

A New Tribe of Fossil Digger Wasps (Insecta: Hymenoptera, Crabronidae) from the Rovno Amber, Eocene of Ukraine

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Abstract—A new tribe of digger wasps, Protomicroidini trib. nov. (Hymenoptera, Crabronidae), including a single known species *Protomicroides sororius* gen. et sp. nov. is described from the Upper Eocene Rovno amber, Ukraine. The new tribe combines features characteristic of several tribes of the Crabroninae and is a sister group of the extant tribe Oxybelini. The most distinctive characters of the new tribe include nonelongate propodeum with strongly developed lateral keel and enclosed dorsal area; semioval postscutellum with a lamellate border; absence of pygidial plate, psammophores, and digging tarsal rakes; and considerably reduced forewing venation.

Key words: Crabronidae, digger wasps, new taxa, Eocene, Rovno Amber, Ukraine.

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INTRODUCTION

Digger wasps of the family Crabronidae are relatively rare in both fossil deposits and resins of various ages. At the later category, the most common genera are the typical xylophilous representatives of Pemphredonini (Pemphredoninae), in which the females of most species build their nests in preexisting borings left by other xylobiotic insects and use plant resinous material for making inner partitions between cells and external plugs of their linear nests. Fossil representatives of this tribe have been found in amber of various ages: Lower Cretaceous Burmese (Albian), Upper Cretaceous New Jersey (Turonian), Siberian (Santonian), and Canadian (Campanian), and Eocene Baltic and Rovno (Evans, 1969, 1973; Sorg, 1986; Budrys, 1993; Antropov, 2000a, 2000b).

Representatives of the Trypoxylini have been found less commonly in fossil resins (Eocene French and Baltic and Miocene Dominican ambers) (Cockerell, 1909; Antropov and Pulawski, 1989, 1996; Prentice and Poinar, 1993; Antropov, 1995; Nel, 2005; Bennett and Engel, 2008). Their females also build nests in similar sites, though construct internal partitions and external plugs of moisten clay.

Finally, representatives of the Crabronini are also known from fossil resins (Cockerell, 1909; Bennett and Engel, 2006). Two samples from the Eocene Baltic amber were attributed to the genus *Tracheliodes* A. Morawitz, 1866, whose extant species either occupy various preexisting cavities in wood and shrub twigs, or dig their nests in soil. In all known cases, females of this genus prey on worker ants of the genera *Liometopum* Mayr, 1861 and *Tapinoma* Förster, 1850 (For-

micidae, Dolichoderinae), which they often gather from tree trunks (Ferton, 1892, 1923; Adlerz, 1904; Bernard, 1934; Grandi, 1934, 1935, 1961; Parker and Bohart, 1966; Krombein, 1967; Zettel et al., 2004). Additionally, a member of the genus *Lindenius* Lepelletier de Saint Fargeau et Brullé, 1834 was described from Miocene Dominican amber (Bennett and Engel, 2006). This discovery is of special interest, because extant members of *Lindenius* do not nest in wood. Preying on ants, also known for *Lindenius* (Bohart and Menke, 1976), may explain its fossilization in resin by analogy with species of *Tracheliodes*.

I have recently examined a fossil crabronid from the Upper Eocene Rovno amber, Ukraine, whose description follows.

The specimen can be assigned to Crabronidae based on the following characters: gaster petiolate with sting, trochanters simple, middle tibiae with one apical spur, hind basitarsomere cylindrical, with cleaning bristles, pronotum short and straight posteriorly, with lateral lobe separated from tegula, and also short pubescence of simple setae. The following place it in the Crabroninae: scutum without expressed parapsidal lines, mesopleuron without scrobal furrow or omaulus but with narrow episternal suture, hardly expressed hypersternaulus, pterostigma not enlarged, and short gastral petiole with undivided proximal and distal parts of tergite I.

The following suite of characters is similar to that found in Miscophini, Crabronini, and Oxybelini: inner eye orbits parallel, antennal sockets touching short clypeus, ocelli unmodified, mandible bidentate apically, without ventral notch or lobe, postscutellum

semioval, with lamellate posterolateral border, propodeum with enclosed dorsal area and conspicuously developed lateral keel, forewing with acute apically marginal cell, one submarginal and one discoidal cells, hindwings with vein RS shorter than r-m, absence of digging bristles on mandibles, temples, and fore legs, and absence of pygidial plate. However, the whole complex of features does not allow assigning the specimen examined to any of them. Consequently, it is placed in a separate tribe, *Protomicroidini* trib. nov., in the *Crabroninae*.

