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A new genus of Hybotidae (Diptera, Empidoidea) from Lower Cretaceous amber of Alava (Spain)

[Eine neue Gattung der Hybotidae (Diptera, Empidoidea) im Bernstein aus der unteren Kreide von Alava (Spanien)]

by
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Abstract	The genus *Alavesia* gen. nov. (Diptera, Empidoidea, Hybotidae) with its type species *A. subiasi* spec. nov. is described from the Lower Cretaceous amber of Alava (Spain). Its phylogenetic relationships are studied.
Key words	Lower Cretaceous, Alava Amber, Insects, Diptera, Empidoidea, Hybotidae, new genus, new species
Zusammenfassung	Aus dem Bernstein der unteren Kreide von Alava (Spanien) wird die Gattung *Alavesia* gen. nov. (Diptera, Empidoidea, Hybotidae) mit der Typusart *A. subiasi* spec. nov. beschrieben. Ihre phylogenetische Position wird diskutiert.
Stichwörter	Unterkreide, Alava Bernstein, Insekten, Diptera, Empidoidea, Hybotidae, neue Gattung, neue Art

Introduction

Amber from Alava (northern Spain), of middle Albian – upper Aptian in age (around 113 Ma), was recently discovered. To date approximately 1500 organic inclusions have been recorded (ALONSO et al. in press), three of which are the remains of flies of the family Hybotidae belonging to a new genus and species.

The oldest known empidoid is *Protempis antennata* USSATCHEV, 1968 from the Upper Jurassic of Karatau (Kazakhstan) redescribed by CHVÁLA (1983). HENNIG (1970, 1971) described *Trichinites cretaceous* and *Microphorites extinctus* from Lower Cretaceous Lebanese amber (Neocomian); the rest of the Mesozoic Empidoidea are known from several Upper Cretaceous sites: *Empis orapaensis* and *Pseudoacarterus orapaensis*, from the Cenomanian of the Orapa diamond mine, Botswana (WATERS 1989a, 1989b); SCHLUTER (1978) described *Ecomniocydromia difficilis* from Cenomanian French amber. Several Empidoidea are known from Coniacian/Santonian Siberian amber: *Archiplatyplapus cretaceus* and *Cretoplatypalpus archaeus* described by KOVALEV (1974, 1978) and *Cretomicrophorus rohdendorfi*, *Archichrysotus hennigi*, *Archichrysotus minor*, and *Retinitus nervosus* described by NEGROBOV (1978). Our knowledge about Mesozoic empidoids has recently considerably grown: GRIMALDI & CUMMING (1999) described *Atelestites senectus*, *Phaetempis lebanensis*, *Microphorites similis*, *Microphorites oculeus*, *Avenaphora hispida*, and *Sympycnites primaevus* from Lebanese amber, *Turonempis styx*, *Emplita casei*, *Nemedromia turonia*, *Neoturonius asymmetrus*, *Neoturonius cretatus*, *Neoturonius vetus*, *Cretomicrophorus novemundus*, and *Archichrysotus incompletus* from Turonian amber from New Jersey (USA) and *Nemedromia campania*, *Nemedromia telescopica*, *Prolatomyia elongata*, *Cretodromia glaesa*, *Cretoplatypalpus americanas*, *Mesoplatypalpus carpenteri*, *Apalocnemis canadambris*, and *Archichrysotus manitobus* from Campanian amber from Canada. Undescribed Cretaceous Empidoidea are recorded in Alaskan amber (EVENHUIS 1994). Cenozoic Empidoidea are frequent, mainly in amber, and are listed by EVENHUIS (op.cit.).

Methods and material

The pieces of amber were embedded in and consolidated with resin (Epotek 301), which facilitates cutting and trimming, and then polished. The fossils were examined using an Olympus BX50 microscope. The specimens were drawn with the aid of a camera lucida. Morphological terminology is based on MCALPINE (1981) and the arrangement of species into higher taxa follows that of CHVALA (1983). However other authors have another view on Empidoidea phylogenetic system, where Oedydromiinae are considered as being paraphyletic with uncertain relationships with respect to Tachydrominae and Hybotinae (CUMMING et al. 1995, SINCLAIR 1995).

