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On the Taxonomic State of a Digger Wasp of the Tribe Crabronini (Hymenoptera, Crabronidae, Crabroninae) from the Dominican Amber

A. V. Antropov

Zoological Museum, Moscow, State University, ul. Bolshaya Nikitskaya 6, Moscow, 125009 Russia
e-mail: antropov@zmmu.msu.ru

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Abstract—"*Lindenius paleomystax*" described from the Miocene Dominican amber has been included into a separate digger wasp genus, *Lindocerus* gen. nov. (Crabronidae, Crabroninae, Crabronini), which is similar to the genus *Crossocerus* Lepeletier de Saint Fargeau et Brullé, 1835, but differs in the well-pronounced hypersternaulus.

Keywords: Crabronidae, Crabronini, digger wasps, new genus, Miocene, Dominican amber
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INTRODUCTION

Fossil resins are of particular interest for studying the insect paleofauna. In contrast to two-dimensional imprints in the deposits of different ages, they are significantly more informative, since they allow the study of inclusions at different angles. At the same time, it should be taken into account that inclusions in fossil resins display only a small part of the diversity of entomofauna of particular periods, since resins mostly enclose insects associated with trees. This relation is closest for actively flying hymenopterans. This is particularly proved by the fact that almost all digger wasps (Hymenoptera, Sphecidae sensu lato) described from fossil resins belong to the taxa extant representatives of which are typical xylobionts, whose females either hide their prey in bark folds or make nests in dry wood and abandoned burrows of xylophagous insects. The first belong to the family Ampulicidae (4 tribes, 5 genera, 6 species) (Nemkov, 1988; Antropov, 2000b; Ohl, 2004); the second are Crabronidae (Pemphredoninae: 5 tribes, 15 genera, 23 species; Crabroninae: 3 tribes, 6 genera, 14 species) (Cockerell, 1909; Evans, 1969, 1973; Sorg, 1986; Antropov and Pulawski, 1989, 1996; Budrys, 1993; Prentice and Poinar, 1993; Antropov, 1995, 2000a, 2000b, 2010, 2011; Nel, 2005; Bennett and Engel, 2008; Antropov and Perkovsky, 2009).

Lindenius paleomystax Bennett et Engel, 2006 (Crabronidae, Crabroninae, Crabronini) described from the Miocene Dominican amber is the only known exception to this rule. The point is that all extant species of the genus *Lindenius* Lepeletier de Saint Fargeau et Brullé, 1835 with the known nesting sites are exclusively terrabiotic with females digging nests in the ground and not related to trees. The genus *Lindenius* is assigned to the basal branch of the subtribe Crabronina, for which terrabiont nests are considered as the initial state and there are no grounds to assume that the ancestral forms of this group used to be xylobionts. Therefore, embedding of an insect representing the genus *Lindenius* in tree resin should be treated as a highly improbable event. The possibility to find several specimens of the same species belonging to this genus tends to zero. However, the material for description of "*Lindenius paleomystax*" consisted of two specimens. In my opinion, this shows the necessity of more careful analysis of features of this taxon.

Unfortunately, for objective reasons beyond my control, I had no possibility to study the type material of "*Lindenius paleomystax*" and, for subjective reasons, over several years of correspondence, I did not receive detailed data from either the authors of the original description or colleagues from the American Museum of Natural History (New York, United States). Thus, all conclusions provided below are based exclusively on the original description of "*Lindenius paleomystax*" and comparison of this species with living representatives of the genus *Lindenius* and similar crabronine taxa.

The authors assigned the described fossil wasps to the genus *Lindenius* based on the following features regarded as diagnostic and taken from the generic diagnosis provided in the revision of digger wasp genera of the world fauna (Bohart and Menke, 1976):

—mandibles acute apically and with even ventral margin;

—ocellar triangle wider than high;

—depression of lower frons behind antennal scapes without ridges;

—hind wing [sic] longer than second cubital (submedial) cell.

In addition to the key features, the authors noted a specific shape of the anterior margin of the clypeus (Bennett and Engel, 2006, text-fig. 4).

However, a detailed consideration of these features shows that they are very formal and prevent reliable assignment of the fossil species studied to the genus *Lindenius*.