The specimen was studied under a stereomicroscope Carl Zeiss Stemi SV 6 with drawing unit. Nikon Coolpix 885 digital camera was used to make photographs, which were subsequently improved when necessary using Adobe Photoshop 7.0 software. The line drawings were prepared using the stereomicroscope drawing unit and CorelDRAW 7 software. All measurements were made with the help of an ocular-micrometer.

SYSTEMATIC PALAEONTOLOGY

Superfamily Apoidea Latreille, 1802

Family Crabronidae Latreille, 1802

Subfamily Crabroninae Latreille, 1802

Tribe *Protomicroidini* Antropov, trib. nov.

Type genus. *Protomicroides* gen. nov.

Diagnosis. (1) Eyes naked; inner eye orbits almost parallel; ocelli unmodified. (2) Antennal sockets contiguous with frontoclypeal suture, antenna unmodified, with 12 joints. (3) Clypeus transverse; labrum short, not projecting beyond anterior margin of clypeus. (4) Mandible without ventral notch or angle. (5) Pronotal collar rounded convex, without medial furrow and transverse ridges (Pl. 9, fig. 1; Fig. 2a); lateral lobe separated from tegula. (6) Scutum with admedial and parapsidal lines not expressed; adlateral lines narrow short furrow-like; scutellum without posterolateral lobes; postscutellum semioval, laterally and posteriorly with translucent lamellate border (Pl. 10, fig. 1; Fig. 2a). (7) Mesopleuron with episternal suture narrow, without areolae; hypersternaulus short furrow-like; scrobal furrow, omaulus, sternaulus, and postspiracular and acetabular carinae absent. (8) Mid coxae separated, hind coxae contiguous; hind femur not truncate apically; mid tibia with one apical spur; tarsomeres unmodified; claws simple; arolia developed; plantulae absent; foretarsal rake absent. (9) Propodeum (Figs. 1a, 1b) not elongate, posteriorly not shorter than dorsally; lateral keels completely and strongly developed; dorsal area margined distinctly laterally. (10) Forewing (Pl. 10, figs. 1, 2; Figs. 2a, 2c) with acute apex of marginal cell (r) narrowly separated from wing margin; single submarginal cell (1m) and single discoidal cell (1mcu) developed; longitudinal radiomedial vein (RS+M) separating submarginal and discoidal cells narrowly

interrupted at proximal end (Pl. 10, fig. 2; Fig. 2c); subdiscoidal cell (2cu-a) closed. (11) Hindwing with two closed cells (Pl. 10, fig. 2; Fig. 2c); vein RS short and directed to wing apex; jugal lobe present. (12) Gaster sessile, without separated petiole (Pl. 9, figs. 1, 2; Figs. 1a, 1b); sternites convex; pygidial plate absent.

Generic composition. Type genus.

Comparison. A similar level of reduction of the forewing venation in *Crabroninae* is found among representatives of the tribes *Crabronini*, *Miscophini*, *Oxybelini*, and *Trypoxylini*.

First of all, the tribe *Protomicroidini* differs from *Trypoxylini*, *Miscophini*, and *Crabronini* in the lamellate border of the postscutellum. Furthermore, the tribe *Protomicroidini* differs from *Trypoxylini* in the nonmarginated inner eye orbits, absence of a supra-clypeal sclerite, antennal socket contiguous with frontoclypeal suture, marginal cell narrowly separated from the wing margin, row of hamuli on the anterior margin of the hindwing not interrupted, and particularly in the shortened vein RS, which is directed to the hindwing apex. It also differs from *Miscophini* in the margined dorsal area and developed lateral keels of the nonelongate propodeum, and from most *Crabronini* and part of *Oxybelini* in the parallel inner eye orbits, marginal cell weakly separated from the wing margin and not truncate apically, and the absence of a pygidial plate. Finally, it differs from *Oxybelini* in its submarginal and discoidal cells not fused and the absence of digging bristles on fore legs and head and the absence of pygidial plate.

The hindwing venation of *Protomicroidini*, with the antefurcal cu-a and conspicuously shortened vein RS directed to the wing apex, are characteristic of *Crabronini* and *Oxybelini*. A similar form of the hindwing medial cell (m) is rarely found in *Pemphredonini* and *Miscophini*, and only among their smallest species. The last is undoubtedly the independent result of the body size minimization accompanying considerable reduction of the wing venation.

