 0.04 Cerapachys sp. (g) **0.04 Haidomyrmex zigrasi (w)** 0.04 Kyromyrma neffi (w) 0.04 Aenictus sp. (w) 0.04 Martialis heureka (w) 0.04 Camponotus pennsylvanicus (w) 0.04 Manica muttica (w) 0.04 Neoponera villosa (w) 0.04 Pseudomyrmex pallidus (w) 0.04 Neoponera villosa (g) 0.04 Acanthoponera mucronata (g) 0.05 Leptanilloides erinys (g) 0.05 Stigmatomma pallipes (g) 0.05 Dolichoderus traschenbergi (g) 0.05 Formica glacialis (g) 0.05 Aenictus pachycerus (g) 0.05 Camponotus pennsylvanicus (g) 0.06 Formica glacialis (w) 0.06 Dyscothyrea sp. (g) 0.06 Pseudomyrmex pallidus (g) 0.06 Tatuidris tatusia (g) 0.06 Leptanilla taiwanensis (g) 0.06 Eotapinoma macalpini 0.06 Linepithema humile (w) 0.06 Ectatomma tuberculatum (g) **0.07 Haidomyrmex scimitarus (g)** **0.07 Boltonimecia canadensis (w)** 0.07 Ectatomma tuberculatum (w) 0.07 Linepithema humile (g) **0.08 Haidomyrmodes mammuthus #2 (w)**	0.02 Ponera pennsylvanica (w) 0.02 Ponera pennsylvanica (g) 0.02 Dorylus sp. (w) 0.02 Aneuretus simoni (w) 0.02 Aphaenogaster honduriana (w) Dorylus rufescens (g) 0.03 Canapone dentata (w) 0.03 Martialis heureka (w) 0.03 Tatuidris tatusia (w) 0.03 Cerapachys sp. (w) 0.03 Acanthoponera mucronata (w) 0.03 Acanthoponera mucronata (g) 0.03 Aneuretus simoni (g) 0.03 Dolichoderus traschenbergi (w) 0.03 Manica muttica (w) 0.03 Aphaenogaster honduriana (g) **0.04 Haidomyrmex zigrasi (w)** 0.04 Kyromyrma neffi (w) 0.04 Chronomyrmex medicinehatensis #1 (w) 0.04 Leptanilloides erinys (w) 0.04 Leptanilla taiwanensis (w) 0.04 Stigmatomma pallipes (w) 0.04 Dyscothyrea sp. (g) 0.04 Cerapachys sp. (g) 0.04 Aenictus sp. (w) 0.04 Pseudomyrmex pallidus (w) 0.04 Manica muttica (g) **0.05 Haidoterminus cippus (w)** 0.05 Brownimecia clavata (w) 0.05 Chronomyrmex medicinehatensis #2 (w) 0.05 Leptanilloides erinys (g) 0.05 Stigmatomma pallipes (g) 0.05 Dyscothyrea sp. (w) 0.05 Aenictus pachycerus (g) 0.05 Dolichoderus traschenbergi (g) 0.05 Formica glacialis (g) 0.06 Eotapinoma macalpini (w) 0.06 Neoponera villosa (w) 0.06 Neoponera villosa (g) 0.06 Eciton hammatum (w) 0.06 Tatuidris tatusia (g) 0.06 Leptanilla taiwanensis (g) 0.06 Eciton hammatum (g) 0.06 Myrmecia gulosa (w) 0.06 Pseudomyrmex pallidus (g) 0.06 Ectatomma tuberculatum (g) 0.06 Linepithema humile (w) 0.06 Formica glacialis (w) 0.06 Camponotus pennsylvanicus (w) **0.07 Pseudarmania rasnitsyni (g)**

0.14 Formica glacialis (w)	**0.08 Zigrasimecia ferox #2 (w)**	0.08 Brownimecia clavata (w)	**0.07 Sphecomyrma freyi #1 (w)**
0.14 Neoponera villosa (g)	**0.08 Haidomyrmodes mammuthus #2 (w)**	0.08 Dyscothyrea sp. (w)	**0.07 Sphecomyrma freyi #3 (w)**
0.14 Neoponera villosa (w)	**0.08 Haidomyrmodes mammuthus #1 (g)**	**0.08 Haidomyrmodes mammuthus #1 (g)**	**0.07 Sphecomyrmodes orientalis (w)**
0.15 Linepithema humile (w)	**0.08 Sphecomyrmodes rugosus (w)**	0.08 Paraponera clavata (w)	**0.07 Sphecomyrma occidentalis (w)**
0.15 Myrmecia gulosa (w)	0.08 Eciton hammatum (w)	0.08 Eciton hammatum (w)	0.07 Paraponera clavata (w)
0.16 Sphecomyrma mesaki (w)	0.08 Leptanilloides erinys (g)	0.08 Eciton hammatum (g)	0.07 Ectatomma tuberculatum (w)
0.17 Pseudarmania rasnitsyni (g)	0.08 Leptanilloides erinys (w)	0.08 Paraponera clavata (g)	0.07 Linepithema humile (g)
0.18 Ectatomma tuberculatum (w)	**0.08 Sphecomyrma occidentalis (w)**	0.09 Myrmecia gulosa (w)	0.07 Camponotus pennsylvanicus (g)
0.18 Linepithema humile (g)	0.08 Dolichoderus traschenbergi (g)	**0.09 Haidoterminus cippus (w)**	**0.08 Sphecomyrma freyi #2 (w)**
0.18 Myrmecia gulosa (g)	0.08 Formica glacialis (g)	**0.10 Sphecomyrmodes magnus (w)**	**0.08 Haidomyrmodes mammuthus #1 (g)**
0.18 Paraponera clavata (w)	0.08 Leptanilla taiwanensis (g)	**0.11 Sphecomyrmodes rugosus (w)**	**0.08 Haidomyrmodes mammuthus #2 (w)**
0.18 Sphecomyrma freyi #2 (w)	0.09 Aenictus sp. (w)	**0.12 Sphecomyrma freyi #3 (w)**	**0.08 Sphecomyrmodes contegus (w)**
0.18 Armania robusta (g)	0.09 Leptanilla taiwanensis (w)	**0.12 Sphecomyrmodes contegus (w)**	**0.08 Sphecomyrmodes magnus (w)**
0.19 Zigrasimecia ferox #1 (w)	0.09 Tatuidris tatusia (g)	0.12 Myrmecia gulosa (g)	**0.08 Sphecomyrmodes pilosus (w)**
0.20 Haidomyrmodes mammuthus #1 (g)	0.09 Ponera pennsylvanica (w)	**0.12 Sphecomyrmodes spiralis (w)**	**0.08 Sphecomyrmodes rubustus (w)**
0.20 Paraponera clavata (g)	0.09 Myrmecia gulosa (g)	**0.12 Zigrasimecia ferox #1 (w)**	0.08 Paraponera clavata (g)
0.21 Sphecomyrmodes contegus (w)	**0.09 Haidoterminus cippus (w)**	**0.12 Sphecomyrmodes rubustus (w)**	0.08 Myrmecia gulosa (g)
0.21 Sphecomyrmodes pilosus (w)	**0.09 Boltonimecia canadensis (w)**	**0.12 Zigrasimecia ferox #2 (w)**	**0.09 Zigrasimecia ferox #2 (w)**
0.21 Zigrasimecia ferox #2 (w)	0.10 Formica glacialis (w)	**0.13 Sphecomyrma freyi #1 (w)**	**0.09 Boltonimecia canadensis (w)**
0.21 Zigrasimecia tonsora (g)	0.10 Chronomyrmex medicinehatensis #2 (w)	**0.13 Sphecomyrma occidentalis (w)**	**0.09 Sphecomyrmodes rugosus (w)**
0.22 Sphecomyrma freyi #1 (w)	0.10 Pseudomyrmex pallidus (g)	**0.13 Sphecomyrma mesaki (w)**	**0.09 Sphecomyrmodes spiralis (w)**
0.25 Sphecomyrmodes tendir (w)	**0.10 Zigrasimecia ferox #1 (w)**	**0.13 Gerontoformica cretacica (w)**	**0.09 Myanmyrma gracilis (w)**
0.27 Boltonimecia canadensis (w)	**0.10 Zigramecia tonsora (w)**	**0.14 Zigramecia tonsora (w)**	**0.09 Gerontoformica cretacica (w)**
0.28 Haidomyrmex cerberus (w)	0.10 Chronomyrmex medicinehatensis #1 (w)	**0.14 Pseudarmania rasnitsyni (g)**	**0.1 Zigrasimecia ferox #1 (w)**
0.29 Sphecomyrmodes spiralis (w)	0.13 Martialis heureka (w)	**0.14 Sphecomyrmodes pilosus (w)**	**0.11 Zigramecia tonsora (w)**
0.30 Sphecomyrmodes gracilis (w)	0.16 Pseudomyrmex pallidus (w)	**0.16 Sphecomyrma freyi #2 (w)**	**0.11 Sphecomyrma mesaki (w)**
0.31 Sphecomyrmodes rugosus (w)		**0.17 Sphecomyrmodes orientalis (w)**	**0.12 Sphecomyrmodes subcuspis (w)**
0.33 Sphecomyrmodes rubustus (w)		**0.17 Myanmyrma gracilis (w)**	**0.15 Haidomyrmex scimitarus (g)**
0.34 Sphecomyrmodes magnus (w)		**0.17 Sphecomyrmodes subcuspis (w)**	
0.35 Myanmyrma gracilis (w)			
0.36 Gerontoformica cretacica (w)			
0.37 Sphecomyrmodes subcuspis (w)			
0.43 Haidomyrmex scimitarus (g)			