First, the mandibles acute apically and with a smooth ventral margin are characteristic of many crabronine genera. At the same time, the inner margin of mandibles in females of *Lindenius* has more or less developed teeth, while that in the figured accompanying description of "*Lindenius paleomystax*" lacks teeth (Bennett and Engel, 2006, text-figs. 2, 4), which is explained by the authors as one of the main differences of the fossil species from extant representatives of *Lindenius*. However, this shape of mandibles is common in, for example, females of the subgenus *Hoplocrabro* Thomson, 1874 of the genus *Crossocerus* Lepeletier de Saint Fargeau et Brullé, 1835.

Second, the ocelar triangle is wider than high in almost all genera of the tribe Crabronini, including even males of some species of the genus *Lestica* Billberg, 1820, which have a head narrowed strongly laterally due to the extremely impressed temples. This feature, which was taken by the authors from the revision of Bohart and Menke reflects incorrectly the actual proportions of this structure, since the width of the ocellar triangle, even in case of an equilateral one, is greater than its height. Actually, the ocelli in females of the genus *Lindenius* form a very obtuse (sometimes even almost flat) triangle, while in "*Lindenius paleomystax*", according to the illustrations (Bennett and Engel, 2006, text-fig. 1), it is right-angled. Furthermore, the head of females of *Lindenius,* as viewed from above, is almost twice wider than long, while that of "*Lindenius paleomystax*" is at most 1.5 times wider (Bennett and Engel, 2006, text-figs. 1, 3). The distance between the lateral ocelli in *Lindenius* is clearly greater than the distance between the lateral ocellus and the nearest eye, while these distances in "*Lindenius paleomystax*" are almost equal (Bennett and Engel, 2006, text-fig. 4). This shape of the head and ocellar triangle is also typical for females of the genus *Crossocerus* (*Hoplocrabro*).

Third, an impression of the lower frons behind the antennal scapes not bordered by ridges is a plesiomorphic condition typical for many crabronine genera.

Fourth, the last feature provided by the authors is puzzling, since the hind wing of all crabronines is a priori longer than the submedial cell of both fore- and hind wings. The mistake made by the authors in interpretation of this feature is that the revision of digger wasp genera discusses only the jugal lobe rather than the length of the entire hind wing in comparison with the submedial cell length of the hind wing (Bohart and Menke, 1976, p. 382, text-fig. 122 A). A possible reason for it might be a typing error that resulted in the loss of indication of the jugal lobe. However, in any case, the length ratio of the jugal lobe to submedial cell of the hind wing in the revision is regarded as the only discrete difference of both sexes of *Lindenius* from the genus *Crabro* Fabricius, 1775, in which the jugal lobe is shorter than the submedial cell rather than as an apomorphic condition of *Lindenius* (males of *Lindenius* also lack protibial broadenings, which are found in some species of *Crabro*). In *Crossocerus* (*Hoplocrabro*), the jugal lobe is also longer than the submedial cell of the hind wing.

Finally, the anterior margin of the clypeus with a concave medial lobe and a pair of lateral teeth, although resemble somewhat the clypei of some extant species of the genus *Lindenius*, but it is not unique to this genus. Females of the genus *Crossocerus* (*Hoplocrabro*), such as Palearctic *C. quadrimaculatus* (Fabricius, 1793) and East Asian *C. pseudopalmarius* (Gussakovskij, 1932), also have a similar shape of the anterior margin of the clypeus (Marshakov, 1979). *Crossocerus pseudopalmarius* is similar to "*Lindenius paleomystax*" in both size and absence of light-colored spots on the abdomen.

