A new genus and species of apoid wasps from Saxonian amber (Hymenoptera: Apoidea: Crabronidae)

Michael Ohl & Daniel J. Bennett

Abstract: Palarpactophilus saxonicus gen.n. and sp.n. is described from Middle Eocene (Lutetian) Saxonian amber from Bitterfeld, Germany. The new genus and species are diagnosed and important characters are illustrated with microphotographs. Within the Crabronidae the fossil is placed in the tribe Pemphredonini, and a possible affinity to the Spilomenina is discussed.

Key words: Palarpactophilus saxonicus, Pemphredoninae, Spilomenina, fossil, new genus, new species, taxonomy, Australasian region, Baltic amber, Saxonian amber.

Introduction

The apoid wasp subfamily Pemphredoninae belongs in the large and diverse clade Crabronidae (PRENTICE 1998; MELO 1999; OHL & BLEIDORN 2006). Pemphredonines are usually small or tiny, and nesting in any kind of pre-existing cavity (hollow stems and twigs in particular) is abundant in the subfamily. In such nests they typically provide their progeny with auchenorrhynchan or sternorrhynchan Hemiptera, but other small insects such as thrips and collembolans are also attacked by a few members (BOHART & MENKE 1976).

The pemphredonine subtribe Spilomenina comprises about 160 species in four genera, namely Arpactophilus, Microstigmus, Spilomena, and Xysma. This subtribe is remarkable among Apoidea for two aspects: at least some species of Arpactophilus and Microstigmus exhibit a high level of social behavior (e.g., MATTHEWS 1991; MATTHEWS & NAUMANN 1989), which rarely occurs in the otherwise usually solitary apoid wasps. The other aspect is the remarkable diversity of recent species, best exemplified by Arpactophilus, which has been progressively revealed by a number of revisionary studies. MENKE (1989) pointed out that Arpactophilus has apparently “exploded”, evolutionarily speaking in the Australasian region and that there exist at least 40 species from Australia alone. He has also seen undescribed species from New Guinea, New Britain, the Solomon Islands, New Caledonia and Fiji. BOHART (1999) described 17 new species from New Caledonia. In the Australian National Insect Collection, Canberra, specimens of Arpactophilus have been sorted into more than 60 morpho-species (NAUMANN unpubl., cited in MATTHEWS & NAUMANN 2002), and nine of them have been described by MATTHEWS & NAUMANN (2002). In total, 43 species of Arpactophilus have been formally described as yet (PUŁAWSKI 2008). In 2005, one of us (MO) received 79 individuals of Arpactophilus from New Caledonia sent by the Queensland Museum for identification. These have been sorted to 24 provisional species, 20 of which cannot be reliably identified with BOHART’S (1999) key to New Caledonian Arpactophilus and probably represent undescribed species (JAENICKE & OHL, unpubl. data). The high morphological and taxonomical diversity on New Caledonia implies a high level of island endemism, and based on the published and unpublished records, the Recent species diversity of Arpactophilus certainly exceeds the currently known number of species considerably.

Among Saxonian amber inclusions from the Museum für Naturkunde in Berlin we recently discovered an apoid wasp that readily keyed out to Arpactophilus with the key to genera in BOHART & MENKE (1976). Although the specimen clearly shows affinities to
Arpactophilus and the Spilomenina, it shows a number of significant differences to Recent species. Thus, the purpose of this paper is to describe Palarpactophilus saxonicus gen.n. and sp.n. and to discuss its affinities to the Spilomenina.

The age of Saxonian amber has been subject to controversial discussions. Weitschat (1997) convincingly demonstrated that Saxonian amber is merely redeposited Baltic amber and, thus, of Middle Eocene age (see also Engel 2001). This led Bennett & Engel (2006) to list the pemphredonine wasp Passaloceus munax Sorg (originally described from Saxonian amber) as originating from Baltic amber. Although this is correct in terms of the mere age of the resin, the relevant information (that Saxonian amber is not true Baltic amber but redeposited Baltic amber) would have been obscured had they not further discussed this nomenclatural problem. Although Baltic and Saxonian ambers are identical in terms of their geological origin, we prefer to use Saxonian amber for the amber from Bitterfeld, Saxony to emphasize its specific geological history and geographic origin, in contrast to true Baltic amber.

Systematic Paleontology

Palarpactophilus Ohl & Bennett, gen.n.

Type species: Palarpactophilus saxonicus Ohl & Bennett, sp.n.

