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A Primitive Aphidiine Wasp in Albian Amber from Spain and a Northern Hemisphere Origin for the Subfamily (Hymenoptera: Braconidae: Aphidiinae)

JAIME ORTEGA-BLANCO,1 DANIEL J. BENNETT,2 XAVIER DELCLOS,1 AND MICHAEL S. ENGEL2

ABSTRACT: A description of a new genus and species of braconid, Archephedrus stolamissus, from Early Cretaceous (Albian) amber from Moraza-Peñacerrada I (Spain) is here provided. This is the first fossil Aphidiinae described in Cretaceous amber. The fossil has some typical characters of the subfamily but possesses a unique assemblage of characters among aphidiines, such as a fairly robust abdomen, with a more pronounced articulation between the first and second, instead of the second and third, metasomal segments, as well as several wing venational traits. The distribution of this and other aphidiine fossils, as well as their putative phylogenetic placement as basal among Aphidiinae, is discussed, supporting a Northern rather than Southern Hemisphere origin for the lineage.

KEY WORDS: Ichneumonoidea, Braconidae, amber, Albian, Spain, paleontology, taxonomy

Members of the highly beneficial braconid subfamily Aphidiinae are well-known for exerting significant top-down control of aphid populations through endoparasitoidism. This is often successfully exploited for the biological control of these pests in agroecosystems and greenhouses, and their presence is frequently indicated by ghostly golden or tan mummified aphid husks which may litter infested plants. Because of their beneficial nature the group has been the subject of considerable attention, which has resulted in a number of biological (Stary, 1970), biogeographical (Belshaw et al., 2000), and phylogenetic investigations using morphology of adults and larvae (Mackauer, 1961; Chou, 1984; Gärdenfors, 1986; O’Donnell, 1989; Finlayson, 1990), embryology (Tremblay and Calvert, 1971), and multiple molecular markers (Belshaw and Quicke, 1997; Belshaw et al., 2000; Kambhampati et al., 2000; Sanchis et al., 2000; Smith et al., 1999; Shi and Chen, 2005).

Modern representatives are easily recognized by their small, aphid-limited size, short ovipositor, flexible suture between metasomal tergites two and three, weakly sclerotized metasoma, 18-segmented or less antenna, smooth scutellar sulcus, hind wing lacking crossvein cu-a, and presence laterally of the occipital carina (Wharton et al., 1997). These characters, along with their consistent host behavior, have long suggested that these wasps comprise a distinct lineage which has at times been given familial-rank status. Several investigations of ichneumonoid phylogeny using molecular data have confirmed the monophyly of Aphidiinae and shown it to fall clearly within the Braconidae (Quicke and van Achterberg, 1990; van Achterberg and Quicke, 1992; Wharton et al., 1992; Belshaw et al., 1998; Dowton et al., 1998; Shi et al., 2005). Most studies have also supported the monophyly of aphidiine tribes.

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[but see Sanchis et al. (2000) who questioned the existence of Aphidiini and Trioxini], but the relative positions of the tribes to each other have been sensitive to data type and taxon sampling. Most authors follow Mackauer’s (1961) classification and divide the subfamily into the four tribes Aclitini, Praini, Ephedrini, and Aphidiini. Others ignore Aclitini due to its unavailability for molecular analysis and raise Trioxina to tribal status (Belshaw and Quicke, 1997; Belshaw et al., 2000) or recognize three tribes only (Sanchis et al., 2000; Smith et al., 1999; Shi and Chen, 2005). Sanchis et al. (2000) also argued that additional components of the Aphidiini may require elevation to tribal status. Belshaw and Quicke (1997), in a combined analysis of three genes (nuclear elongation factor-1α, mitochondrial cytochrome b, and nuclear 28S D2 rRNA), recovered Ephedrini + (Praini + (Aphidiini + Trioxini)). The same arrangement was found when the 28S D2 rRNA gene was analyzed alone (Belshaw and Quicke, 1997; Belshaw et al., 2000). Ephedrini was also found to be basal using 18S rRNA gene sequence data alone (Sanchis et al., 2000) and in combination with 16S rRNA and ATPase 6 gene sequence data (Shi and Chen, 2005). However, none of these studies included the putatively basal Aclitini.

Kambhampati et al. (2000), based on mitochondrial 16S rRNA gene sequence data, found Aclitini + (Praini + (Ephedrini + Aphidiini)). After removing a number of taxa including Aclitini from the analysis due to missing data they found the same pattern for the remaining tribes in a combined analysis of DNA sequence data from 16S rRNA, NADH1 dehydrogenase, and 28S rRNA genes. Mitochondrial NADH1 dehydrogenase gene sequence data analyzed alone and without the Aclitini also recovered the same pattern among the remaining tribes (Smith et al., 2000).