Table S2 (continued)

SL/FL	AL/HL	SL/AL
0.10 Myanmyrma gracilis (w)	1.05 Oxybellus sp. (C)	**0.09 Myanmyrma gracilis (w)**
0.11 Sphecomyrmodes contegus (w)	1.09 Dasypoda plumipes (Me)	**0.10 Sphecomyrmodes orientalis (w)**
0.12 Sphecomyrmodes magnus (w)	1.10 Pseudomyrmex pallidus (g)	**0.10 Sphecomyrmodes contegus (w)**
0.12 Sphecomyrmodes rubustus (w)	1.12 Dorylus rufescens (g)	**0.11 Sphecomyrmodes magnus (w)**
0.12 Sphecomyrmodes orientalis (w)	1.17 Apis mellifera (Ap)	**0.11 Sphecomyrmodes rubustus (w)**
0.14 Pseudarmania rasnitsyni (g)	1.20 Panurgus calcaratus (An)	0.11 Methoca ichmeumonoides (T)
0.15 Sphecomyrmodes occidentalis (w)	1.22 Andrena hattorfiana (An)	0.13 Agrogorytes mystaceus (C)
0.15 Sphecomyrmodes pilosus (w)	1.24 Bombus pascuorum (Ap)	0.13 Ammophila sabulosa (Sp)
0.17 Sphecomyrmodes spiralis (w)	1.26 Euodynerus disconotatus (V)	0.13 Gorytes quadrifasciatus (C)
0.17 Sphecomyrma freyi #3 (w)	1.26 Megachile lagopoda (Mg)	0.13 Polochrum repandum (Sa)
0.17 Sphecomyrma mesaki (w)	1.28 Crossocerus sp. (C)	**0.13 Sphecomyrmodes pilosus (w)**
0.18 Zigrasimecia tonsora (g)	1.29 Crabro cribrarius (C)	**0.13 Pseudarmania rasnitsyni (g)**
0.19 Haidomyrmex scimitarus (g)	1.29 Pseudomyrmex pallidus (w)	**0.13 Sphecomyrmodes occidentalis (w)**
0.19 Zigrasimecia ferox #2 (w)	1.31 Discothyrea sp. (w)	0.13 Sphex funerarius (Sp)
0.20 Zigrasimecia ferox #1 (w)	1.38 Bombus lapidarius (Ap)	0.14 Sapyga caucasica (Sa)
0.22 Sphecomyrmodes rugosus (w)	1.38 Bradynobaenus gayi (B)	**0.14 Sphecomyrma freyi #3 (w)**
0.23 Sphecomyrmodes subcuspis (w)	1.38 Mutilla europaea (Mu)	**0.14 Sphecomyrma mesaki (w)**
0.25 Sphecomyrma freyi #1 (w)	1.40 Bombus hypnorum (Ap)	0.15 Proscolia spectator (Sc)
0.26 Haidomyrmex zigrasi (w)	1.41 Eucera dentata (Ap)	**0.15 Sphecomyrmodes spiralis (w)**
0.27 Boltonimecia canadensis (w)	1.41 Tatuidris tatusia (w)	**0.15 Zigrasimecia tonsora (g)**
0.27 Haidomyrmodes mammuthus #1 (g)	1.42 Symmorphus sp. (V)	**0.16 Haidomyrmex scimitarus (g)**
0.27 Gerontoformica cretacica (w)	1.46 Dorylus sp. (w)	**0.16 Zigrasimecia ferox #2 (w)**
0.27 Pseudomyrmex pallidus (g)	1.48 Meria discussa (T)	**0.17 Zigrasimecia ferox #1 (w)**
0.28 Sphecomyrma freyi #2 (w)	1.49 Canapone dentata (w)	0.17 Typhoctes peculiaris (B)
0.32 Leptanilloides erinys (g)	1.50 Leptanilla taiwanensis (w)	**0.18 Sphecomyrmodes rugosus (w)**
0.33 Leptanilla taiwanensis (g)	1.50 Discothyrea sp. (g)	0.18 Fedtschenkia indigotea (Sa)
0.36 Haidomyrmodes mammuthus #2 (w)	1.52 Acanthoponera mucronata (w)	0.18 Meria discussa (T)
0.38 Eciton hamatum (g)	1.56 Ancistrocerus parietinus (V)	0.19 Eucera longicornis (Ap)
0.39 Leptanilloides erinys (w)	1.56 Andrena rosae (An)	0.19 Fedtschenkia anthracina (Sa)
0.42 Pseudomyrmex pallidus (w)	1.57 Bombus lucorum (Ap)	**0.19 Sphecomyrmodes subcuspis (w)**
0.45 Martialis heureka (w)	1.57 Tiphia femorata (T)	0.20 Myrmosa atra (Mu)
0.45 Eciton hamatum (w)	1.58 Vespa crabro (V)	**0.20 Sphecomyrma freyi #1 (w)**
0.45 Leptanilla taiwanensis (w)	1.60 Polistes gallicus (V)	0.21 Eucera dentata (Ap)
0.47 Aenictus sp. (w)	1.61 Eucera longicornis (Ap)	**0.21 Gerontoformica cretacica (w)**
0.48 Haidoterminus cippus (w)	1.61 Stigmatomma pallipes (g)	**0.21 Haidomyrmex zigrasi (w)**
0.48 Cerapachys sp. (w)	1.65 Fedtschenkia anthracina (Sa)	**0.21 Haidomyrmodes mammuthus #1 (g)**
	1.65 Tatuidris tatusia (g)	0.21 Pseudomyrmex pallidus (g)
	1.65 Leptanilla taiwanensis (g)	

0.49 Chronomyrmex medicinehatensis #1 (w)
0.49 Cerapachys sp. (g)
0.51 Brownimecia clavata (w)
0.52 Stigmatomma pallipes (w)
0.53 Stigmatomma pallipes (g)
0.56 Aenictus pachycerus (g)
0.57 Acanthoponera mucronata (g)
0.58 Paraponera clavata (w)
0.58 Ectatomma tuberculatum (g)
0.60 Neoponera villosa (w)
0.60 Neoponera villosa (g)
0.60 Manica invidia (g)
0.61 Acanthoponera mucronata (w)
0.61 Dolichoderus taschenbergi (w)
0.61 Manica invidia (w)
0.62 Chronomyrmex medicinehatensis #2 (w)
0.62 Linepithema humile (w)
0.64 Dorylus sp. (w)
0.64 Myrmecia gulosa (w)
0.64 Dolichoderus taschenbergi (g)
0.64 Linepithema humile (g)
0.64 Camponotus pennsylvanicus (w)
0.65 Eotapinoma macalpini (w)
0.65 Formica glacialis (g)
0.67 Tatuidris tatusia (w)
0.67 Ectatomma tuberculatum (w)
0.68 Paraponera clavata (g)
0.68 Ponera pennsylvanica (w)
0.70 Aphaenogaster honduriana (w)
0.71 Ponera pennsylvanica (g)
0.71 Aneuretus simoni (g)
0.72 Kyromyrma neffi (w)
0.72 Formica glacialis (w)
0.72 Camponotus pennsylvanicus (g)
0.73 Tatuidris tatusia (g)
0.77 Myrmecia gulosa (g)
0.77 Dorylus rufescens (g)
0.78 Aneuretus simoni (w)
0.80 Canapone dentata (w)
0.90 Discothyrea sp. (g)
0.91 Discothyrea sp. (w)
0.94 Aphaenogaster honduriana (g)

