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

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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 (Starý, 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-1 α , 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-rs 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 (Delclòs *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 1. Compression (C) and amber (A) fossil Aphidiinae.

Taxon	Deposit	Age	References	Notes
<i>Aphidius maximus</i> Théobald	Aix-en-Provence, France (C)	Oligocene	Théobald, 1937; Starý 1970, 1973	lost
<i>Archeophedrus stotamissus</i> n. gen, n. sp.	Moraza-Peñacerrada, Spain (A)	Cretaceous (Albian)	herein	
<i>Archipraon gausai</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Praon</i>
<i>Ephedrus mirabilis</i> Timon-David	Marseille Basin, France (C)	Oligocene	Timon-David, 1944; Starý 1970, 1973	lost
<i>E. prinordialis</i> Brues	Baltic (A)	Eocene (Lutetian)	Brues, 1933; Starý 1970, 1973	lost
<i>Holocnomus braconiformis</i> Quilis	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost
<i>Oligoaphidius sannoniensis</i> Quilis	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	
<i>Palaeoxys fuscus</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Diaeretus</i>
<i>P. primgentis</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Trioxys</i>
<i>Praeaphidius macrophalms</i> (Brues)	Baltic (A)	Eocene (Lutetian)	Brues, 1933; Starý 1970; 1973	lost; described in <i>Aphidius</i>
<i>P. microphalms</i> (Brues)	Baltic (A)	Eocene (Lutetian)	Brues, 1933; Starý 1970; 1973	lost; described in <i>Aphidius</i>
<i>Promonocentia quevrenuxi</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970; 1973	described in <i>Aphidius</i>
<i>Propraon cellulare</i> Brues	Baltic (A)	Eocene (Lutetian)	Brues, 1933; Starý 1970; 1973	lost
<i>Protacanthoides fossilis</i> (Mackauer)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Mackauer, 1959; Starý 1970; 1973	described as <i>Trioxys obscuriformis</i>
<i>Protophedrus terciarius</i> Quilis	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	Quilis probably lost
<i>Protodiaeretiella berlandti</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Diaeretus</i>
<i>Pseudaphidius cenozoicus</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Aphidius</i>
<i>P. fosiliferus</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Aphidius</i>
<i>P. lysiphleboides</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Aphidius</i>
<i>P. nigrofacies</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Aphidius</i>
<i>P. oligoarundinis</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Aphidius</i>
<i>P. oligocenus</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Aphidius</i>
<i>P. premedicagnis</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Aphidius</i>
<i>P. pseudogranarius</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Aphidius</i>
<i>P. saliniferus</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	described in <i>Aphidius</i>
<i>P. torneli</i> (Quilis)	Haut-Rhin, France (C)	Oligocene	Quilis, 1940; Starý 1970, 1973	probably lost; described in <i>Aphidius</i>