Finally, *Protomicroidini* differs from representatives of all tribes with similar forewing venation in the proximally interrupted longitudinal radiomedial vein RS+M.

Genus *Protomicroides* Antropov, gen. nov.

Type species. *Protomicroides sororius* sp. nov.

Etymology. From the Greek *protos* (before, ahead) and a part of the generic name *Belomicroides*. Masculine gender.

Diagnosis. Head (Pl. 10, fig. 3; Fig. 2b) thickened; frontal carinae absent; malar space narrow; ocelli placed in obtuse-angled triangle; occipital carina thin, not forming complete circle, not reaching hypostomal carina; clypeus with roundly convex medial lobe; scape ecarinate ventrally; mandibles bidentate apically; palpi short, palpal formula unknown. Scutum uniformly convex, somewhat



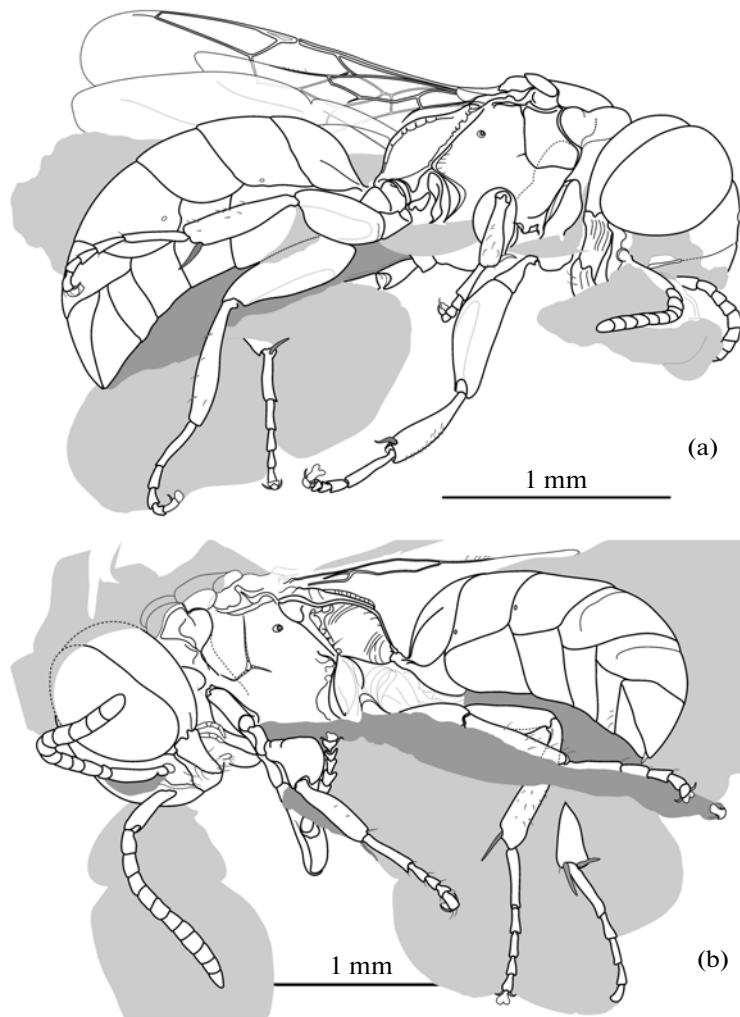


Fig. 1. *Protomicroides sororius* gen. et sp. nov., female, holotype IZ, no. K-3386: (a) total view from right side; (b) total view from left side.

higher than pronotal level; scutellum flat-convex, trapezoid, somewhat broader than long; mesopleuron uniformly convex; precoxal tubercle flat triangular and rounded apically (Pl. 9, figs. 1, 2; Figs. 1a, 1b). Mid and hind coxae each with oblique dorsal carina; tibiae with sparse, short, thick spines; arolia twice as long as claws. Forewing with acute apically marginal cell (r) and narrow, open distally additional cell; submarginal cell (1rm) larger than discoidal cell (1mcu); recurrent vein (1m-cu) ending somewhat distally of midlength of submarginal cell; cu-a antefurcal, longer than 2M+Cu; subdiscoidal cell closed. Hindwing with vein RS considerably shorter than r-m and shorter than cu-a, directed towards wing apex; cu-a antefurcal; anterior margin with uninterrupted row of five hamuli;