Another important feature provided in the description of "*Lindenius paleomystax*" and not included in the diagnosis of the genus should be mentioned: the shape and sculpture of the pygidial plate in females. In contrast to known species of the genus *Lindenius*, the pygidial plate of which similarly to other terrabiont forms of digger wasps without digging structures (psammophores and digging rakes), is covered with dense hairs hiding the cuticle sculpture, the description of "*Lindenius paleomystax*" reads that the flat triangular pygidial plate is longer than wide, evenly narrowed toward its truncate apex, and has dense punctures, which is even denser near the apex. The description provides no data on hairs covering the pygidial plate of "*Lindenius paleomystax*" and the illustrations (Bennett and Engel, 2006, text-fig. 1) show only sparse setae at the base of the pygidial plate sides. However, it is plausible that, if hairs in the pygidial plate of "*Lindenius paleomystax*" were similar to that in female *Lindenius*, they would have been distinctly seen. This shape and sculpture of the pygidial plate are characteristic of females of the nominative subgenus *Crossocerus* and also *Crossocerus* (*Hoplocrabro*), which are xylobionts.

Thus, detailed consideration of the key features of fossil crabronine wasps prevents the assignment of these forms to the genus *Lindenius*. Most features in the description make this species close to the genus *Crossocerus*, especially to the subgenus *Crossocerus* (*Hoplocrabro*). However, "*Lindenius paleomystax*" differs from all recent species of the genus *Crossocerus* in the pronounced hypersternaulus and from species of

the subgenus *Crossocerus* (*Hoplocrabro*) in the absence of terminal teeth at the ends of the occipital carina. Consequently, "*Lindenius paleomystax*" cannot be assigned to the genus *Crossocerus*. As concerns the hypersternaulus, in the genus *Lindenius,* it is only present in the species group *L. mesopleuralus*, in which females are distinguished by the well-developed teeth on the inner margin of mandibles and by the wide, rounded apically pygidial plate densely covered with appressed hairs.

As a result, I come to the conclusion that the fossil species "*Lindenius paleomystax*" should be referred to as a separate genus of crabronine digger wasps, which is phylogenetically close to the genus *Crossocerus*.

Judging from the mandibular structure (absence of apical teeth and ventral lobes and notches), the absence of psammophores on mandibles, temples, and forefemora, absence of foretarsal digging rakes, and the pygidial plate of females without hairs, this species was a typical xylobiont, whose females did not produce burrows in wood, making their nests in the burrows abandoned by xylophagous insects. This solves the problem of the occurrence of these wasps in a fossil resin.

The systematic position of the new genus and its diagnosis are given below.

SYSTEMATIC PALEONTOLOGY

Superfamily Apoidea Latreille, 1802

Family Crabronidae Latreille, 1802

Subfamily Crabroninae Latreille, 1802

Tribe Crabronini Latreille, 1802

Genus *Lindocerus* Antropov, gen. nov.

Etymology. From the parts of the generic names *Lindenius* and *Crossocerus*.

Type species. *Lindenius paleomystax* Bennett et Engel, 2006; designated here by monotypy.

Diagnosis. Head thickened, dorsally about 1.5 times wider than long. Ocelli disposed in right-angled triangle, with distance between lateral ocelli equal to distance from lateral ocellus to nearest eye; ommatidia in lower part of eye noticeably larger than in upper part. Occipital carina without terminal teeth. Depression of frons behind antennal scapes without ridges; clypeus short, with medial lobe slightly apically concave and with pair of lateral teeth; mandibles simply apically pointed, with even outer ventral margin, without lobes and notches, without teeth on inner margin. Postspiracular, epicnemial, and acetabular carinae well-developed; episternal sulcus grooved; scrobal sulcus, mesopleuralus, verticaulus, and sternaulus absent; hypersternaulus developed. Forewing with antefurcal vein cu-a; recurrent vein connected with submarginal cell at its middle. Abdomen not petiolate; pygidial plate of females flat, triangular, evenly narrowed to truncate apex, with dense punctures, denser near apex, not covered with dense appressed hairs.

Species composition. *Lindocerus paleomystax* (Bennett et Engel, 2006) from the Miocene Dominican amber.

Remarks. Type material: holotype AMNH, no. DR-14-1091, female, Dominican Republic; Early Miocene (Burdigalian) amber, specific mine unknown. Paratype AMNH DR-14-236, female, Dominican Republic; Early Miocene (Burdigalian) amber, northern mines. Types (by original description, *Lindenius paleomystax* Bennett et Engel, 2006) are stored in the collection of amber fossils of the Division of Invertebrate Zoology, American Museum of Natural History.

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