Diagnosis: Palarpactophilus is here classified with reference to Bohart & Menke (1976), Menke (1989), and Prentice (1998) but follows the latter two with regards to subtribal categories. The fossil is recognized as belonging to the Pemphredoninae by the combination of its small size, cuboidal head, normal ocelli, sub-parallel inner orbits, simple mandible exteroventrally, and single midtibial spur. Of the two pemphredonine tribes it is recognized as belonging to the Pemphredonini by the two submarginal cells (three in Psenini, two or fewer in Pemphredonini); toruli positioned against the frontoclypeal sulcus; mandibles bidentate apically; and low, broad pronotal collar. Palarpactophilus is excluded from all subtribes of the Pemphredonini as represented by modern taxa as follows: from Pemphredonina by its two discoidal cells (as opposed to three), hind wing medial cell not extended much beyond origin of radial sector, and without facial fovea extended onto frontal area (however, the relative size of the marginal cell to the pterostigma is arguably more like this subtribe in the fossil than the others); from Ammoplanina by the orthognathous head (rather than prognathous), longer marginal cell, presence of an acetabular carina, and less-reduced fore and hind wing venations; from Stignmina by the lack of both a long maxillary palpus and long petiole; from Spilomenina by its six-segmented maxillary palpus (rather than five) and strong mesopleural sulcus; and from Spilomenina other than Arpactophilus by the presence of an occipital carina. The fossil and Arpactophilus also share a very short petiole, short first sement of maxillary palpus, forewing with elongate, closed marginal cell (Fig. 1d), and hind wing media diverging before cu-a (Fig. 1d). In addition to the number of palpal segments, Palarpactophilus differs from Arpactophilus in that the occipital carina in Palarpactophilus is in close contact to the hypostomal carina (Fig. 2a) (as opposed to its position considerably behind the oral fossa in even the putatively most plesiomorphic species of Arpactophilus) and in that the forewing basal veinlet of discoidal cell 1 (a section of M) is markedly bent, forming an angle between 90° and 120° (veinlet straight or indistinctly bent, angle 180° or slightly less in Arpactophilus) (Fig. 1d).

Etymology: The name is a combination of the prefix pal-, which refers to the Greek palaiós, meaning ancient, and Arpactophilus, a close relative of the new genus. The name is masculine.

Remarks: Despite the differences of Palarpactophilus to the pemphredonine subtribes noted above, the body of evidence suggests an affinity to Spilomenina, possibly as a stem-group to the subtribe or to Arpactophilus only. The morphology of Arpactophilus is remarkably diverse and character-rich, and this includes a significant diversity of integument sculpture, clypeal and labral dentition, and general body shape. An interesting character in Arpactophilus, which is not diagnostic for the genus, is the frontal line between frontoclypeal sulcus and midcellus, which is usually raised to an elevated carina (interantennal carina sensu Bohart & Menke 1976). Menke (1989) pointed out that in some species that lack coarse sculpture, the frontal carina might be fine, but it is discrete in any case. In many described and undescribed species of Arpactophilus, the frontal carina is markedly raised into significant lamellae or other elaborate facial features. The newly discovered fossil also has the frontal carina raised into a significant thorn-like structure between the antennal sockets. This and the other characters listed above, as well as the general body shape, suggest an association with Arpactophilus. Hence, it is tempting to interpret the fossil as a rather plesiomorphic, that is, basal species in Arpactophilus. However, if the reduced palpal formula 5-4 is really a synapomorphic trait of Arpactophilus, Spilomena, Xysma, and Microstigmus as proposed by Menke (1989) and Prentice (1998), it was likely present in the stem species of Arpactophilus as well. If this interpretation is true, placement of the fossil in Arpactophilus is contradictory. Additionally, Spilomena, Xysma, and Microstigmus lack an occipital carina and a raised frontal carina and have an
indistinguishable point of divergence of the hind wing media from Cu. Thus, the fossil is clearly not more closely related to any of these genera. Even though the exact phylogenetic position of the new fossil cannot be absolutely assured yet, placement in a new genus as a consequence of its unique combination of characters is logically consistent with the several possibilities, i.e. as the stem group to Spilomenina, *Arpactophilus* only, or further removed from Spilomenina altogether.

**Palarpactophilus saxonicus** **OHL & BENNETT**, sp.n. (Figs 1-2)

**Diagnosis**: As for the genus (vide supra). However, if paralleled with the enormous diversity in *Arpactophilus*, it can be expected that other characters of the fossil are also of specific value. Candidates are: head and thoracic dorsum microsculptured, without ridges or punctures (Fig. 2b); most mesopleural sulci coarsely pitted (Fig. 2c); with a peg-like process between antennal sockets in a deeply impressed scapal basin (Fig. 1c); propodeal dorsum coarsely areolate (Fig. 2d); and tergite VI narrowly truncate apically.

**Holotype**: ♀. Saxonian amber [redeposited Baltic amber; Lutetian stage, middle Eocene], labeled "Serie 10", Bitterfeld, Germany (Museum für Naturkunde, Berlin, paleontological collection; MB 1.5438). Preserved in a clean, polished, irregularly oval piece of amber (size about 17 x 15 x 4 mm).