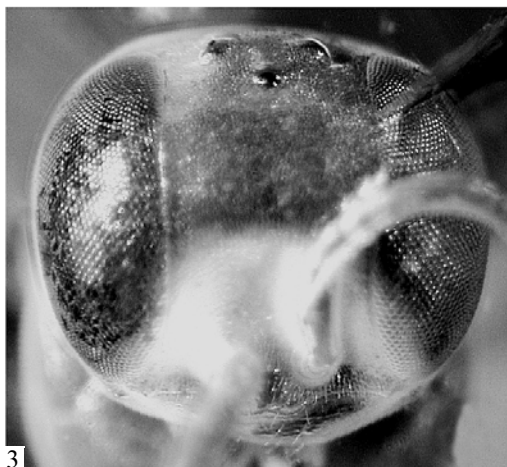
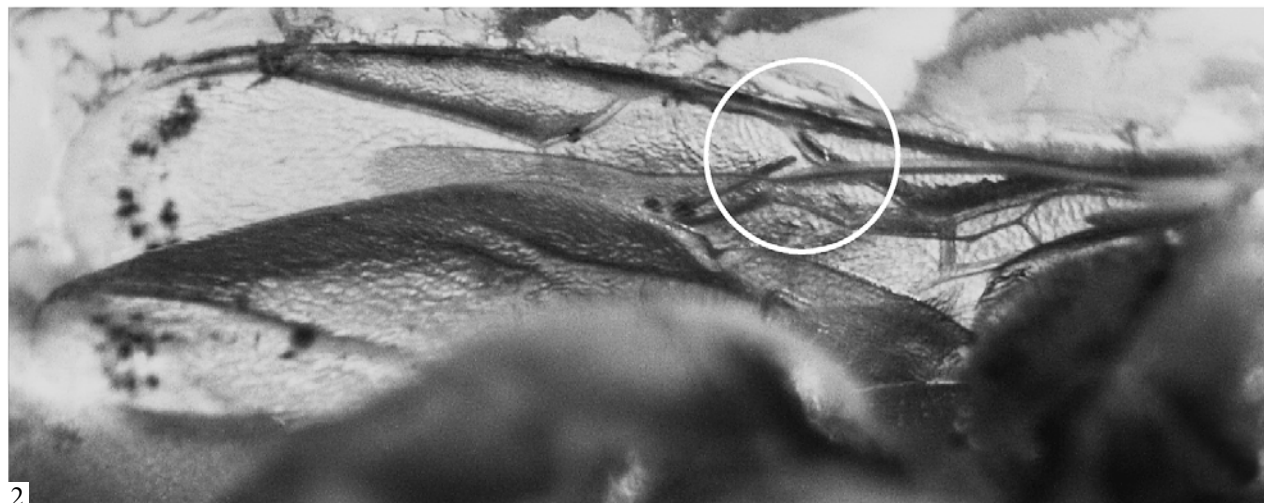
jugal lobe rounded, approximately half length of submedial cell (cua). Propodeal lateral keel translucent, high (not lower than half of foretarsal width), with posterior angle curved inwards; propodeal enclosure reaching posterior border of dorsum, distinctly emarginated laterally and separated from lateral parts by distinct furrow, and transgressing onto posterior surface. Only gastral tergum I with lateral carina; transverse basal depressions of terga absent.

Species composition. Type species.

Remarks. Several fossil representatives of the Trypoxylini and Crabronini are known. They have the same degree of reduction of the forewing venation.

Explanation of Plate 9

Figs. 1–2. *Protomicroides sororius* gen. et sp. nov., holotype IZ, no. K-3386, female: (1) total view from right side; (2) total view from left side.