1.67 Sphecomyrma mesaki (w)
1.68 Stigmatomma pallipes (w)
1.71 Acanthoponera mucronata (g)
1.71 Brownimecia clavata (w)
1.71 Fedtschenkia indigotea (Sa)
1.73 Leptanilloides erinys (w)
1.74 Eumenes pedunculatus (V)
1.76 Proscolia spectator (Sc)
1.77 Ponera pennsylvanica (w)
1.78 Pseudophotopsis sp. (Mu)
1.78 Leptanilloides erinys (g)
1.80 Ponera pennsylvanica (g)
1.81 Aenictus pachycerus (g)
1.81 Brachycistis carinata (T)
1.82 Smicromyrme rufipes (Mu)
1.86 Manica invidia (w)
1.86 Sphecomyrmodes orientalis (w)
1.87 Haidomyrmodes mammuthus #2 (w)
1.87 Vespula vulgaris (V)
1.88 Apterogyna sp. (B)
1.92 Aenictus sp. (w)
1.92 Sphecomyrma freyi #3 (w)
1.93 Sphecomyrmodes occidentalis (w)
1.94 Cerapachys sp. (w)
1.94 Eciton hamatum (w)
1.95 Cerapachys sp. (g)
1.96 Myrmosa atra (Mu)
2.00 Sphex funerarius (Sp)
2.03 Eotapinoma macalpini (w)
2.04 Sapyga caucasica (Sa)
2.04 Typhoctes peculiaris (B)
2.05 Gorytes quadrifasciatus (C)
2.07 Camponotus pennsylvanicus (g)
2.08 Manica invidia (g)
2.09 Methoca ichmeumonoides (T)
2.10 Ammophila sabulosa (Sp)
2.14 Eciton hamatum (g)
2.15 Haidoterminus cippus (w)
2.15 Zigrasimecia tonsora (g)
2.15 Zigrasimecia ferox #1 (w)
2.61 Zigrasimecia ferox #2 (w)
2.16 Aneuretus simoni (g)
2.18 Ectatomma tuberculatum (g)
2.19 Dolichoderus taschenbergi (w)
2.27 Sphecomyrma freyi #2 (w)
2.28 Agrogorytes mystaceus (C)
2.28 Aneuretus simoni (w)
2.29 Chronomyrmex medicinehatensis #2 (w)
2.30 Dolichoderus taschenbergi (g)
2.31 Formica glacialis (g)
2.39 Camponotus pennsylvanicus (w)
2.40 Martialis heureka (w)
2.42 Myrmecia gulosa (g)
2.45 Chronomyrmex medicinehatensis #1 (w)
2.55 Aphaenogaster honduriana (g)
2.56 Linepithema humile (g)
2.60 Neoponera villosa (w)
2.61 Formica glacialis (w)
2.62 Linepithema humile (w)
2.62 Polochrum repandum (Sa)
2.63 Ectatomma tuberculatum (w)
2.63 Kyromyrma neffi
2.66 Paraponera clavata (g)
2.67 Neoponera villosa (g)
2.69 Pseudarmania rasnitsyni (g)
2.72 Myrmecia gulosa (w)
2.77 Paraponera clavata (w)
2.79 Haidomyrmodes mammuthus #1 (g)
2.87 Sphecomyrmodes pilosus (w)
2.91 Sphecomyrmodes contegus (w)
3.02 Aphaenogaster honduriana (w)
3.11 Haidomyrmex zigrasi (w)
3.13 Sphecomyrma freyi #1 (w)
3.18 Boltonimecia canadensis (w)
3.23 Haidomyrmex scimitarus (g)
3.52 Sphecomyrmodes subcuspis (w)
3.67 Sphecomyrmodes rugosus (w)
3.68 Sphecomyrmodes spiralis (w)
4.09 Myanmyrma gracilis (w)

0.22 Boltonimecia canadensis (w)
0.22 Dasypoda plumipes (Me)
0.22 Sphecomyrma freyi #2 (w)
0.23 Andrena rosae (An)
0.23 Apterogyna sp. (B)
0.23 Brachycistis carinata (T)
0.23 Megachile lagopoda (Mg)
0.23 Pseudophotopsis sp. (Mu)
0.23 Tiphia femorata (T)
0.24 Leptanilloides erinys (g)
0.25 Leptanilla taiwanensis (g)
0.25 Eumenes pedunculatus (V)
0.25 Oxybellus sp. (C)
0.25 Smicromyrme rufipes (Mu)
0.25 Vespula vulgaris (V)
0.26 Haidomyrmodes mammuthus #2 (w)
0.26 Mutilla europaea (Mu)
0.26 Symmorphus sp. (V)
0.26 Vespa crabro (V)
0.27 Eciton hamatum (g)
0.27 Panurgus calcaratus (An)
0.28 Andrena hattorfiana (An)
0.28 Bradynobaenus gayi (B)
0.28 Leptanilloides erinys (w)
0.30 Ancistrocerus parietinus (V)
0.30 Crossocerus sp.(C)
0.30 Polistes gallicus (V)
0.30 Pseudomyrmex pallidus (w)
0.31 Eciton hamatum (w)
0.31 Leptanilla taiwanensis (w)
0.31 Martialis heureka (w)
0.32 Aenictus sp. (w)
0.32 Apis mellifera (Ap)
0.32 Cerapachys sp. (w)
0.32 Euodynerus disconotatus (V)
0.32 Haidoterminus cippus (w)
0.33 Cerapachys sp. (g)
0.33 Chronomyrmex medicinehatensis #1 (w)
0.33 Crabro cribrarius(C)
0.34 Brownimecia clavata (w)
0.34 Stigmatomma pallipes (w)
0.35 Bombus lucorum (Ap)
0.35 Bombus pascuorum (Ap)
0.35 Stigmatomma pallipes (g)
0.36 Acanthoponera mucronata (g)
0.36 Aenictus pachycerus (g)
0.36 Bombus hypnorum (Ap)
0.36 Bombus lapidarius (Ap)
0.37 Ectatomma tuberculatum (g)
0.37 Neoponera villosa (w)
0.37 Paraponera clavata (w)
0.38 Acanthoponera mucronata (w)
0.38 Chronomyrmex medicinehatensis #2 (w)
0.38 Dolichoderus taschenbergi (w)
0.38 Linepithema humile (w)
0.38 Manica invidia (g)
0.38 Manica invidia (w)
0.38 Neoponera villosa (g)
0.39 Camponotus pennsylvanicus (w)
0.39 Dolichoderus taschenbergi (g)
0.39 Dorylus sp. (w)
0.39 Eotapinoma macalpini (w)
0.39 Linepithema humile (g)
0.39 Myrmecia gulosa (w)
0.40 Ectatomma tuberculatum (w)
0.40 Formica glacialis (g)
0.40 Ponera pennsylvanica (w)
0.40 Tatuidris tatusia (w)
0.41 Aneuretus simoni (g)
0.41 Aphaenogaster honduriana (w)
0.41 Paraponera clavata (g)
0.42 Camponotus pennsylvanicus (g)
0.42 Formica glacialis (w)
0.42 Kyromyrma neffi (w)
0.42 Tatuidris tatusia (g)
0.42 Ponera pennsylvanica (g)
0.43 Myrmecia gulosa (g)
0.43 Dorylus rufescens (g)
0.44 Aneuretus simoni (w)
0.44 Canapone dentata (w)

	4.27 Gerontoformica cretacica (w)	0.47 Discothyrea sp. (g)
	4.31 Sphecomyrmodes rubustus (w)	0.48 Discothyrea sp. (w)
	4.47 Sphecomyrmodes magnus (w)	0.49 Aphaenogaster honduriana (g)