Although fossils, and the unique character combinations they embody, are known to be critical in phylogenetic analyses (Grimaldi and Engel, 2005), they are infrequently included in cladistic studies of insect relationships. Furthermore, presumably since such fossils cannot be sequenced for molecular markers, the impact of aphidiine fossils on aphid wasp phylogeny has never been investigated. This is not owing to a complete absence of material. Indeed, 25 fossils of aphid wasps have hitherto been described from a diversity of Tertiary deposits, mostly as compressions from the Oligocene of Europe, but also including several from middle Eocene Baltic amber (Table 1). The latter fossils are certainly preserved with sufficient fidelity to permit coding in analyses with modern counterparts.

Herein we report the discovery of the oldest aphidiine wasp, a single male preserved in Early Cretaceous (Albian) amber from Moraza-Peñacerrada I (Spain) (Figs. 1–2). The species is allied to the aphidiinae on the basis of its small size, habitus, occipital carina, short antennae, and Ephedrus-like wing venation. However, it retains notable plesiomorphies relative to all other Aphidiinae including, most notably, a relatively robust abdomen. Morphological terminology for the description follows Wharton et al. (1997) except for r-rrr crossvein (named R in Wharton et al.’s treatment) and pterostigma (referred to as stigma in Wharton et al.).

Geological Setting

The amber piece was recovered from the Peñacerrada I (Moraza) locality in Spain (Delelòs et al., 2007). The outcrop is located along the southern margin of the Basque-Cantabrian Basin, in the Sierra de Cantabria. The area with amber localities is located close to the meridional margin of the Peñacerrada diapire, situated in the
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Deposit</th>
<th>Age</th>
<th>References</th>
<th>Notes</th>
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</thead>
<tbody>
<tr>
<td>Aphidius maximus</td>
<td>Théobald, Aix-en-Province, France (C)</td>
<td>Oligocene</td>
<td>Théobald, 1937; Starý 1970, 1973</td>
<td>lost</td>
</tr>
<tr>
<td>Archephedrus stolamissus n. gen, n. sp.</td>
<td>Moarza-Peña, moraza, Spain (A)</td>
<td>Cretaceous (Albian)</td>
<td>herein</td>
<td></td>
</tr>
<tr>
<td>Archipraon gausai (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Praon</td>
</tr>
<tr>
<td>Ephedrus mirabilis Timon-David</td>
<td>Marseille Basin, France (C)</td>
<td>Oligocene</td>
<td>Timon-David, 1944; Starý 1970, 1973</td>
<td>lost</td>
</tr>
<tr>
<td>E. primordialis Brues</td>
<td>Baltic (A)</td>
<td>Eocene (Lutetian)</td>
<td>Brues, 1933; Starý 1970, 1973</td>
<td>lost</td>
</tr>
<tr>
<td>Holocnomus braconiformis Quilis</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost</td>
</tr>
<tr>
<td>Oligoaphidius sannoniensis Quilis</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Diaeretus</td>
</tr>
<tr>
<td>Palaeoxys fuscus (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Diaeretus</td>
</tr>
<tr>
<td>P. primigenius (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Trioxys</td>
</tr>
<tr>
<td>Praeaphidius macropthalmus (Brues)</td>
<td>Baltic (A)</td>
<td>Eocene (Lutetian)</td>
<td>Brues, 1933; Starý 1970, 1973</td>
<td>lost; described in Aphidius</td>
</tr>
<tr>
<td>P. microphthalmus (Brues)</td>
<td>Baltic (A)</td>
<td>Eocene (Lutetian)</td>
<td>Brues, 1933; Starý 1970, 1973</td>
<td>lost; described in Aphidius</td>
</tr>
<tr>
<td>Propronocota quieveuxi (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>Proprona cellulare Brues</td>
<td>Baltic (A)</td>
<td>Eocene (Lutetian)</td>
<td>Brues, 1933; Starý 1970, 1973</td>
<td>lost</td>
</tr>
<tr>
<td>Protacanthoides fossilis (Mackauer)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Mackauer, 1959; Starý 1970, 1973</td>
<td>described as Trioxys obscuriformis</td>
</tr>
<tr>
<td>Protephedrus terciarius Quilis</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost</td>
</tr>
<tr>
<td>Protodiaeretiella berdlandi (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Diaeretus</td>
</tr>
<tr>
<td>Pseudaphidius cenozoius (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>P. fosiliferus (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Aphidius</td>
</tr>
<tr>
<td>P. lysophileoides (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Aphidius</td>
</tr>
<tr>
<td>P. nigrofacies (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Aphidius</td>
</tr>
<tr>
<td>P. oligoarundinis (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>P. oligocenus (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>P. preredicaginis (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>P. pseudogranarius (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>P. saliniferus (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>described in Aphidius</td>
</tr>
<tr>
<td>P. torneli (Quilis)</td>
<td>Haut-Rhin, France (C)</td>
<td>Oligocene</td>
<td>Quilis, 1940; Starý 1970, 1973</td>
<td>probably lost; described in Aphidius</td>
</tr>
</tbody>
</table>
Amber occurs in organic-rich clays from the Escucha Formation (Lower Albian), an essentially siliciclastic unit, with thin carbonate and coal levels deposited in a transitional marine to continental paleoenvironment. In the Iberian Peninsula, the Escucha Formation is subdivided into three lithostratigraphic units related with the vertical evolution of a deltaic system (progradation – retrogradation of this system), that correspond to a regional episode of marine regression – transgression. The coal and organic-matter rich clay levels of this formation contain the major proportion of amber pieces, and are related with the fill of the interdistributary bay deposits. These levels correspond to the maximum regressive marine episode and the maximum deltaic progradation, representing the second lithostatigraphic unit. The depositional environment where resins have been deposited is related with a proximal facies of a delta plain with little marine influence (Arostegui and Sanguesa, 2003) under a hot and humid climate around 30°N latitude (Larrasoña et al., 2003).