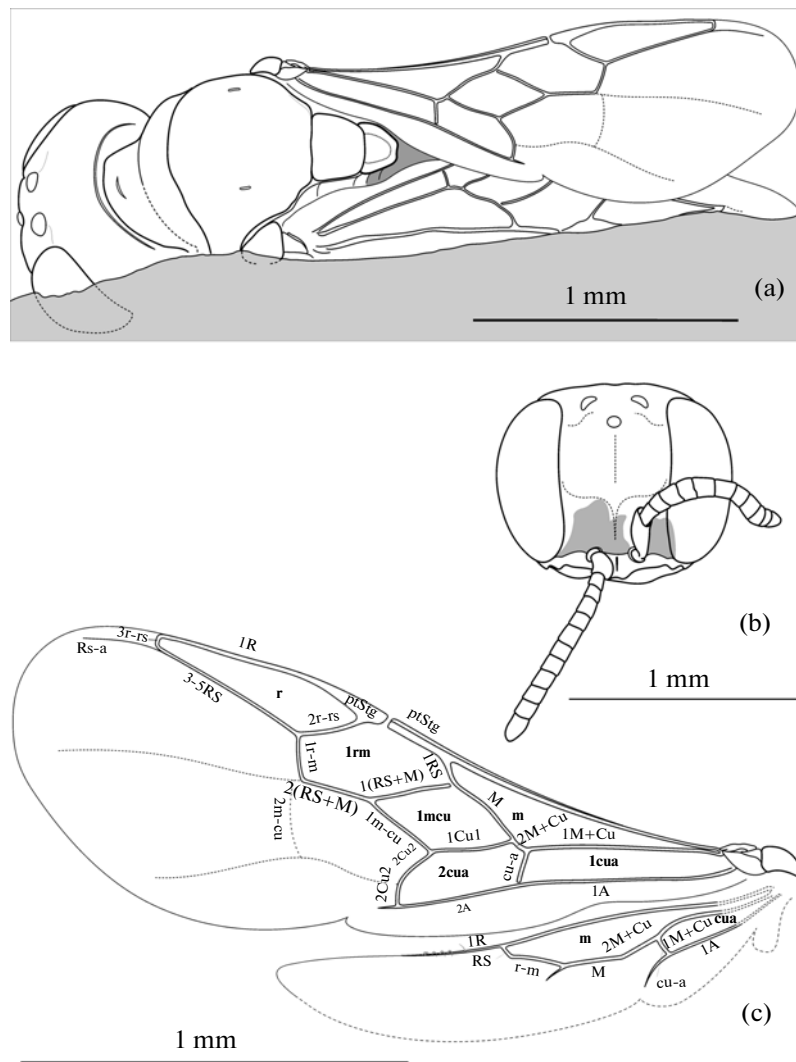


Fig. 2. *Protomicroides sororius* gen. et sp. nov., female, holotype IZ, no. K-3386: (a) total view from above; (b) head, frontal view; (c) wing venation.

In the first tribe, four species of *Trypoxylon* Latreille, 1796 have been described from the Miocene Dominican amber (*T. dominicanum* Prentice et Poinar, 1993, *T. eucharis* Prentice et Poinar, 1993, *T. pallidiventre* Prentice et Poinar, 1993, and *T. electrum* Antropov, 1995). They clearly differ from *Protomicroides* in such features as the deeply emarginated inner eye orbits, developed supraclypeal sclerite, the antennal sockets distinctly separated from the dorsal clypeal margin, the apically acute forewing marginal cell touching the wing margin, the hindwing vein RS directed towards the wing base and considerably longer than r-m, and the row of hamuli divided into

two groups, and the elongate gastral segments, particularly basal one.

Representatives of three genera have been described in Crabronini: *Lindenius* Lepeletier de Saint Fargeau et Brullé, 1835 (*L. paleomystax* Bennet et Engel, 2006 from Miocene Dominican amber), *Tracheliodes* A. Morawitz, 1866 [*T. succinalis* (Cockerell, 1909), *T. tornquisti* (Cockerell, 1909) from Eocene Baltic amber and *T. mortuellus* Cockerell, 1906 from Lower Oligocene shale beds of Florissant]. There are also records of compressions of *Ectemnius longoevus* (Cockerell, 1910) in Lower Oligocene shales of Florissant and of the extant species *E. continuus* (Fabricius, 1804) from the Lower Miocene of Germany (Meu-

Explanation of Plate 10

Figs. 1–3. *Protomicroides sororius* gen. et sp. nov., holotype IZ no. K-3386, female: (1) total view from above; (2) fragments of the right wings, ventral view; (3) head, frontal view.

nier, 1911), but these have not been sufficiently substantiated and require confirmation.

All genera of Crabronini differ from *Protomicroides* in the distinctly apically truncate forewing marginal cell, and in the presence of the more or less developed pygidial plate in females. Furthermore, *Tracheliodes* differs from *Protomicroides* in the elongate fore trochanters and thickened hind tibiae, the absence of the propodeal lateral keels, and the hindwing jugal lobe being equal to its submedial cell. *Lindenius* differs from *Protomicroides* in the inner eye orbits distinctly converging below in the lower part of the face, the apically edentate mandibles, and the hindwing jugal lobe longer than its submedial cell. *Ectemnius* differs from *Protomicroides* in the distinctly ventrally converging inner orbits, the antennal sockets positioned close to each other, the almost complete occipital carina, and the forewing recurrent vein joining the submarginal cell in its distal third.