Table S3. Male's antennal indexes sorted in acsending order

Cretaceous species are in bold

SL/HL	FL/HL	PL/HL
0.14 Tatuidris tatusia	1.36 Aenictogiton fossiceps	0.07 Dorylus sp.
0.16 Ectatomma tuberculatum	1.73 Dorylus sp.	0.08 Myrmecia sp.
0.18 Baikuris mandibularis	1.83 Leptanilla sp.	0.09 Aneuretus simoni
0.18 Neoponera villosa	1.86 Camponotus pennsylvanicus	**0.09 Baikuris mandibularis**
0.18 Ponera pennsylvanica	1.88 Linepithema humile	0.09 Discothyrea sp.
0.19 Myrmecia sp.	2.11 Discothyrea sp.	0.09 Paraponera clavata
0.22 Baikuris maximus	2.21 Eciton hamatum	0.09 Stigmatomma pallipes
0.22 Acanthoponera mucronata	2.22 Pseudomyrmex pallidus	0.10 Cerapachys sp.
0.22 Aneuretus simoni	2.35 Tatuidris tatusia	0.10 Manica invidia
0.22 Manica invidia	2.36 Aphaenogaster honduriana	**0.10 Baikuris maximus**
0.22 Stigmatomma pallipes	2.44 Stigmatomma pallipes	**0.11 Dlusskyidris zherichini**
0.25 Linepithema humile	2.71 Formica glacialis	**0.11 Shecomyrma sp.**
0.27 Paraponera clavata	3.06 Dolichoderus taschenbergi	0.11 Tatuidris tatusia
0.27 Pseudomyrmex pallidus	**3.20 Baikuris mandibularis**	0.11 Ectatomma tuberculatum
0.20 Cerapachys sp.	3.43 Aenictus sp.	0.11 Pseudomyrmex pallidus
0.31Dolichoderus taschenbergi	**3.54 Dlusskyidris zherichini**	0.13 Linepithema humile
0.31 Dlusskyidris zherichini	3.74 Leptanilloides mckennae	0.14 Ponera pennsylvanica
0.32 Baikuris casei	3.75 Ponera pennsylvanica	0.15 Aenictogiton fossiceps
0.33Leptanilla sp.	3.84 Cerapachys sp.	0.15 Aphaenogaster honduriana
0.36 Aphaenogaster honduriana	3.85 Aneuretus simoni	**0.15 Archaeopone taylori**
0.37 Shecomyrma sp.	3.80 Manica invidia	**0.15 Baikuris casei**
0.40 Discothyrea sp.	4.04 Myrmecia sp.	0.16 Dolichoderus taschenbergi
0.46 Aenictogiton fossiceps	4.43 Acanthoponera mucronata	0.17 Acanthoponera mucronata
0.50 Archaeopone taylori	**4.44 Shecomyrma sp**.	0.17 Leptanilla sp.
0.51 Leptanilloides mckennae	5.45 Paraponera clavata	0.17 Neoponera villosa
0.60 Dorylus sp.	**5.56 Baikuris maximus**	0.18 Eciton hamatum
0.72 Eciton hamatum	**5.73 Baikuris casei**	0.19 Formica glacialis
1.07 Formica glacialis	6.21 Neoponera villosa	0.21 Camponotus pennsylvanicus
1.17 Camponotus pennsylvanicus	6.44 Ectatomma tuberculatum	0.23 Leptanilloides mckennae
1.22 Aenictus sp.		0.27 Aenictus sp.

Table S3 (continued)

F1L/HL	F2L/HL	SL/FL
0.07 Dorylus sp.	0.06 Aenictogiton fossiceps	0.02 Ectatomma tuberculatum
0.07 Aenictogiton fossiceps	0.08 Leptanilla sp.	0.03 Neoponera villosa
0.08 Leptanilla sp.	0.11 Dorylus sp.	0.04 Leptanilloides mckennae
0.13 Camponotus pennsylvanicus	0.15 Aphaenogaster honduriana	**0.04 Baikuris maximus**
0.15 Tatuidris tatusia	0.15 Tatuidris tatusia	**0.05 Baikuris mandibularis**
0.20 Aphaenogaster honduriana	0.17 Aneuretus simoni	0.05 Acanthoponera mucronata
0.21 Eciton hamatum	0.18 Discothyrea sp.	0.05 Paraponera clavata
0.22 Discothyrea sp.	0.18 Stigmatomma pallipes	0.05 Ponera pennsylvanica
0.22 Stigmatomma pallipes	0.21 Camponotus pennsylvanicus	0.05 Cerapachys sp.
0.24 Formica glacialis	0.21 Eciton hamatum	0.05 Myrmecia sp.
0.27 Pseudomyrmex pallidus	0.21 Formica glacialis	**0.06 Baikuris casei**
0.29 Aneuretus simoni	0.22 Dolichoderus taschenbergi	0.06 Aneuretus simoni
0.30 Aenictus sp.	0.22 Pseudomyrmex pallidus	0.06 Tatuidris tatusia
0.30 Cerapachys sp.	0.27 Aenictus sp.	0.06 Manica invidia
0.31 Dolichoderus taschenbergi	0.30 Manica invidia	**0.08 Sphecomyrma sp.**
0.32 Ponera pennsylvanica	0.31 Linepithema humile	**0.09 Dlusskyidris zherichini**
0.36 Manica invidia	0.32 Ponera pennsylvanica	0.09 Stigmatomma pallipes
0.36 Dlusskyidris zherichini	**0.33 Dlusskyidris zherichini**	0.10 Dolichoderus taschenbergi
0.37 Shecomyrma sp.	**0.34 Baikuris mandibularis**	0.12 Pseudomyrmex pallidus
0.38 Linepithema humile	**0.35 Shecomyrma sp.**	0.13 Linepithema humile
0.38 Leptanilloides mckennae	0.36 Leptanilloides mckennae	0.15 Aphaenogaster honduriana
0.43 Acanthoponera mucronata	0.40 Cerapachys sp.	0.18 Leptanilla sp.
0.46 Myrmecia sp.	0.46 Myrmecia sp.	0.19 Discothyrea sp.
0.50 Baikuris mandibularis	0.48 Acanthoponera mucronata	0.33 Eciton hamatum
0.63 Baikuris casei	**0.55 Archaeopone taylori**	0.34 Aenictogiton fossiceps
0.68 Paraponera clavata	**0.57 Baikuris maximus**	0.35 Dorylus sp.
0.69 Ectatomma tuberculatum	0.59 Paraponera clavata	0.35 Aenictus sp.

0.71 Neoponera villosa **0.72 Baikuris maximus** **1.00 Archaeopone taylori**	**0.67 Baikuris casei** 0.69 Ectatomma tuberculatum 0.69 Neoponera villosa	0.39 Formica glacialis 0.63 Camponotus pennsylvanicus

Table S3 (continued)

PL/(AL-PL)	**F1L/(AL-F1L)**	**F2L/(AL-F2L)**
0.02 Paraponera clavata 0.02 Ectatomma tuberculatum **0.02 Baikuris maximus** 0.02 Myrmecia sp. 0.02 Aneuretus simoni **0.02 Shecomyrma sp.** **0.03 Baikuris casei** 0.03 Cerapachys sp. 0.03 Manica muttica **0.03 Baikuris mandibularis** 0.03 Neoponera villosa **0.03 Dlusskyridris zherihini** 0.03 Dorylus sp. 0.03 Stigmatomma pallipes 0.04 Acanthoponera mucronata 0.04 Tatuidris tatusia 0.04 Dyscothyrea sp. 0.04 Ponera pennsylvanica 0.05 Pseudomyrmex pallidus 0.05 Dolichoderus traschenbergi 0.05 Formica glacialis 0.06 Leptanilloides mckennae 0.06 Aphaenogaster honduriana 0.06 Aenictus sp. 0.06 Linepithema humile 0.06 Eciton hammatum 0.08 Camponotus pennsylvanicus 0.08 Leptanilla sp. 0.09 Aenictogiton fossiceps	0.03 Dorylus sp. 0.04 Aenictogiton fossiceps 0.04 Leptanilla sp. 0.04 Camponotus pennsylvanicus 0.06 Tatuidris tatusia 0.07 Aenictus sp. 0.07 Formica glacialis 0.08 Aneuretus simoni 0.08 Aphaenogaster honduriana 0.08 Eciton hammatum 0.08 Cerapachys sp. **0.08 Shecomyrma sp.** 0.09 Ponera pennsylvanica 0.09 Stigmatomma pallipes 0.10 Leptanilloides mckennae 0.10 Dyscothyrea sp. 0.10 Acanthoponera mucronata 0.10 Manica muttica **0.10 Dlusskyridris zherihini** 0.10 Dolichoderus traschenbergi **0.12 Baikuris casei** 0.12 Ectatomma tuberculatum 0.12 Pseudomyrmex pallidus 0.12 Myrmecia sp. 0.13 Neoponera villosa 0.14 Paraponera clavata **0.14 Baikuris maximus** **0.17 Baikuris mandibularis** 0.21 Linepithema humile	0.03 Aenictogiton fossiceps 0.04 Leptanilla sp. 0.04 Aneuretus simoni 0.05 Dorylus sp. 0.06 Aphaenogaster honduriana 0.06 Formica glacialis 0.06 Tatuidris tatusia 0.06 Aenictus sp. 0.07 Dolichoderus traschenbergi 0.07 Stigmatomma pallipes 0.08 Camponotus pennsylvanicus 0.08 Eciton hammatum 0.08 Dyscothyrea sp. **0.08 Shecomyrma sp.** 0.08 Manica muttica 0.09 Ponera pennsylvanica 0.09 Leptanilloides mckennae **0.09 Dlusskyridris zherihini** 0.10 Pseudomyrmex pallidus 0.11 Cerapachys sp. 0.11 Acanthoponera mucronata **0.11 Baikuris maximus** **0.11 Baikuris mandibularis** 0.12 Paraponera clavata 0.12 Ectatomma tuberculatum 0.12 Neoponera villosa 0.12 Myrmecia sp. **0.12 Baikuris casei** 0.17 Linepithema humile

