

The First Find of the Formicoidea (Hymenoptera) in the Lower Cretaceous of the Northern Hemisphere

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Abstract—*Armania pristina* sp. nov., *A. capitata* sp. nov. and *Khetania mandibulata* gen. et sp. nov. (Armaniidae) are described from the Albian of Eastern Siberia. They are the earliest formicoids known from the Northern Hemisphere (and possibly worldwide). The genus *Armaniella* Dlussky, 1983 is synonymized with *Armania* Dlussky, 1983. *Khetania* is distinct from other armaniids in the construction of the cranio-mandibular system. The systematic position of other Cretaceous formicoids is discussed.

INTRODUCTION

Up to now only two species of Lower Cretaceous insects were interpreted as ants (Hymenoptera, Formicidae). However, this assignment raised some doubt (Darling and Sharkey, 1990). A poorly preserved specimen (fragments of the wings, body and legs) from the Lower Cretaceous deposits of the Koonwarra locality, Australia was described as a male of the ant *Cretoformica explicata* Jell et Duncan (Jell and Duncan, 1986). Later Naumann (1993) redescribed the *C. explicata* holotype and reinterpreted its wing venation. He excluded this species from the family Formicidae without assigning it to any other family of the Hymenoptera. A better preserved specimen of *Caridris bipetiolata* Brandão et Martins-Neto (Brandão et al., 1989) was described from the Santana Formation, Brazil dated as Early Aptian. According to the original interpretation this insect possessed geniculate antennae and a two-segmented waist. The authors assigned this species to the subfamily Myrmeciinae, represented in modern fauna by a single genus *Myrmecia* Fabricius, 1804 which is restricted to Australia. However, A.P. Rasnitsyn (pers. comm.) has doubted such an interpretation on the basis that *C. bipetiolata* should be transferred to the subfamily Ampulicinae in the family Sphecidae.

All Upper Cretaceous Formicoidea known to date are found in the Northern Hemisphere and belong to the families Armaniidae (11 described species) and Formicidae, the latter represented by the subfamilies Sphecomyrminae (11 species) and Ponerinae (one species). Both Armaniidae and Sphecomyrminae demonstrate the wing venation typical of ants, a single-segmented waist, and no constriction between the III and IV abdominal segments. It is worth remembering that formicoids like other Hymenoptera have the functional thorax (mesosoma) formed by the thoracic segments proper plus the first abdominal segment. Hence, the ant waist is homologous either to the genuine abdominal II

segment (petiole) or to the segments II and III (petiole and postpetiole). The first segment of the functional abdomen corresponds to either genuine abdominal segment III or IV, respectively. Therefore, to avoid confusion, the term 'metasomal segments' is used to designate the segments of the functional abdomen (metasoma), and 'abdominal segments' for those of the morphological abdomen.

The Sphecomyrminae, and possibly Armaniidae as well, possessed the metapleural glands (characteristic feature of ants). Their females were distinct from those of modern ants in the bidentate mandibles similar to those of the primitive solitary wasps, the relatively short antennal scape, and the long and flexible flagellum. In the Armaniidae the petiole was scarcely separated, more primitive than in the Amblyoponini (Formicidae, Ponerinae) and similar to that of some Scoliidae (Sierolomorphidae), whereas in the Sphecomyrminae it was nodiform, with a distinct tergo-sternal fusion, as in the modern Aneuretinae and Nothomyrmecinae. Some other characters likewise indicate that the Armaniidae were more primitive than the Sphecomyrminae. In armaniids, only males and winged females are known, whereas in sphecomyrminae only males and wingless females, interpreted as the workers by many authors (Wilson et al., 1967; Wilson, 1987; Grimaldi et al., 1997).

The Armaniidae are known from sedimentary rocks of the Cenomanian of Northeastern Siberia (Dlussky, 1983) and the Turonian of Kazakhstan (Dlussky, 1975), and the Sphecomyrminae from fossil resins of the Turonian of New Jersey (Wilson et al., 1967; Grimaldi et al., 1997), the Santonian of Taimyr (Dlussky, 1975), the Campanian of Canada (Wilson, 1985), and the Upper Cretaceous (not dated more precisely) of Taimyr (Baikura-Neru locality) and Burma (Dlussky, 1987, 1996). Both Armaniidae and Sphecomyrminae are not recorded in the Cenozoic and probably became extinct by the end of the Late Cretaceous. The oldest represen-

tative of an extant ant subfamily Ponerinae is found in the same New Jersey fauna as the earliest Sphecomyrminae. Previously these resins were dated as Coniacian–Santonian, but now are shown to be of Turonian age (Grimaldi *et al.*, 1997).