Systematic account

Superfamily Empidoidea (sensu CHVALA 1983)
Family Hybotidae CHVALA 1983
Subfamily Oedydromiinae (sensu CHVALA 1983)
Genus *Alavesia* gen. nov.

Type and only known species: *Alavesia subiasi* spec. nov.
Derivation of generic name: from the province of Alava

Diagoosis: Cell dm present, very small and closed (with distinct dm-cu vein) emitting two veins (M_2 and CuA_1). Cell cup shorter than cell bm, with CnA_2 forming distinct angle with basal part of A_1. Cells br, bm and cup short, M_2 and CuA_1 long (greater than half wings length). Vein C is not circumambient but ends at wing tip (at M_2). Vein Sc does not reach wing margin but ends freely in wing membrane after running alongside R_1 for most of its length. Anal lobe well developed with alula not developed. Vein R_{4+5} is not forked. R_1 and R_{2+3} are short as they curve anteriorly approximately midway along wing length. Branch of vein M distinct, not evanescent. Vein Rs is longer than the length of the distance from humeral vein to its origin. Femora are a little thickened, mainly hind femora. Forelegs near the others and distant from the head. The mid and hind coxae are approximately two thirds of the length of the fore coxae. Antennae with basal flagellomere extremely large, blunt at apex, leaf shaped. Style short and 3-articulated, being basal 2 articles very small. Hypopygium small, much smaller than pregenital segments.

Alavesia subiasi spec. nov.

(Figs 1-5)

Holotype (sex of this specimen questionable but most possibly a male, see description). Museum of Natural Sciences of Alava, Spain (MCNA-8837) from Lower Cretaceous (middle Albian-upper Aptian) amber of Sierra de Cantabria, near Peñacerrada, 30 km south of Vitoria (Alava, Spain)
Paratypes: Museum of Natural Sciences of Alava, Spain. (MCNA-8841 [possibly a male, see description]) and (MCNA-8838 [possibly a female, see description])

Description

Holotype is almost complete (Fig.1a), only some terminal tarsomeres and one antennal apex have been lost. The wing is 1.1 mm long, the antenna is 0.5 mm, the length of the head with the thorax is 5.5 mm. The body (without the antennae) is approximately 1.5 mm long. Due to the shape of the piece of amber the holotype is best viewed in the dorsal position although head is also clearly visible in lateral view (Fig.1b). Wings (1.1 mm length) appear crossed over the body, so in dorsal view it is not possible to see the abdomen (with genitalia) and the halteres.