Representatives of several extant genera of various tribes of Crabronidae have the same kind of forewing venation as in *Protomicroides*, consisting of the more or less apically acute forewing marginal cell, one submarginal cell and one discoidal cell.

Microstigmus Ducke, 1907 (Pemphredoninae, Pemphredonini, Spilomenina) and *Ammoplanops* Gussakovskij, 1931 (Pemphredoninae, Pemphredonini, Ammoplanina) differ from *Protomicroides* in the marginal cell not separated apically from the wing margin, the considerably enlarged pterostigma, comparable in size with the discoidal cell, the hindwing jugal lobe comparable in length with the submedial cell, the completely or mostly absent occipital carina, the nonmargined dorsal propodeal enclosure, and the absence of its lateral keels. Furthermore, *Microstigmus* differs from *Protomicroides* in its very short forewing prestigma (prStg), the hindwing vein RS longer than r-m and directed at an angle to the anterior wing margin, the transverse ridge of the pronotal collar, and the hind tibiae without spines. *Ammoplanops* differs from *Protomicroides* in the shorter forewing marginal cell (not longer than the pterostigma), the hind tibiae with many spines, and the presence of a pygidial plate in females. Furthermore, the recurrent vein (1m-cu) in *Ammoplanops* joins the submarginal cell near its free distal angle; as a result, veins 1m-cu, 1r-m, and 3-5RS are positioned within the same almost straight line.

Nitela Latreille, 1809 (Crabroninae, Miscophini) is similar to *Protomicroides*, but differs in the discoidal cell being larger than the submarginal cell, the recurrent vein joining the submarginal cell near its free distal angle (just as in *Ammoplanops*, veins 1m-cu, 1r-m, and 3-5RS in *Nitela* are within an almost straight line), the absence of the distal segment of the forewing anal vein (2A) and of all veins in the hindwing, which has an elongate jugal lobe, and also in the more or less developed frontal keels, short and unmodified postscutellum without a lamellate border, and the elongate

propodeum without a margined dorsal enclosure and well-developed lateral keels.

Pisoxylon Menke, 1968 and *Trypoxylon* (Crabroninae, Trypoxylini) differ from *Protomicroides* in the marginal cell touching apically the wing margin, and the hindwing vein RS considerably longer than r-m and directed towards the wing base, the strongly emarginated inner orbits, the well-developed supraclypeal sclerite, the antennal sockets separated from the dorsal clypeal margin, and the absence of a lamellate border of the postscutellum. In addition, *Trypoxylon* differs from *Protomicroides* in the more or less elongate gastral segments (particularly the first segment), while *Pisoxylon* differs in the presence of frontal keels and the absence of a margined dorsal enclosure and lateral keels of the propodeum.

Finally, *Protomicroides* shows obvious similarity to genera of the tribe Oxybelini that have no propodeal mucro and lateral carinae of abdominal tergites, such as *Minimicroides* Antropov, 2000, *Gessus* Antropov, 2001, and *Belomicroides* Kohl, 1899 (particularly of the *pictus* species-group), sharing with them structural details of the postscutellum and propodeum and wing venation.

Minimicroides differs from *Protomicroides* in the ventrally converging inner orbits, apically edentate mandibles, complete hypersternaulus, narrow posterolateral lamellae of the scutellum, narrow and apically interrupted lamellate border of the postscutellum, conspicuously broadened oval dorsal metapleural flange, merged forewing submarginal and discoidal cells, reduced hindwing venation and jugal lobe, and the deep transverse basal depressions of gastral terga II-III.

Gessus differs from *Protomicroides* in the elongate medial lobe of the clypeus; apically acute mandible, with developed ventral lobe, psammophores on the mandibles, temples, fore trochanters and femora and with foretarsal rakes; lamellate posterolateral lobes of the scutellum; deeply apically interrupted, lamellate border of the postscutellum; fused forewing submarginal and discoidal cells with acute free distal angle; the jugal lobe almost equal in length to the submedial cell; and the distinct pygidial plate.