A new rich Lower Cretaceous entomofauna was discovered by an expedition of the Arthropod Laboratory, Paleontological Institute, Russian Academy of Sciences (PIN) in East Siberia (Khetana River, Ul'ia River Basin, Okhotsk District, Khabarovsk Territory). The deposit was dated as the Albian (Gromov *et al.*, 1993). All the specimens are poorly preserved impressions in tuffaceous argillite; 77 insects were determined as either Scolioidea or Formicoidea, 30 of them as Armaniidae, and 22 of them as the members of the genus *Armania*. Only seven specimens turned out to be appropriate for describing the species.

SYSTEMATIC PALEONTOLOGY

Superfamily Formicoidea Latreille, 1802

Family Armaniidae Dlussky, 1983

Genus *Armania* Dlussky, 1983

Armaniella: Dlussky, 1983, p. 71 (syn. nov.)

Type species. *A. robusta* Dlussky, 1983; Upper Cretaceous; Northeastern Siberia.

Diagnosis. Winged females. Head oval, without occipital angles. Mandibles short, with two teeth (apical and subapical). Eyes oval, weakly convex, situated about the middle of sides of the head. Antennae filiform. Scape (first antennal segment) short and thick, several times as long as wide. Second antennal segment very short, about as long as wide. Third antennal segment about as long as scape. Forewing with closed cells 1r+2r, 3r, rm and mcu. Hind trochanter single-segmented. Hind tibia with two spurs, one simple and one pectinate. Waist single-segmented. Petiole broadly attached to first metasomal segment, scarcely separated from it dorsally and laterally with slight depression, less than 1.5 times shorter than first metasomal tergite. Depression between first and second metasomal segments absent or scarcely indicated. Sting developed, massive, curved upwards.

Composition. *A. robusta* and *A. curiosa* (Dlussky, 1983) from the Upper Cretaceous (Cenomanian) of Northeastern Siberia, and two new species.

Comparison. Five genera of Armaniidae are known: *Archaeopone* Dlussky (Cenomanian–Turonian), *Poneropterus* Dlussky (Cenomanian), *Armania* Dlussky (Albian–Cenomanian), *Pseudarmania* Dlussky (Cenomanian), *Dolichomyrma* Dlussky (Turonian) (Dlussky, 1975, 1983). Two former genera are known from the males only, and the others from the females only. One can not exclude the possibility that *Armania* are the females of *Archaeopone* although it is not possible to confirm. *Armania* is distinct from *Dolichomyrma* in the head shape: oval with short mandibles and roughly midlateral eye position in *Armania*, elongate with the

eyes displaced backwards in *Dolichomyrma*. It is distinct from *Pseudarmania* in the forewing venation (fused cells 1r and 2r), one-segmented hind trochanter and shorter petiole.

Remarks. The genus *Armaniella* with the only species, *A. curiosa*, described from the same locality as *A. robusta*, was separated because of differences in the petiole and metasoma structure. In *A. curiosa* the petiole is evenly convex in profile, not forming a node, whereas in *A. robusta*, the only species originally assigned to *Armania*, the petiole is raised posteriorly to form a node, clearly seen in profile. Besides that, *A. curiosa* shows a slight constriction between the first and second metasomal (abdominal III and IV) segments, absent in *A. robusta*. Two new species described below have neither the node on the petiole nor the constriction between the first and second metasomal segments, and therefore are in a sense intermediate between *A. robusta* and *A. curiosa*. In light of the new data one should regard *Armaniella* as the junior synonym of *Armania*.

Armania pristina Dlussky, sp. nov.

Etymology. From Latin *pristinus* (primitive).

Holotype. PIN, no. 3800/100, poorly preserved winged female; Khetana River, Ul'ia River Basin, Okhotsk District, Khabarovsk Territory; Lower Cretaceous, Albian, Emanra Formation, outcrop 2/19.