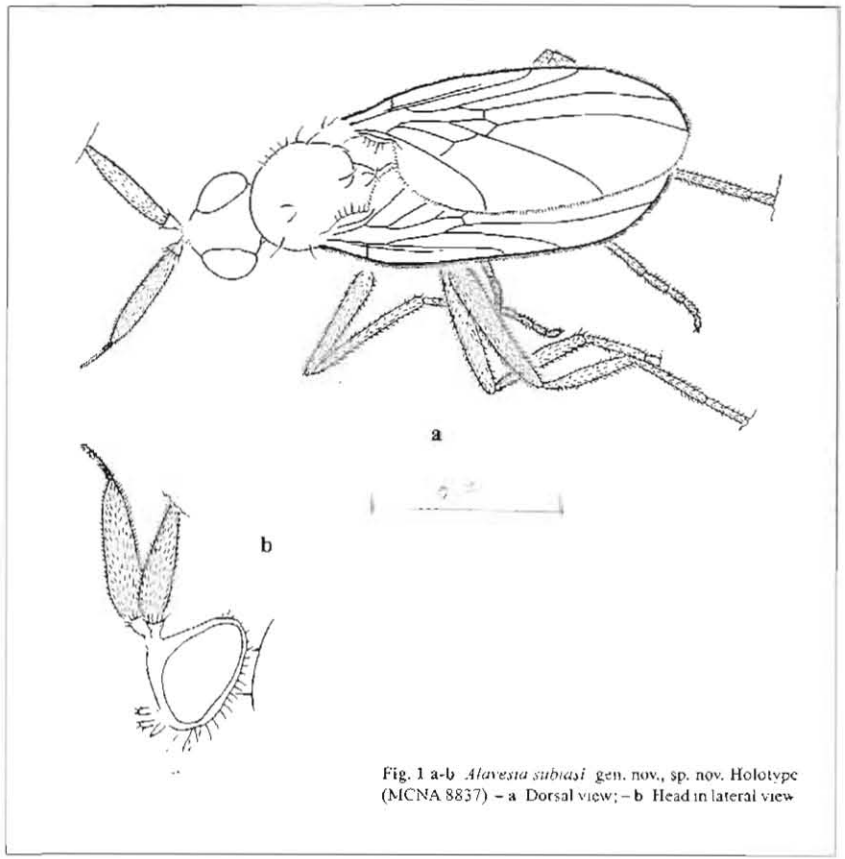

Fig. 1 a-b *Alavesia subiasi* gen. nov., sp. nov. Holotype (MCNA 8837) – a Dorsal view; – b Head in lateral view

Bristles are clearly seen on some areas of the body but the piece of amber is too large and too dark for viewing the complete chaetotaxy. The same problem appears on the head where ocelli and the shape of the eyes are not perfectly visible. Some mouthparts are clearly visible. The membrane of the wing is entirely covered with microtrichia. The genitalia are difficult to interpret in ventral view but it seems to be a male.

Paratype (MCNA-8841) (Fig. 2) is best observed in lateral view, the specimen appears to be nearly complete but some tibiae and tarsomeres are lost. The total length of the body is slightly shorter than the holotype (around 1.3 mm). The shape of the antennae is clearly distinguishable. The genitalia are difficult to interpret in lateral view (possibly a male)

Paratype (MCNA-8838) (Fig. 3) is also almost complete although head and thorax are not well preserved. Its size is almost identical to that of the holotype. The specimen is best observed in anterolateral view (one haltere is clearly visible in this position). All the legs are completely preserved. The specimen seems to be a female.

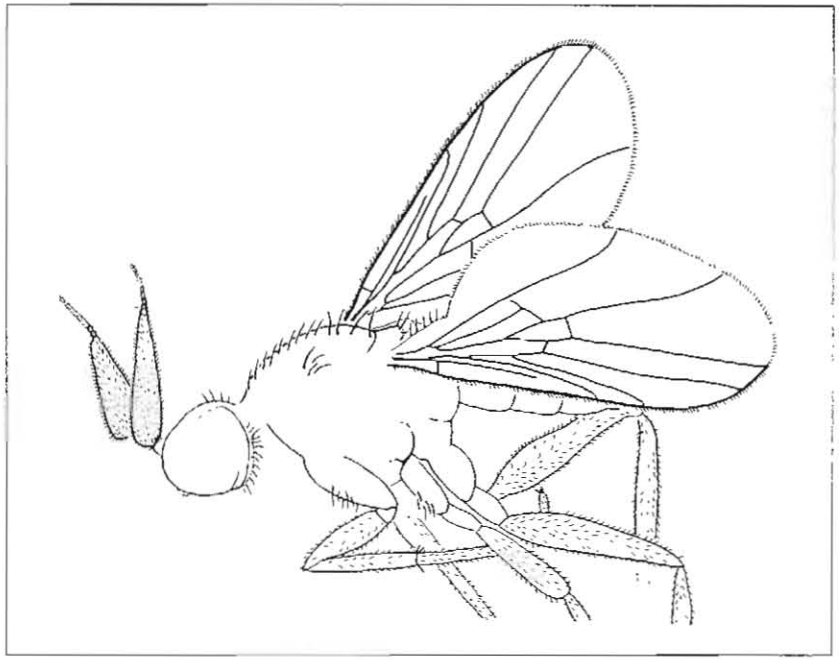

Fig. 2: *Alavesia subiasi* gen. nov., spec. nov. Paratype (MCNA 8841)

Derivatio nominis: Derivation of the specific epithet: after Dr. LUIS S. SUBIAS, acarologist from the Complutense University, Madrid, Spain.