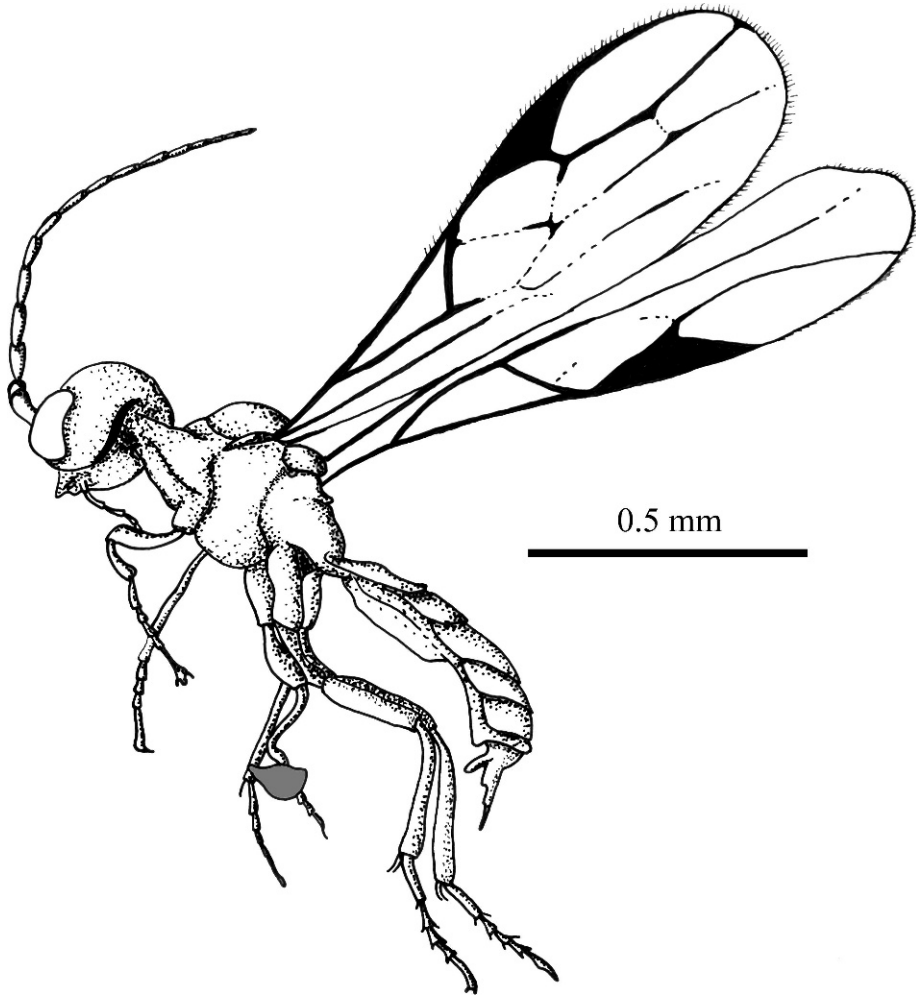


Fig. 1. Camera lucida drawing of holotype male of *Archephedrus stolamissus*, new genus and species (MCNA 8785), lateral habitus.

septentrional margin of the thrust sheet of Sierra de Cantabria (Martínez-Torres *et al.*, 2003). 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 Sangüesa, 2003) under a hot and humid climate around 30°N latitude (Larrasoña *et al.*, 2003).