Description (Figs. 1a, 1b). Winged female. The head is oval, without conspicuous occipital angles, about as long as wide, and (as measured in the holotype and paratype no. 3800/116) about 60% as long as the mesosoma. The first antennal segment (scape) is short and thick, the second one is about as long as wide, the third one is about as long as the scape. The scutum is evenly and weakly convex. The propodeum lacks spines or teeth. The petiole is evenly convex in profile, without a node, twice as wide as long, widest at junction to the first metasomal (abdominal III) segment. No constriction between the first and second metasomal segments.

Measurements (mm): body length (holotype), about 18; mesosoma length, 4.6–5.2 (holotype, 5.2); head length, 2.8 (paratype no. 3800/116) to 3.2 (holotype); petiole length, 1.03–1.1 (holotype, 1.05); length of hind femur, 3.4 (paratype no. 3800/66); length of hind tibia, 3.3 (holotype).

Material. Holotype and paratypes from the same locality: PIN, nos. 3800/66 (outcrop 2/19), 3800/99, 116, 159 (outcrop 2/20), poorly preserved winged females.

Comparison. Similar to *A. robusta* from the Upper Cretaceous of Northeastern Siberia in most of the visible characters, being distinct in the very broad petiole and larger head (in *A. robusta* the petiole is longer than wide, and the head is 60% as long as the mesosoma).

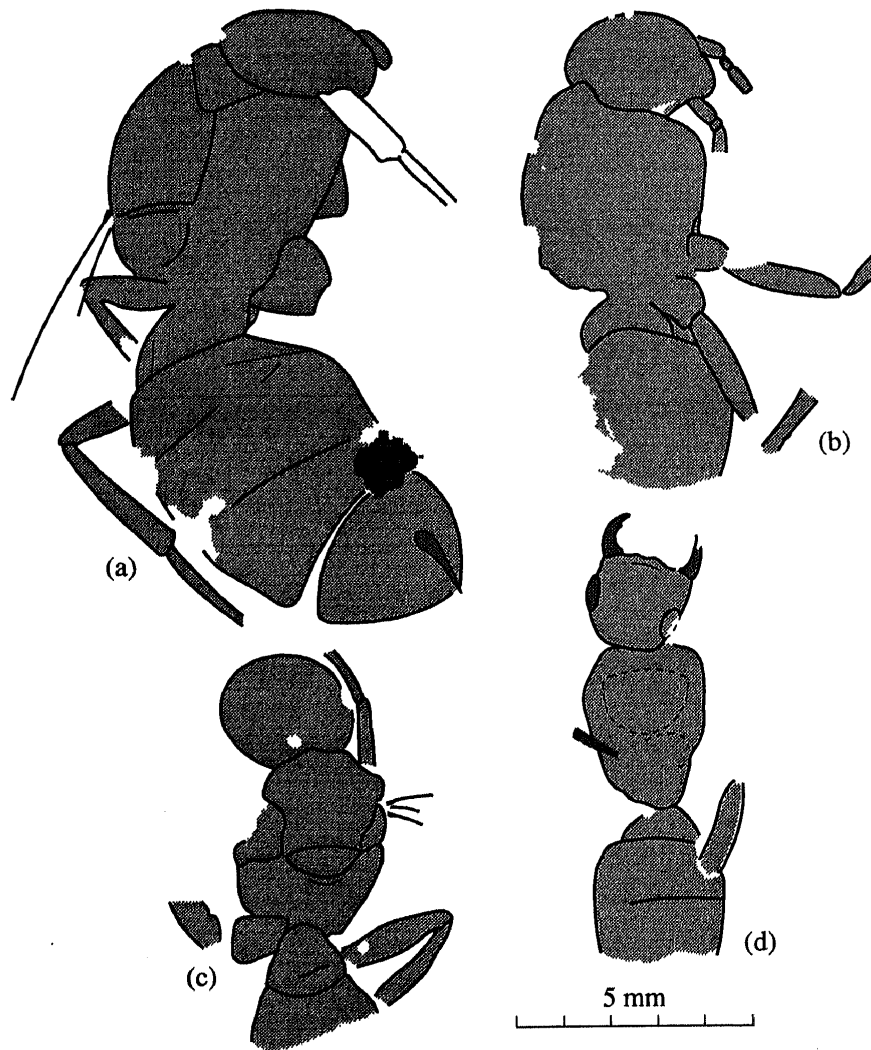


Fig. 1. Lower Cretaceous Armaniidae: (a, b) *Armania pristina* sp. nov.: (a) holotype PIN, no. 3800/100; (b) paratype PIN, no. 3800/116; (c) *A. capitata* sp. nov., holotype PIN, no. 3800/157; (d) *Khetania capitata* sp. nov., holotype PIN, no. 3800/67. Preserved portions of charred chitin in black. Scale bar division 1 mm.