Members of the *pictus* species-group of the genus *Belomicroides* differ from *Protomicroides* in the elongate medial lobe of the clypeus; the apically acute mandible, with distinct ventral lobe, psammophores on the mandibles, temples, fore trochanters, and femora and with foretarsal rakes; the apically interrupted lamellate border of the postscutellum; the fused forewing submarginal and discoidal cells, with acute free distal angle, the developed pygidial plate, and the laterally compressed apical gastral sternum.

Protomicroides sororius Antropov, sp. nov.

Plate 9, figs. 1 and 2; Plate 10, figs. 1–3

E t y m o l o g y. After *sororius*, the Latin masculine adjective, meaning “belonging to the sister”.

H o l o t y p e. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (IZ), no. K-3386, completely preserved female inside a sample of $24.5 \times 6 \times 6$ mm; Ukraine, Rovno Region, town of Klesov, "Pugach" mine; Late Eocene.

Description (Figs. 1, 2). The upper frons is convex, the lower frons is concave; the orbital foveae are absent; the flagellomeres are slightly longer than wide, the apical joint is almost twice as long as wide; the mandible is bidentate apically, the posterior tooth is almost twice as long as anterior one; the translucent lamellate border of the postscutellum is not emarginated apically; the hypersternaulus is short, furrow-like, extends from a broad shallow pit on the episternal suture; the precoxal tubercle is lobe-like, flat, triangular, rounded apically; the fore femur is uniformly rounded, without a ridge along the external margin; the middle femur is broadly anteriorly concave; the hind femur is uniformly rounded, broadened medially, narrowed basally and apically, without a dorsoapical carina.

The frons is shiny, uniformly densely punctate (the interspaces are equal or slightly broader than the puncture diameter); the vertex is densely micropunctate (practically without interspaces), half-matt; the gena is shiny, inpunctate but vertically microstriate; the medial clypeal lobe is glabrous anteriorly and along the medial line, unsculptured, polished. The pronotal collar is densely punctate (like the vertex), half-matt; the scutum is uniformly finely, densely punctate (shiny interspaces are slightly broader than the puncture diameter); the scutellum punctures are similar though slightly sparser; the postscutellum is inpunctate; the mesopleuron is uniformly, finely punctate, although somewhat coarser than the scutum (shiny interspaces are equal to, or slightly broader than, the puncture diameter). The propodeal dorsum is densely coriaceous, matt lateral to the dorsal enclosure; the propodeal sides are smooth, shiny, with scarcely visible smoothed oblique ridges in the posterior angle; the posterior propodeal surface is invisible. The gastral terga and sterna have micropunctures at the bases of appressed microsetae; the interspaces are smooth, shiny, broader than the puncture diameter; the apical tergum is smooth, without pygidial structures.

The body pubescence is inconspicuous, not concealing the surface sculpture. The frons has scarcely visible, very short and sparse semierect setae; the vertex has similar setae; the lateral clypeal lobes have short appressed setae directed downwards and almost hiding the sculpture; the scutum and mesopleurae have scarcely visible appressed microsetae; sternal preapical bristles are absent; the gastral apical segment is not setose.

M e a s u r e m e n t s in points of ocular-micrometer at a magnification of 50. Head width, 48; head height, 40; head length, 30; clypeal width, 25; clypeal length, 5; breadth of clypeal apical margin, 6; mandible

length, 20; length of scape, 16; thickness of scape, 4; length (along medial line) of: scutum, 23; scutellum, 10; postscutellum, 5; breadth of postscutellum, 11. Distance between inner eye orbits: at medial ocellus level, 20; in the middle of frons, 22; at antennal socket level, 21. Distance between inner orbit and lateral ocellus, 4; diameter of lateral ocellus, 4; distance between lateral ocelli, 5. Diameter of antennal socket, 3; distance between antennal socket and inner orbit, 6; distance between antennal sockets, 5; distance between antennal socket and nearest outer angle of clypeal medial lobe, 4.

M e a s u r e m e n t s in mm. Body length, nearly 3; forewing: length, 1.82; prStg, 0.17; ptStg, 0.18; 1R, 0.44; 3r-rs, 0.03; 2r-rs, 0.16; 3-5RS, 0.43; 1(RS+M), 0.21; 2(RS+M), 0.19; 1r-m, 0.12; 1M+Cu, 0.5; 2M+Cu, 0.045; M, 0.21; 1RS, 0.075; 1Cu1, 0.22; 1Cu2, 0.12; 2Cu2, 0.055; 1m-cu, 0.2; cu-a, 0.08; 1A, 0.56; 2A, 0.32. Hindwing: length, 1.25; 1R, 0.25; 2M+Cu, 0.1; M, 0.15; r-m, 0.13; RS, 0.04; cu-a, 0.06.