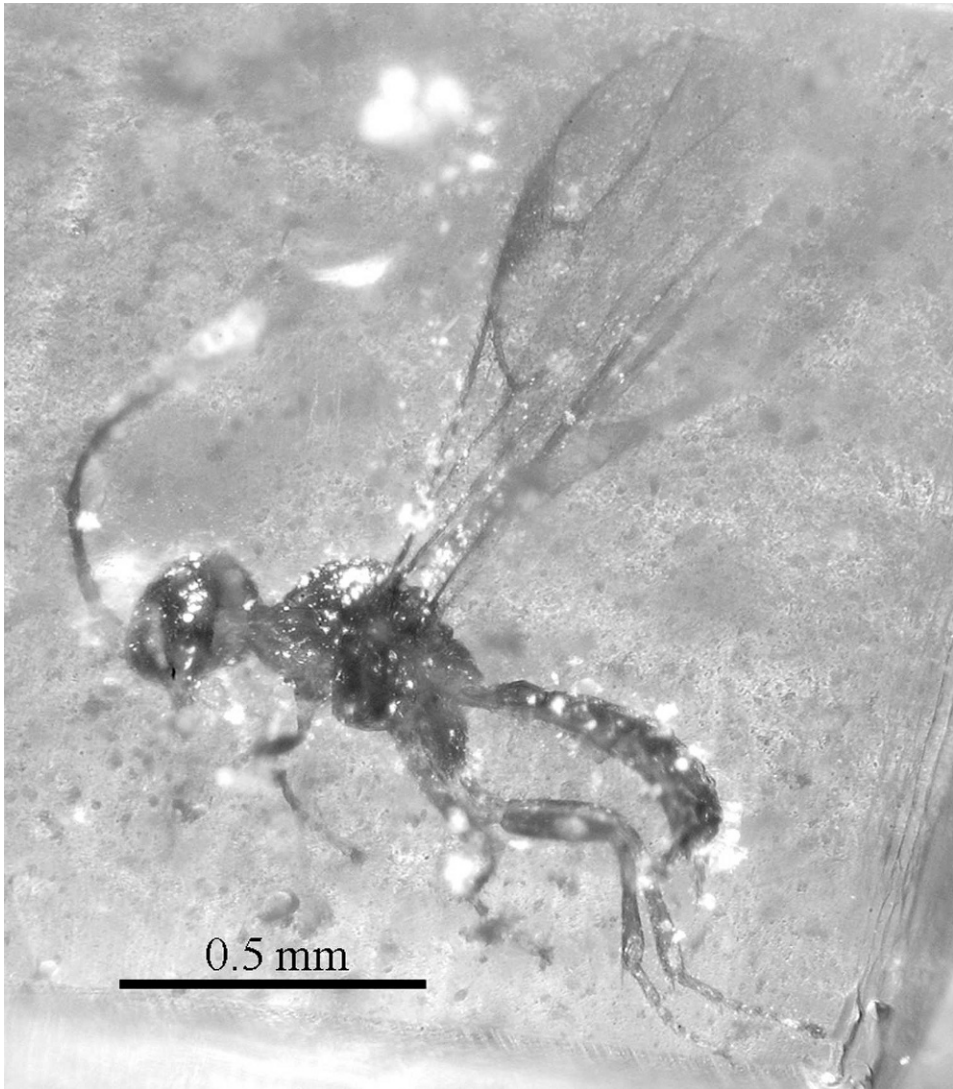


Fig. 2. Photomicrograph of holotype male of *Arcephedrus stolamissus*, new genus and species (MCNA 8785).

Systematic Paleontology

Family BRACONIDAE Nees von Esenbeck

Subfamily Aphidiinae Haliday

Arcephedrus, new genus

TYPE SPECIES: *Arcephedrus 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;

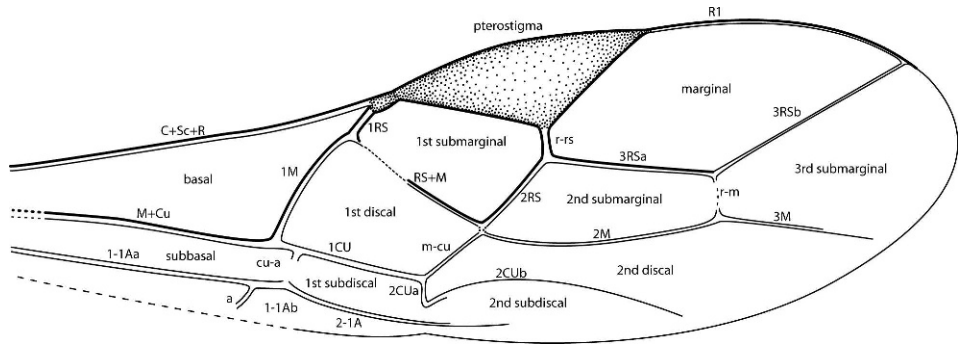


Fig. 3. Forewing venation for *Archephedrus stolamissus*, new genus and species (MCNA 8785), showing standard vein nomenclature (table 2 translates between Stary's vein and cell nomenclature and more modern usage).

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"; epicnemial 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;

Table 2. Aphidiine forewing terminology systems.

Veins <i>sensu</i> Wharton <i>et al.</i> , 1997	Veins <i>sensu</i> Starý, 1970	Cells <i>sensu</i> Wharton <i>et al.</i> , 1997	Cells <i>sensu</i> Starý, 1970
C + Sc + R	C + Sc	marginal	pterostigmal
R1	metacarpus	1 st submarginal	radial cell I
1M	basal	2 nd submarginal	radial cell II
Rs + M	median	3 rd submarginal	radial cell III
2RS	interradial vein I	basal	basal
r	radial	1 st discal	median
3RSa	radial	2 nd discal	not indicated
3RSb	radial	subbasal	cubital cell I
M + Cu	cubital	1 st subdiscal	cubital cell II
1CU	cubital	second subdiscal	not indicated
m-cu	intermedian		
2M	median		
3M	median		
cu-a	nervulus		
2Cub	cubital		
1A	anal		
a	not indicated		

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 *Archephedrus*, 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 *Holocnomus* 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
sternum 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 easily 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 (Belshaw *et al.*, 2000). This support rests on the plesiomorphic Southern Hemisphere aphidiine 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 aphidiine 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 aphidiine 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). *Archeophedrus* suggests that there may have been significant extinction among basal aphidiines and that the initial origin and radiation of these remarkable parasitoids was in the Northern Hemisphere.

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