Table S4. P values for comparison of indexes SL/HL, females

Data from ANOVA with planned comparison of selected groups. Data below the name of the group: arithmetic mean ± standard deviation; [max; min]; n = number of specimens. Crown - all recent crown ants from Table S1; Cretaceous crown - genera *Kyromyrma*, *Canapone*, *Eotapinoma*, *Chronomyrmex*; Sphecomyrmini - genera *Sphecomyrma*, *Sphecomyrmodes*, *Zigrasimecia*; Haidomyrmecini - genera *Haidomyrmex*, *Haidomyrmodes*, *Haidoterminus*; Sphecomyrminae - Sphecomyrmini+Haidomyrmecini; Armaniinae - genera *Armania*, *Pseudarmania*, *Orapia*.

	crown 0.76±0.23 [0.33; 1.24] n=47	Cretaceous crown 0.84±0.16 [0.66; 1.10] n=5	Sphecomyrmini 0.41±0.14 [0.19; 0.67] n=18	Haidomyrmecini 0.57±0.08 [0.49; 0.69] n=6	Armaniinae 0.29±0.07 [0.20; 0.34] n=3	Sphecomyrminae 0.45±0.15 [0.19; 0.69] n=24	Sphecomyrminae+Armaniinae 0.43±0.15 [0.19; 0.69] n=27
crown		0.34	<0.0001	0.08	<0.0001	<0.0001	<0.0001
Sphecomyrmini				0.01	0.12		
Haidomyrmecini					0.003		
Armaniinae						0.01	

Table S5. P values for comparison of indexes FL/HL, females

See Table S4 for detailes.

	crown 1.27±0.29 [0.63; 1.78] n=47	Cretaceous crown 1.32±0.32 [0.83; 1.64] n=5	Sphecomyrmini 2.40±0.80 [1.43; 4.00] n=16	Haidomyrmecini 2.04±0.60 [1.37; 2.72] n=5	Sphecomyrminae 2.32±0.76 [1.37; 4.00] n=21
crown		0.71	<0.0001	<0.0001	<0.0001
Sphecomyrmini				0.28	

Table S6. P values for comparison of indexes PL/HL, females

See Tables S4 for details

	crown 0.13±0.04 [0.04; 0.27] n=47	Cretaceous crown 0.14±0.06 [0.07; 0.22] n=5	Sphecomyrmini 0.15±0.04 [0.09; 0.26] n=18	Haidomyrmecini 0.15±0.04 [0.10; 0.20] n=6	Armaniinae 0.11±0.005 [0.11; 0.12] n=2	Sphecomyrminae 0.15±0.04 [0.09; 0.26] n=24	Sphecomyrminae+Armaniinae 0.15±0.04 [0.09; 0.26] n=26
crown		0.59	0.03	0.24	0.89	0.04	0.28
Sphecomyrmini				0.82	0.33		
Haidomyrmecini					0.45		
Armaniinae						0.37	

Table S7. P values for comparison of indexes F1L/HL, females

See Tables S4 for details

	crown 0.10±0.05 [0.04; 0.26] n=47	Cretaceous crown 0.08±0.02 [0.05; 0.11] n=5	Sphecomyrmini 0.32±0.09 [0.20; 0.52] n=18	Haidomyrmecini 0.17±0.03 [0.11; 0.20] n=6	Armaniinae 0.33±0.002 [0.33; 0.34] n=2	Sphecomyrminae 0.28±0.10 [0.11; 0.52] n=24	Sphecomyrminae+Armaniinae 0.29±0.10 [0.11; 0.52] n=26
crown		0.69	<0.0001	0.001	<0.0001	<0.0001	<0.0001
Sphecomyrmini				0.002	0.83		
Haidomyrmecini					0.04		
Armaniinae						0.22	

Table S8. P values for comparison of indexes F2L/HL, females

See Table S4 for details

	crown 0.09±0.05 [0.03; 0.28] n=47	Cretaceous crown 0.09±0.03 [0.05; 0.11] n=5	Sphecomyrmini 0.23±0.08 [0.12; 0.37] n=18	Haidomyrmecini 0.21±0.12 [0.11; 0.43] n=6	Armaniinae 0.17±0.01 [0.17; 0.18] n=2	Sphecomyrminae 0.23±0.09 [0.11; 0.43] n=24	Sphecomyrminae+Armaniinae 0.22±0.08 [0.11; 0.43] n=26

crown		0.77	<0.0001	<0.0001	0.03	<0.0001	<0.0001
Sphecomyrmini				0.51	0.50		
Haidomyrmecini					0.81		
Armaniinae						0.64	

Table S9. P values for comparison of indexes SL/FL, females

See Table S4 for details

	crown 0.60±0.15 [0.27; 0.94] n=47	Cretaceous crown 0.66±0.11 [0.49; 0.80] n=5	Sphecomyrmini 0.18±0.05 [0.11; 0.28] n=16	Haidomyrmecini 0.31±0.11 [0.19; 0.48] n=5	Sphecomyrminae 0.21±0.09 [0.11; 0.48] n=21
crown		0.43	<0.0001	<0.0001	<0.0001
Sphecomyrmini				<0.0001	

Table S10. P values for comparison of indexes PL/(AL-PL), females

See Table S4 for details

	crown 0.07±0.02 [0.03; 0.16] n=47	Cretaceous crown 0.07±0.03 [0.05; 0.10] n=5	Sphecomyrmini 0.06±0.02 [0.03; 0.10] n=16	Haidomyrmecini 0.06±0.02 [0.03; 0.09] n=5	Sphecomyrminae 0.06±0.02 [0.03; 0.10] n=21
crown		0.94	0.34	0.69	0.43
Sphecomyrmini				0.86	

Table S11. P values for comparison of indexes F1L/(AL-F1L), females

See Table S4 for details

	crown 0.05±0.02 [0.02; 0.12] n=47	Cretaceous crown 0.04±0.01 [0.03; 0.06] n=5	Sphecomyrmini 0.13±0.02 [0.10; 0.17] n=16	Haidomyrmecini 0.07±0.02 [0.04; 0.09] n=5	Sphecomyrminae 0.12±0.03 [0.04; 0.17] n=21
crown		0.20	<0.0001	0.06	<0.0001
Sphecomyrmini				0.01	

Table S12. P values for comparison of indexes F2L/(AL-F2L), females

See Table S4 for details

	crown 0.05±0.02 [0.02; 0.08] n=47	Cretaceous crown 0.04±0.009 [0.03; 0.06] n=5	Sphecomyrmini 0.09±0.01 [0.07; 0.12] n=16	Haidomyrmecini 0.08±0.04 [0.04; 0.15] n=5	Sphecomyrminae 0.08±0.02 [0.04; 0.15] n=21
crown		0.84	<0.0001	0.07	0.002
Sphecomyrmini				0.51	

Table S13. P values for comparison of indexes SL/AL, females

Data from ANOVA with planned comparison between selected groups. Data on Vespoidea and Apoidea are from Dlussky and Fedoseeva (1988), assigned to families in accordance with the current classification. Vespoidea: Sapygidae, Scoliidae, Tiphiidae, Mutillidae, Bradynobaenidae,Vespidae. Apoidea: Sphecidae, Crabronidae, Andrenidae, Melittidae, Megachilidae, Apidae. Social Hymenoptera: *Vespa sp*., *Vespula sp., Polistes sp., Apis sp.* (1 species each), *Bombus sp.* (4 species). Stem ants: all studied here Cretaceous stem ants from Table S1. Crown ants: all studied here Crown ants from Table S1. Data below the name of the group: arithmetic mean ± standard deviation; [max; min]; n = number of specimens.