Fig. 1. Camera lucida drawing of holotype male of Archephedrus stolamissus, new genus and species (MCNA 8785), lateral habitus.
Systematic Paleontology

Family Braconidae Nees von Esenbeck
Subfamily Aphidiinae Haliday

Archehedrus, new genus

TYPE SPECIES: Archehedrus stolamissus Ortega-Blanco, Bennett, Delclòs, and Engel, new species.

DIAGNOSIS: Antenna 16-segmented; notauli present; forewing (Fig. 3) with pterostigma triangular; marginal cell closed; forewing venation rather complete but some sectors very faint as proximal half of Rs + M; m-cu very faint but present;
hind wings with one tubular vein on anterior margin; basal metasoma not tube-shaped, with segments not so weakly sclerotized, suture between first and second metasomal segments less rigid in contrast to that of second and third metasomal segments.

**ETYMOLOGY:** The new genus-group name is a combination of the Greek archaios, meaning “ancient”, and the generic name Ephedrus, type genus of one of the putatively primitive tribes of Aphidiinae. The name is masculine.

**Archephedrus stolamissus**, new species

(Figs. 1–3)

**DIAGNOSIS:** As for the genus (*vide supra*).

**DESCRIPTION:** Male. Body length ca. 1.06 mm; forewing length 1.08 mm. Integument largely cleared, light reddish brown. Head rounded, compound eyes occupying more than half lateral surface; gena relatively wide, nearly as broad as compound eye in lateral view (Figs. 1–2); ocelli not visible in lateral view. Mandible endodont, apparently bidentate; maxillary palpus long, 5-segmented. Occipital carina present (at least laterally). Antenna 16-segmented; scape about four times longer than wide; pedicel as long as wide; flagellomeres cylindrical, long and narrow, progressively shorter, ultimate segment tapered distally.

Mesosoma high; notauli present; long propleuron forming a distinct “neck”; epinemial carina seemingly weakly present. Forewing (Fig. 3) with rather complete venation (see Table 2 for terminology); C + Sc + R fused anterobasally; pterostigma triangular, with r-rs arising from it medially; R1 present to just short of forewing apex; RS + M present in at least its apical half, separating first submarginal and first discal cells, very weak and possibly lacking in part basally; 2RS present, separating first and second submarginal cells; M + Cu tubular throughout at least apical two-third; 3RS present to wing margin, thus marginal cell closed; crossvein r-m very weakly indicated; 1M, 2M, and 3M mostly well defined, though the latter not tubular apically and seemingly ending short of wing margin; 2Cu nebulous or spectral; cu-a crossveins apparently not complete (1cu-a) or absent (2cu-a); short anal crossvein opposite 1M present. Hind wing likely with only one anterior vein, seemingly differentiated into C + Sc + R basally, Sc + R medially, and R1 apically;
both fore and hind wings with short setae along their apical margins becoming slightly longer posteroapically. Long and cylindrical coxae and femora except profemur, widest distally; metatibia long and thin, with fine spicules; tibial spur formula 1-2-2; each leg with short second to fourth tarsomeres, all combined, about as long as basitarsus; fifth tarsomeres elongate, almost as long as corresponding basitarsi.

Metasoma attached to mesosoma by sessile tergum and sternum (i.e., not petiolate); metasoma 7-segmented, flattened, apparently with a more mobile junction between first and second segments; terga well sclerotized; first three terga without carapace. Long, thin, and sharp aedeagal valves, flattened dorso-ventrally and distinctly broadened in basal halves; parameres wide, with some distinct apical setae.

**HOLOTYPE**: Male, MCNA 8785, labeled as Early Cretaceous (Albian); Peñacerrada [Peñacerrada I = Moraza, Burgos], Álava, Spain. Deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

**ETYMOLOGY**: The specific epithet is a combination of the Latin *stolo*, meaning “branch”, and *amissus*, meaning “lost”, and is a reference to this being an extinct branch of aphidiines.