Armania capitata Dlussky, sp. nov.

E t y m o l o g y. From Latin *capitatus* (big-headed).

H o l o t y p e. PIN, no. 3800/157, poorly preserved winged female; Khetana River, Ul'ia River Basin, Okhotsk District, Khabarovsk Territory; Lower Cretaceous, Albian, Emanra Formation, outcrop 2/20.

D e s c r i p t i o n (Fig. 1c). Winged female. The head is oval, without conspicuous occipital angles, about 1.15 times as long as wide, and about 64% as long as the mesosoma. The scutum is clearly longer than wide; the scutellum is transverse. The propodeum lacks spines or teeth. The petiole is trapezoidal in dorsal aspect, about as long as wide, widest at junction to the first metasomal (abdominal III) segment. No constriction between the first and second metasomal segments.

M e a s u r e m e n t s (mm): body length (estimated from the preserved portion), about 12; mesosoma

length, 3.6; head length, 2.3; head width, 2.0; petiole length, 1.45; length of hind femur, 2.3.

M a t e r i a l. Holotype.

C o m p a r i s o n. Similar to *A. robusta* and *A. pristina* sp. nov. in most of the visible characters, being distinct in the smaller size, moderately broad petiole and very large head.

Genus *Khetania* Dlussky, gen. nov.

E t y m o l o g y. From the Khetana River.

T y p e s p e c i e s. *Khetania mandibulata* sp. nov.

D i a g n o s i s. Winged female. Head trapezoidal, widening forwards, with feebly convex sides and rounded occipital angles. Eyes large and convex, elongate elliptical. Bases of mandibles far apart. Mandibles weakly curved, linear, with apical and subapical teeth. Waist single-segmented. Petiole transverse, broadly

attached to first metasomal segment, and twice shorter than its tergite. Depression between first and second metasomal segments absent.

Composition. Type species.

Comparison. Distinct from all known Armaniidae and Sphecomyrminae in the trapezoidal head with broadly separated bases of linear mandibles. In other members of these groups the head is oval or elongate, and mandibles either short or (in *Haidomyrmex* Dlussky, 1996) of completely different structure.

Remarks. The only specimen of *Kh. mandibulata* is very poorly preserved, but nevertheless some conclusions can be drawn. Although the wings are not preserved, the thoracic structure (the scutum and scutellum well-developed) clearly indicates that the insect was able to fly. The shape of the petiole and the structure of the mandibles make its assignment to the superfamily Formicoidea and the family Formicidae very probable, although such important characters as the structure of antennae, the wing venation and the presence of metapleural glands remain unknown. A peculiar structure of the cranio-mandibular system indicates that the species merits generic separation. A similar type of the cranio-mandibular system is recorded in some recent ants (*Myrmecia*, *Amblyopone* Erichson, *Thaumatomyrmex* Mayr, some *Leptogenys* Rog.) with a primitive social organization and specialized hunting behavior.

Khetania mandibulata Dlussky, sp. nov.

Etymology. From Latin *mandibulatus* (with large mandibles).

Holotype. PIN, no. 3800/67, poorly preserved winged female; Khetana River, Ul'ia River Basin, Okhotsk District, Khabarovsk Territory; Lower Cretaceous, Albian, Emanra Formation, outcrop 2/19.

Description (Fig. 1d). Winged female. The head length is equal to its maximal width, and twice less than the length of the mesosoma. The clypeus is narrow, with two small lobes at the front margin. The propodeum lacks spinules or teeth. The petiole is transverse, 2.5 times as wide as long, twice shorter than the first metasomal sternite.

Measurements (mm): body length (estimated from the portion preserved), about 8.5; mesosoma length, 3; head length, 1.6; head width, 1.6; petiole length, 0.5.

Material. Holotype.

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