	Crown ants 0.37±0.06 [0.21; 0.49] n=47	Stem ants 0.17±0.05 [0.09; 0.32] n=25	Vespoidea 0.21±0.06 [0.11; 0.32] n=20	Apoidea 0.22±0.07 [0.13; 0.33] n=14	Social 0.32±0.04 [0.25; 0.36] n=8
Crown ants		<0.0001	<0.0001	<0.0001	0.02
Stem ants			0.009	0.01	<0.0001

Table S14. P values for comparison of indexes AL/HL, females

See Table S13 for details

	Crown ants 2.03±0.48 [1.10; 3.02] n=47	Stem ants 2.90±0.85 [1.7; 4.5] n=25	Vespoidea 1.75±0.31 [1.3; 2.6] n=20	Apoidea 1.53±0.41 [1.1; 2.3] n=14	Social 1.48±0.22 [1.2; 1.9] n=8
Crown ants		<0.0001	0.01	0.002	<0.0001
Stem ants			<0.0001	<0.0001	<0.0001

Table S15. P values for comparison of male's indexes

Data from Student’s unpaired t test. Species listed in Table S3

index	Cretaceous	crown	P value
SL/HL	0.32±0.11 [0,18; 0,50] n=6	0.41±0.32 [0.14; 1.22] n=24	0.73
FL/HL	4.49±1.14 [3.20; 5.73] n=5	3.21±1.39 [1.36; 6.44] n=24	0.07
PL/HL	0.12±0.02 [0.09; 0.15] n=6	0.14±0.05 [0.07; 0.27] n=24	0.43
F1L/HL	0.59±0.24 [0.36; 1.00] n=6	0.31±0.18 [0.07; 0.71] n=24	0.01
F2L/HL	0.47±0.15 [0.33; 0.67] n=6	0.29±0.18 [0.06; 0.69] n=24	0.03
SL/FL	0.06±0.02 [0.04; 0.09] n=5	0.17±0.15 [0.02; 0.63] n=24	0.02
PL/(AL-PL)	0.03±0.004 [0.02; 0.03] n=5	0.04±0.02 [0.02; 0.09] n=24	0.05
F1L/(AL-F1L)	0.12±0.03 [0.08; 0.17] n=5	0.09±0.04 [0.03; 0.21] n=24	0.08
F2L/(AL-F2L)	0.08±0.04 [0.08; 0.12] n=5	0.08±0.03 [0.03; 0.17] n=24	0.20

Table S16. Comparison of flagellomers with each other

P value from Student’s paired t test. See tables S3, S4 for details of groups

group	F1L and PL		F2L/PL		F1L/F2L	
	(F1L/PL)× 100, %	P value	(F2L/PL)× 100, %	P value	(F1L/F2L) ×100, %	P value

Recent crown females	81	<0.0001	77	<0.0001	105	0.27
Cretaceous crown females	66	0.07	71	0.07	90	0.13
Sphecomyrmini	219	<0.0001	154	<0.0001	144	<0.0001
Haidomyrmecini	119	0.35	167	0.38	93	0.45
Shecomyrminae	193	<0.0001	158	<0.0001	132	0.003
Crown males	254	<0.0001	237	0.001	108	0.09
Cretaceous males	504	0.004	413	0.001	137	0.13

Table S17. Female's discriminant scores used in Fig.7 and Fig.8, sorted in acsending order
w – worker, g – gyne. Stem ants are in bold. See relevant figures for details

Fig.7	**Fig.8**
-4.48 Dorylus rufescens (g) -1.51 Aneuretus simoni (w) -1.49 Ponera pennsylvanica (g) -1.48 Dorylus sp. (w) -1.47 Canapone dentata (w) -1.46 Ponera pennsylvanica (w) -1.40 Aphaenogaster honduriana (g) -1.39 Tatuidris tatusia (w) -1.34 Acanthoponera mucronata (w) -1.31 Discothyrea sp. (g) -1.22 Discothyrea sp. (w) -1.22 Pseudomyrmex pallidus (w) -1.20 Aneuretus simoni (g) -1.19 Stigmatomma pallipes (w) -1.13 Manica invidia (g) -1.13 Acanthoponera mucronata (g) -1.11 Pseudomyrmex pallidus (g) -1.11 Aphaenogaster honduriana (w) -1.08 Dolichoderus taschenbergi (w) -1.07 Stigmatomma pallipes (g) -1.07 Manica invidia (w) -1.05 Tatuidris tatusia (g) -1.05 Cerapachys sp. (w) -1.04 Leptanilloides erinys (w) -1.02 Chronomyrmex medicinehatensis #2 (w) -0.98 Leptanilla taiwanensis (w) -0.97 Cerapachys sp. (g) -0.89 Kyromyrma neffi (w) -0.89 Aenictus pachycerus (g) -0.87 Camponotus pennsylvanicus (g) -0.86 Aenictus sp. (w) -0.76 Eotapinoma macalpini (w) -0.74 Camponotus pennsylvanicus (w) -0.74 Formica glacialis (g) -0.72 Dolichoderus taschenbergi (g) -0.68 Chronomyrmex medicinehatensis #1 (w) -0.67 Leptanilloides erinys (g) -0.65 Brownimecia clavata (w) -0.62 Martialis heureka (w) -0.59 Leptanilla taiwanensis (g) -0.58 Neoponera villosa (w) -0.58 Neoponera villosa (g) -0.51 Formica glacialis (w) -0.48 Ectatomma tuberculatum (g) -0.33 Eciton hamatum (w) -0.29 Linepithema humile (w) **-0.26 Haidomyrmodes mammuthus #2 (w)** -0.08 Ectatomma tuberculatum (w) -0.05 Linepithema humile (g) **-0.03 Haidoterminus cippus (w)** -0.02 Eciton hamatum (g) 0.09 Paraponera clavata (g) **0.17 Haidomyrmex zigrasi (w)**	-4.07 Dorylus rufescens (g) -1.69 Aneuretus simoni (w) -1.56 Ponera pennsylvanica (g) -1.53 Ponera pennsylvanica (w) -1.49 Canapone dentata (w) -1.49 Aphaenogaster honduriana (g) -1.45 Stigmatomma pallipes (w) -1.44 Dorylus sp. (w) -1.42 Tatuidris tatusia (w) -1.42 Manica invidia (g) -1.40 Chronomyrmex medicinehatensis #2 (w) -1.40 Acanthoponera mucronata (w) -1.31 Aphaenogaster honduriana (w) -1.28 Pseudomyrmex pallidus (w) -1.23 Aneuretus simoni (g) -1.21 Dolichoderus taschenbergi (w) -1.21 Camponotus pennsylvanicus (w) -1.20 Camponotus pennsylvanicus (g) -1.20 Cerapachys sp. (w) -1.18 Pseudomyrmex pallidus (g) -1.16 Stigmatomma pallipes (g) -1.12 Leptanilla taiwanensis (w) -1.12 Leptanilloides erinys (w) -1.12 Cerapachys sp. (g) -1.10 Tatuidris tatusia (g) -1.08 Discothyrea sp. (g) -1.06 Acanthoponera mucronata (g) -1.04 Kyromyrma neffi (w) -1.01 Neoponera villosa (g) -1.01 Neoponera villosa (w) -1.01 Aenictus sp. (w) -1.00 Manica invidia (w) -0.99 Aenictus pachycerus (g) -0.98 Discothyrea sp. (w) -0.97 Chronomyrmex medicinehatensis #1 (w) -0.88 Formica glacialis (g) -0.87 Eotapinoma macalpini (w) -0.87 Dolichoderus taschenbergi (g) -0.82 Leptanilloides erinys (g) -0.77 Leptanilla taiwanensis (g) -0.67 Formica glacialis (w) -0.63 Ectatomma tuberculatum (g) -0.53 Martialis heureka (w) -0.48 Linepithema humile (w) -0.44 Brownimecia clavata (w) -0.25 Ectatomma tuberculatum (w) -0.25 Eciton hamatum (w) -0.23 Linepithema humile (g) -0.09 Paraponera clavata (g) 0.08 Eciton hamatum (g) 0.14 Paraponera clavata (w) **0.24 Boltonimecia canadensis (w)** **0.63 Sphecomyrma mesaki (w)** 0.71 Myrmecia gulosa (w)