**Key to Fossil Genera of Aphidiinae**
(modified from Starý, 1973)

1. Forewing with three submarginal cells ........................................... 2
   – Forewing venation reduced ...................................................... 4
2. Forewing marginal cell complete ................................................. 3
   – Forewing marginal cell incomplete ........................... *Protephedrus* Quilis
3. Antenna 11-segmented; RS + M complete and tubular . . . . *Ephedrus* Haliday
   – Antenna 16-segmented; RS + M proximally faint . . . . *Archehedrus*, n. gen.
4. 2RS absent; first submarginal and first discal cells separated .......... 5
   – Wing venation not as described above ................................. 6
5. RS + M fully developed; antenna 30-segmented ............ *Propraon* Brues
RS + M indicated; antennae 18-segmented .......... Archipraon Starý
6. Marginal cell distinctly complete ........................................ 7
– Marginal cell incomplete, sometimes with 3RS elongate .......... 8
7. Propodeum more or less areolate; 3M not reaching wing margin ................................ Praeaphidius Starý
– Propodeum smooth; 3M reaching wing margin ........... Holocnemus Quilis
8. First submarginal and first discal cells confluent, demarcated by r-m apically
and 1CU, m-cu, and 2M posteriorly ........................................ 9
– Submarginal and discal cells absent, only r-rs and 3RS present apically .... 11
9. Ovipositor sheaths curved downwards. ................................. 10
– Ovipositor sheaths straight or slightly curved upward. ... Pseudaphidius Starý
10. Ovipositor sheaths plough-share-shaped ........ Promonoctonia Starý
– Ovipositor sheaths gradually narrowed to apex ... Protacanthoides Mackauer
11. Propodeum smooth; abdomen lanceolate, with first tergum triangular or
much longer than wide ........................................................... 12
– Propodeum more or less carinate; metasoma piriform, stout and short, with
first tergum subquadrate; overall appearance robust. .... Oligoaphidius Quilis
12. First tergum three times longer than wide; ovipositor sheaths straight; apical
terumn not bearing accessory prongs ........................ Protodiaeretiella Starý
– First tergum triangular; ovipositor sheaths presumed to be curved
downward; apical sternum bearing accessory prongs .... Palaeoxys Mackauer

Discussion

The fossil is easy recognized as a member of the Braconidae by the fused costa,
subcosta, and radial veins, and the lack of crossvein 2m-cu in the forewing. The
habitus, small size, short antennae, occipital carina, and Ephedrini-like forewing
venation associate it with the Aphidiinae. However, its fairly robust abdomen
suggests placement outside all other known aphidiines and indicate it to be a stem
group.

Perhaps the most interesting aspect of the discovery of Archephedrus is its possible
implications for understanding the origins of aphid parasitoids. Modern aphidiines
are overwhelmingly Holarctic in distribution. Despite this, a Gondwanan origin for
the Aphidiinae has been postulated by Schlinger (1974), which was more recently
supported by parsimony and likelihood methods of ancestral distribution estimation
(Belschaw et al., 2000). This support rests on the plesiomorphic Southern Hemisphere
aphidine genera Parephedrus, Pseudephedrus, and Choreopraon and the Southern
Hemisphere distribution of Aspilodemon and Mesostoa, which in their analysis
formed the sister group of the Aphidiinae. It must be noted that although all of the
fossil aphidine wasps derive from Northern Hemisphere deposits and none were
included in the aforementioned analysis, nor were the possible implications of these
putatively primitive aphidiines and their distributions discussed in regard to the
impact they might wield on the historical biogeography of the subfamily. Given that
Archephedrus is a stem group to Aphidiinae, the fossil makes less clear the
reconstruction of a Southern Hemisphere origin for the basal node of the subfamily.
Instead, this suggests that the earliest aphidiines were already present in the
Northern Hemisphere by the latter part of the Early Cretaceous. This pattern is also
in accordance with the biogeography of aphidiiine hosts. Aphididae (Hemiptera) are
common and diverse principally in the Holarctic region and aphids are abundant in many Cretaceous and Tertiary ambers. It is quite common that fossils critically revise our understanding of biogeographic patterns based solely on modern taxa. Numerous putatively “Gondwanan” clades among insects have been proven to not be of Gondwanan origin and the distribution has instead been formed through a combination of global climate change (frequently during the Eocene-Oligocene transition) and significant levels of extinction (e.g., Grimaldi and Engel, 2005, 2006; Engel and Grimaldi, 2007). *Archeaphedrus* suggests that there may have been significant extinction among basal aphidines and that the initial origin and radiation of these remarkable parasitoids was in the Northern Hemisphere.

Acknowledgments

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