R e m a r k s. Though the biology of *Protomicroides* is unknown, an analysis of some female structures permits the hypotheses regarding its nesting places and nest material to be generated. In particular, the absence of any digging structures (clypeal projections, modified mandibles, digging foretarsal rake, psammophores on mandibles, temples, fore trochanters and femora, flat sculptured and densely setose pygidial plate) indicates that females were not able to dig nests in soil. Their moderately broadened temples and apically bidentate mandibles with no broadened or flattened lobes and the apical gastral tergum without specialized pygidial plate point to a wasp that nested in soft dead wood or twigs with a soft core. Females of *Protomicroides* were probably capable of gnawing out their nest cavities themselves and used excavated material to build inner partitions and external plugs, but they did not use their own silk excretions, plant resins, or moistened clay.

M a t e r i a l. Holotype.

DISCUSSION

In my opinion, the features defining the tribe Protomicroidini and allied tribes of the Crabronidae should be divided into two groups. First of all, the extent to which the pygidial plate or digging bristles on the fore legs and head are developed as well as certain mandible shapes are directly connected with the female nesting activity and, hence, liable to parallel development, reductions, and reversions. This is confirmed by their multiple and independent appearances and disappearances not only in the Crabronidae, but also in other families of aculeate Hymenoptera (for example, Tiphidae, Scoliidae, Pompilidae, and Apidae). For these reasons, attempts at phylogenetic interpretations based on such features are questionable. On the other hand, features not linked directly with biological peculiarities, obviously reflect deeper

relationships between taxa, and their analysis may be more productive for phylogenetic reconstructions. I suppose that structural details of the propodeum, thorax (particularly of the postscutellum), and, to a lesser degree, head, should be mentioned among them. Finally, the details of the wing venation in Crabronidae may be most significant in phylogenetic reconstructions because of the irreversibility of the veins' and cells' reductions.

Based on the above data, I conclude that Mischophini, Crabronini, and Oxybelini are very similar to Protomicroidini. However, the first differs considerably in the absence of a lateral keel and margined dorsal enclosure of the elongate propodeum and of a lamellate border of the postscutellum. Members of Crabronini, some of which are similar to Protomicroidini in the structure of the propodeum and, particularly, in the hindwing venation, differ in the apically truncate forewing marginal cell, the absence of the lamellate border of the postscutellum (more or less developed short vertical ridges around the strongly transverse postscutellum in some species of *Encopognathus* Kohl, 1897 have different structure and undoubtedly independent origin), and in the inner orbits distinctly convergent below (excluding only *Tsunekiola* Antropov, 1986 and several species of *Tracheliodes* A. Morawitz, 1866).

The tribe Oxybelini is most similar to Protomicroidini in the structure of the propodeum and postscutellum and the hindwing venation. The main difference is only in the complete absence of the forewing longitudinal radiomedial vein (RS+M) in Oxybelini. However, it is quite possible that the proximal break of RS+M in Protomicroidini is the first step in its complete reduction, which is observed in extant Oxybelini.

At the same time, it seems impossible to attribute Protomicroidini and Oxybelini to the same phylogenetic lineage because of the obvious differences in the way their submarginal cells are reduced. In particular, the weakly expressed trace of forewing recurrent vein II (2m-cu) of *Protomicroides* ends somewhat distally from the obtuse free angle of the submarginal cell, whereas it ends before the usually acute free angle in the majority of Oxybelini. I suppose that this character demonstrates the probable way of forming a single submarginal cell in Protomicroidini through reduction of submarginal cells III and II, like in some Mischophini and all Crabronini, and not through merging submarginal cells I and II, like in Oxybelini.

Moreover, the preservation of submarginal cell II in one of extant genera of Oxybelini (*Wojus* Antropov, 1999) also indicates that Protomicroidini cannot be ancestral to Oxybelini. Both these tribes obviously constitute a pair of sister groups, originating from a common ancestral form, which was similar to some extant Mischophini with petiolate forewing submarginal cell II and shortened hindwing medial cell. This ancestral group had xylobiotic habits, indicating that the exclusively terrabiotic habits of extant Oxybelini

are of secondary origin, as was ascertained for some other groups of Crabronidae (Budrys, 2001).

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