0.21 Paraponera clavata (w) 0.28 Myrmecia gulosa (w) 0.38 Myrmecia gulosa (g) **0.53 Sphecomyrma mesaki (w)** **0.58 Sphecomyrma freyii #3 (w)** **0.75 Sphecomyrmodes occidentalis (w)** **0.84 Haidomyrmodes mammuthus #1 (g)** **0.94 Zigrasimecia ferox #1 (w)** **1.16 Boltonimecia canadensis (w)** **1.18 Sphecomyrmodes orientalis (w)** **1.25 Zigrasimecia tonsora (g)** **1.48 Sphecomyrma freyii #2 (w)** **1.65 Zigrasimecia ferox #2 (w)** **1.66 Haidomyrmex scimitarus (g)** **2.09 Pseudarmania rasnitsyni (g)** **2.17 Sphecomyrma freyii #1 (w)** **2.17 Sphecomyrmodes contegus (w)** **2.37 Sphecomyrmodes pilosus (w)** **2.82 Sphecomyrmodes rugosus (w)** **3.05 Sphecomyrmodes spiralis (w)** **3.86 Gerontoformica cretacica (w)** **3.88 Sphecomyrmodes magnus (w)** **3.90 Sphecomyrmodes subcuspis (w)** **4.20 Sphecomyrmodes rubustus (w)** **5.21 Myanmyrma gracilis (w)**	**0.86 Sphecomyrma freyii #3 (w)** 0.89 Myrmecia gulosa (g) **0.96 Zigrasimecia ferox #1 (w)** **1.26 Sphecomyrmodes occidentalis (w)** **1.33 Zigrasimecia tonsora (g)** **1.88 Zigrasimecia ferox #2 (w)** **2.00 Sphecomyrmodes orientalis (w)** **2.30 Sphecomyrma freyii #2 (w)** **2.43 Sphecomyrmodes contegus (w)** **2.72 Sphecomyrma freyii #1 (w)** **2.79 Sphecomyrmodes rugosus (w)** **2.98 Pseudarmania rasnitsyni (g)** **3.07 Sphecomyrmodes pilosus (w)** **3.21 Sphecomyrmodes spiralis (w)** **3.57 Sphecomyrmodes magnus (w)** **4.31 Gerontoformica cretacica (w)** **4.49 Sphecomyrmodes rubustus (w)** **4.53 Sphecomyrmodes subcuspis (w)** **6.38 Myanmyrma gracilis (w)**

Table S18. Phylogenetic nomenclature of subclades of *Formicidae*^{P}

Reference phylogenies: Ward 1990; Baroni-Urbani *et al.* 1992; Brandão *et al.* 1999; Brady *et al.* 2006, 2014; Moreau *et al.* 2006; Ward *et al.* 2010; Schmidt 2013; Ward *et al.* 2014

Converted clade name	Clade definition
Martialinae^{P} Rabeling, Brown & Verhaagh 2008	The clade consisting of *Martialis heureka* Rabeling, Brown & Verhaagh 2008 and all species that share a more recent common ancestor with *Martialis heureka* Rabeling, Brown & Verhaagh 2008 than with *Leptanilla revelierii* Emery, 1870
Leptanillinae^{P} Wheeler, 1923	The clade originating with the most recent common ancestor of *Leptanilla revelierii* Emery, 1870, *Protanilla rafflesi* Bolton, 1990 and *Anomalomyrma taylori* Bolton, 1990
Proceratiinae^{P} Bolton, 2003	The clade originating with the most recent common ancestor of *Proceratium silaceum* Roger, J. 1863 and *Probolomyrmex tani* Fisher, 2007
Amblyoponinae^{P} Forel, 1893	The clade originating with the most recent common ancestor of *Amblyopone australis* Erichson, 1842, *Onychomyrmex hedleyi* Emery, 1895a and *Bannapone mulanae* Xu, 2000
Ponerinae^{P} Ashmead, 1905	The clade originating with the most recent common ancestor of *Ponera coarctata* (Latreille, 1802), *Platythyrea punctata* (Smith, F., 1858) and *Anochetus mayri* Emery, 1884
Paraponerinae^{P} Bolton, 2003	The clade consisting of *Paraponera clavata* (Fabricius, 1775) and all species that share a more recent common ancestor with *Paraponera clavata* (Fabricius, 1775) than with *Tatuidris tatusia* Brown & Kempf, 1968
Agroecomyrmecinae^{P} Bolton, 2003	The clade originating with the most recent

	common ancestor of *Tatuidris tatusia* Brown & Kempf, 1968 and *Ankylomyrma coronacantha* Bolton, 1973
Dorylinae^{P} Ashmead, 1905	The clade originating with the most common ancestor of *Dorylus helvolus* (Linnaeus, 1764),*Vicinopone conciliatrix* (Brown, 1975) and *Leptanilloides biconstricta* Mann, 1923
Myrmeciinae^{P} Ashmead, 1905	The clade originating with the most recent common ancestor of *Myrmecia gulosa* (Fabricius, 1775) and *Nothomyrmecia macrops* Clark, 1934
Pseudomyrmecinae^{P} Smith, 1952	The clade originating with the most recent common ancestor of *Pseudomyrmex gracilis* (Fabricius, 1804), *Myrcidris epicharis* Ward, 1990 and *Tetraponera punctulata* Smith, F., 1877
Ectatomminae^{P} Bolton, 2003	The clade originating with the most recent common ancestor of *Ectatomma tuberculatum* (Olivier, 1792) and *Gnamptogenys striatula* Mayr, 1884
Heteroponerinae^{P} Bolton, 2003	The clade originating with the most recent common ancestor of *Heteroponera carinifrons* Mayr, 1887, *Acanthoponera mucronata* (Roger, 1860) and *Aulacopone relicta* Arnol'di, 1930
Aneuretinae^{P} Clark,1951	The clade consisting of *Aneuretus simoni* Emery, 1893a and all species that share a more recent common ancestor with *Aneuretus simoni* Emery, 1893a than with *Dolichoderus attelaboides* (Fabricius, 1775)
Dolichoderinae^{P} Forel, 1893	The clade originating with the most recent common ancestor of *Dolichoderus attelaboides* (Fabricius, 1775), *Tapinoma sessile* (Say, 1836) and *Linepithema humile* (Mayr, 1868)
Formicinae^{P} Ashmead, 1905	The clade originating with the most recent common ancestor of *Formica rufa* Linnaeus, 1761, *Myrmelachista flavocotea* Longino, 2006, and *Camponotus pennsylvanicus* (De Geer, 1773)
Myrmicinae^{P} Ashmead, 1905	The clade originating with the most recent common ancestor of *Myrmica rubra* (Linnaeus, 1758), *Temnothorax rugatulus* (Emery, 1895b) and *Monomorium pharaonis* (Linnaeus, 1758)

References

Arnol'di, K. V. (1930) Studien über die Systematik der Ameisen. IV. Aulacopone, eine neue Ponerinengattung (Formicidae) in Russland. *Zoologischer Anzeiger*, 89, 139-144.

Ashmead, W. H. (1905) A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. *Canadian Entomologist*, 37, 381-384.

Baroni Urbani, C., Bolton, B., & Ward, P.S. (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). Systematic Entomology, 17.4, 301-329.

Baroni Urbani, C., & De Andrade, M. L. (2006) A new *Protanilla* Taylor, 1990 (Hymenoptera: Formicidae: Leptanillinae) from Sri Lanka. *Myrmecologische Nachrichten*, 8, 45-47.

Bharti, H. (2003) Queen of the army ant *Aenictus pachycerus* (Hymenopetra, Formicidae, Aenictinae). *Sociobiology*, 42, 715-718.

Bolton, B. (1973) A remarkable new arboreal ant genus (Hym. Formicidae) from West Africa. The Entomologist's monthly magazine, 108, 234-237.

Bolton, B. (1990) The higher classification of the ant subfamily Leptanillinae (Hymenoptera: Formicidae). Systematic Entomology, 15, 267-282.

Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1-370.

Borowiec, M.L., & Longino J.T. (2011) Three new species and reassessment of the rare Neotropical ant genus *Leptanilloides* (Hymenoptera, Formicidae, Leptanilloidinae). *ZooKeys*, 133, 19-48.

Brady, S. G., Schultz, T.R., Fisher, B. L., & Ward P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. Proceedings of the National Academy of Sciences, 103, 18172-18177.