**Description**: Based on the holotype, ♀.

Body length (without appendages) 3.9 mm; forewing length 2.7 mm; head width 1.1 mm.

Head: Orthognathous; face rather rounded in frontal view, not elongate; integument microsculptured throughout; eyes slightly diverging below; ocular-ocellar distance 1.2x midocellar diameter (Fig. 1a); scapal basin depressed, dorsal margin probably carinate; with peg-like process between antennal sockets, almost perpendicular to scapal basin, process about as long as twice maximum scapal width, parallel-sided in basal two-thirds, sharply pointed apically (Fig. 1c); scape dorsally extending beyond scapal basin; flagellomeres about as wide as long, terminal flagellomeres twice as long as wide, tapering apically; mandible with two subequal apical teeth;
labrum not protruding, apex shallowly emarginate; palpal formula 6-4, basal segment of maxillary palpus very short, segments 2-3 slightly broadened, segments 4-6 elongate; gena behind eye narrow, not more than one-third eye width; malar space absent; occipital carina a complete circle, subcontiguous with hypostomal carina (Fig. 2a).

Mesosoma: Thoracic dorsum microsculptured except for coarsely pitted grooves along anterior scutellar and posterolateral scutal margins (Fig. 2b); pronotum short, with a low, transverse carina dorsally; propleuron with pair of shiny impressions anteroventrally; ventral angle of pronotum with transverse rugulae; mesopleuron with postspiracular groove, mesepisternal sulcus, acetabular sulcus, scrobal sulcus, and hypersternaulus (Fig. 1c); all mesopleural sulci coarsely pitted, postspiracular groove and scrobal sulcus less so; midventral line flanked by shallowly pitted grooves; precoxal groove coarsely pitted; metasternum (= propodeal dorsum) coarsely areolate (Fig. 2d), carina in posterolateral angle raised to form low lamella; hindtibia with a few bristles; forewing (Fig. 1d) with two submarginal cells, the second being much smaller; marginal cell closed, very long and broad basally; pterostigma large, but significantly smaller than marginal cell; section of M at discoidal cell I (= basal veinlet of discoidal cell I) markedly bent at an angle of 90°-120°; hind wing media diverging before cuba (Fig. 1d).

Metasoma: petiole present but indistinct; tergites microsculptured; tergite VI narrowly truncate at apex, pygidial plate absent.

Discussion
Spilomenina is essentially worldwide in distribution; Spilomena is widespread, Xysma is known from the New World and South Africa, Microstigmus is Neotropical, and Arpactophilus is Australasian, as has been more fully noted above (Bohart & Menke 1976; Pulawski 2008). The locality of Palarpactophilus combined with its similarities to Arpactophilus make an interpretation in which these taxa together comprise a clade within the Spilomenina that underwent extinction in the northern hemisphere a tempting argument. This may
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Literature


very well be the case. However, based on the plesiomorphic number of labial palp segments, it seems more likely (as discussed above) that Palarpactophilus is the sister group to all other Spilomenina or further removed from the subtribe, in which case such a conclusion is not necessarily warranted.

The small body size and nesting habits of Pemphredoninae make them good candidates to be preserved in fossil resin. Indeed, most apoid wasps known from amber deposits belong in the Pemphredoninae (ANTROPOV 2000a, b; BENNETT & ENGEL 2006), this despite being outnumbered in the modern fauna by the Bembicinae, Philanthinae, and, by about four and a half times, the Crabroninae (PULAWSKI 2008). Five species from Baltic amber have been described in a modern genus, Passalocerus, by SORG (1986) and BUDRYS (1993), and 15 more species from various amber deposits have been placed in 11 extinct genera (BUDRYS 1993; ANTROPOV 2000a, b; EVANS 1969, 1973). The antiquity of the Pemphredonini is solidly indicated by the Cretaceous fossils Psolime-na electra ANTRPOV (2000a), Prolemistus apiformis ANTRPOV (2000b), and Lisponema singularis EVANS (1969). Whether or not Spilomenina or the other pemphredonine subtribes are as ancient as is disputed by the plesiomorphic number of labial palp segments, it seems more likely that the fossil within the Spilomenina or in any pemphredonine subtribe. Palarpactophilus represents yet another pemphredonine genus with uncertain phylogenetic affinities. A phylogenetic analysis of the Pemphredoninae which takes into account the numerous fossil taxa is needed and might well clarify these ambiguities, providing insight into the age, diversification, and subsequent extinction of pemphredonine taxa.

Zusammenfassung


Address of authors:

Michael OHL
Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin
Museum für Naturkunde, Sektion Entomologie
Invalidenstr. 43
10115 Berlin, Germany
E-Mail: michael.ohl@museum.hu-berlin.de

Daniel J. BENNETT
Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology
University of Kansas
1501 Crestline Drive, Suite 140
Lawrence Kansas 66049-2811, USA
E-Mail: danben@ku.edu
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