Brady, S. G., Fisher, B. L., Schultz, T. R., & Ward, P. S. (2014) The rise of army ants and their relatives: diversification of specialized predatory doryline ants. *BMC Evolutionary Biology*, 14, 93.

Brandão, C. R. F., Diniz, J. L. M., Agosti, D., & Delabie, J. H. (1999) Revision of the Neotropical ant subfamily Leptanilloidinae. *Systematic Entomology*, 24, 17-36.

Brown, W. L., Jr. (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. *Search Agriculture (Ithaca N. Y.)*, 5, 1-115.

Brown, W. L., Jr., & Kempf, W. W. (1968) Tatuidris, a remarkable new genus of Formicidae (Hymenoptera). *Psyche (Cambridge)*, 74, 183-190.

Clark, J. (1934) Notes on Australian ants, with descriptions of new species and a new genus. *Memoirs of the National Museum of Victoria*, 8, 5-20.

Clark, J. (1951) *The Formicidae of Australia.* Vol. 1. Subfamily Myrmeciinae. CSIRO, Melbourne, Australia.

Creighton, W. S. (1950) The ants of North America. *Bulletin of the Museum of Comparative Zoology*, 104, 1-585.

De Geer, C. (1773) *Mémoires pour servir à l'histoire des insectes*. Tome troisième. Pierre Hesselberg, Stockholm.

Donoso, D. A. (2012) Additions to the taxonomy of the armadillo ants (Hymenoptera, Formicidae, Tatuidris). *Zootaxa,* 3503, 61-81.

Emery, C. (1870) Studi mirmecologici. *Bullettino della Società Entomologica Italiana*, 2, 193-201.

Emery, C. (1884) Materiali per lo studio della fauna Tunisina raccolti da G. e L. Doria. III. Rassegna delle formiche della Tunisia. *Annali del Museo Civico di Storia Naturale*, 21, 373-384.

Emery, C. (1893a) [Untitled. Introduced by: "M. C. Emery, de Bologne, envoie les diagnoses de cinq nouveaux genres de Formicides".]. *Bulletin Bimensuel de la Société Entomologique de France* 1892: cclxxv-cclxxvii.

Emery, C. (1893b) Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, 7, 633-682.

Emery, C. (1895a) Descriptions de quelques fourmis nouvelles d'Australie. *Annales de la Société Entomologique de Belgique*, 39, 345-358.

Emery, C. (1895b) Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. (Schluss). *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, 8, 257-360.

Emery, C. (1901) Note sulle Doriline. *Bollettino della Societa Entomologica Italiana*, 33, 43-56.

Erichson, W. F. (1842) Beitrag zur Insecten-Fauna von Vandiemensland, mit besonderer Berücksichtigung der geographischen Verbreitung der Insecten. *Archiv für Naturgeschichte*, 8, 83-287.

Fabricius, J. C. (1775) *Systema entomologiae, sistens insectorum classes, ordines, genera, species adiectis synonymis, locis, descriptionibus, observationibus*. Korte, Flensburg and Leipzig, Germany.

Fabricius, J. C. (1804) *Systema Piezatorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*. C. Reichard, Brunswick.

Fisher, B. L. (2007) A new species of Probolomyrmex from Madagascar. *Memoirs of the American Entomological Institute*, 80, 146-152.

Forel, A. (1893) Sur la classification de la famille des Formicides, avec remarques synonymiques. *Annales de la Société Entomologique de Belgique*, 37, 161-167.

Ketterl, J., & Verhaagh, M. (2004) *Acanthoponera mucronata* (Roger, 1860) (Hymenoptera: Formicidae), first record in Peru and Rio Grande do Sul, Brazil, with description of its male. *Revista Peruana de Entomologia*, 44, 65-68.

Latreille, P. A. (1802) Description d'une nouvelle espèce de fourmi. *Bulletin des Sciences par la Société Philomathique de Paris*, 3, 65-66.

Longino, J.T. 2006. A taxonomic review of the genus *Myrmelachista* in Costa Rica. Zootaxa. 1141: 1-54.

Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Salvii, Stockholm, Sweden.

Linnaeus, C. (1761) *Fauna suecica sistens animalia Sueciae regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes*. Editio altera, auctior. Salvii, Stockholm, Sweden.

Linnaeus, C. (1764) *Museum S:ae R:ae M:tis Ludovicae Ulricae Reginae Svecorum, Gothorum, Vandalorumque, &c. In quo animalia rariora, exotica, imprimis.* Insecta & Conchilia describuntur & determinantur. Salvii, Stockholm, Sweden.

Longino, J. T. (2003) A new Costa Rican species of *Leptanilloides* (Hymenoptera: Formicidae: doryline section: Leptanilloidinae). *Zootaxa*, 264, 1-6.

Mann, W. M. (1922) Ants from Honduras and Guatemala. *Proceedings of the United States National Museum*, 61, 1-54.

Mann, W. M. (1923) Two new ants from Bolivia. (Results of the Mulford Biological Exploration. - Entomology.). Psyche (Cambridge), 30, 13-18.

Mayr, G. (1868) Formicidae novae Americanae collectae a Prof. P. de Strobel. *Annuario della Società dei Naturalisti e Matematici, Modena*, 3, 161-178.

Mayr, G. (1884) [Untitled. Descriptions of eight new species.]. *In* Fourmis de Cayenne Française. *Edited by* O. Radoszkowsky. Trudy Russkogo Entomologicheskago Obshchestva, Russia. Pp. 31-38.

Mayr, G. (1887) Südamerikanische Formiciden. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 37, 511-632.

Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., & Pierce, N.E. (2006) Phylogeny of the ants: Diversification in the Age of Angiosperms. *Science*, 312, 101–104.

Ogata, K., Terayama, M., & Masuko, K. (1995) The ant genus *Leptanilla*: discovery of the worker-associated male of *L. japonica*, and a description of a new species from Taiwan (Hymenoptera: Formicidae: Leptanillinae). *Systematic Entomology*, 20, 27-34.

Olivier, A. G. (1792) *Encyclopédie méthodique. Histoire naturelle. Insectes.* Tome 6. (pt. 2). Panckoucke, Paris, France.

Rabeling, C., Brown, J. M., and Verhaagh, M. (2008) Newly discovered sister lineage sheds light on early ant evolution. *Proceedings of the National Academy of Sciences*, 105 (39), 14913-14917.

Roger, J. (1860) Die Ponera-artigen Ameisen. *Berliner Entomologische Zeitschrift*, 4, 278-312.

Roger, J. (1863) Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses nebst Ergänzung einiger früher gegebenen Beschreibungen. Berliner Entomologische Zeitschrift, 7, 131-214.

Santschi, F. (1915) Nouvelles fourmis d'Afrique. Annales de la Société Entomologique de France, 84, 244-282.

Say, T. (1836) Descriptions of new species of North American Hymenoptera, and observations on some already described. *Boston Journal of Natural History*, 1, 209-305.

Schmidt, C. (2013) Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). *Zootaxa*, 3647, 201-250.

Smith, F. (1858) *Catalogue of hymenopterous insects in the collection of the British Museum.* Part VI. Formicidae. British Museum, London, England.

Smith, F. (1877) Descriptions of new species of the genera Pseudomyrma and Tetraponera, belonging to the family Myrmicidae. *Transactions of the Entomological Society of London*, 1877, 57-72.

Smith, M. R. (1952) The correct name for the group of ants formerly known as Pseudomyrma (Hymenoptera). *Proceedings of the Entomological Society of Washington*, 54, 97-98.

Ward, P. S. (1990) The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): generic revision and relationship to other formicids. *Systematic Entomology*, 15, 449-489.

Ward, P. S., Brady, S. G., Fisher, B. L., & Schultz, T. R. (2010) Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Systematic Biology*, 59, 342-362.

Ward, P.S., Brady, S.G., Fisher, B.L., & Schultz, T.R. (2014) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*.

Wheeler, W. M. (1923) *Social life among the insects*. Harcourt, Brace and Co., New York, USA.

Wheeler, W. M. (1925) The finding of the queen of the army ant *Eciton hamatum* Fabricius. *Biological Bulletin (Woods Hole)*, 49, 139-149.

Wilson, E.O., Eisner, T., Wheeler, G.C., & Wheeler J. (1956) *Aneuretus simoni* Emery, a major link in ant evolution. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 115, 81-99.

Xu, Z.-H. (2000) Two new genera of ant subfamilies Dorylinae and Ponerinae (Hymenoptera: Formicidae) from Yunnan, China. *Zoological Research*, 21, 297-302.