Discussion

Alavesia subiasi spec. nov. is placed within the phylogenetic system of CHVÁLA (1983), where the Empidoidea comprise four distinct families: Empididae, Hybotidae, Atelestidae, and Microphoridae. The family Hybotidae, a clearly defined monophyletic group, consists of the subfamilies Ocydromiinae, Hybotinae and Tachydromiinae. Hybotids include about 1300 recent species. The presumed phylogeny of the family is given in figure 4. It is thought that the Ocydromiinae include the most primitive groups of the family, whilst the Hybotinae and Tachydromiinae, which form a natural subgroup within the family, have more apomorphic characters. (A set of apomorphic characters is present in the Tachydromiinae). The subfamily Ocydromiinae, to which *Alavesia* belongs, includes 17 recent genera which are classified into three fairly well-defined tribes (Ocydromiini, Trichinini, Oedaleini), based mostly on the structure of antennae, wing venation and male genitalia. As to the phylogeny of this subfamily, the tribe Trichinini is clearly the most primitive as it has a full set of plesiomorphic characters. The other taxa of the subfamily, tribes Oedaleini and Ocydromiini, appear to have evolved along two parallel lines (CHVÁLA 1981). *Alavesia* is now the oldest known member of the subfamily and contains a combination of apomorphic and plesiomorphic characters.

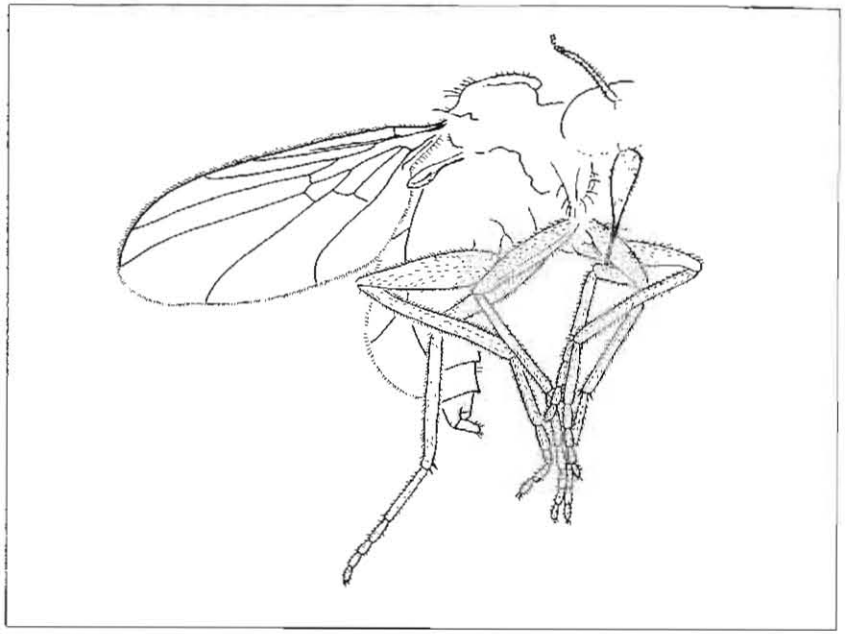

Fig. 3 *Alavesia subiasi* gen. nov., spec. nov. Paratype (MCNA 8838).

The presumed origins of the three subfamilies of Hybotidae were suggested to be Upper Cretaceous (CHVÁLA 1983). Then the fossil *Pseudoacarterus* (WATERS 1989b) lowered the age of the Hybotinae to the Cenomanian (middle Cretaceous, 94-100 Myrs old), and now *Alavesia* extends the age of the Ocydromiinae even further, to the Albian-Aptian (around 113 Ma). The origin of the three subfamilies are thus now believed to be Lower Cretaceous. The age of the origin of the tribes is still under debate.

Alavesia's systematic position is not entirely obvious. First the identifying characters are not always consistent with the grounplan characters distinguishing the Ocydromiinae. It must be mentioned here, however, that the members of the subfamily are much more heterogeneous than the more specialised and rather homogeneous Hybotinae (CHVÁLA 1981). Secondly, in the list of characters shared with and differing from the three tribes Ocydromiini, Trichinini, Oedaleini, *Alavesia* has a combination of characteristics distinguishing these groups. It is important to take a close look at how *Alavesia* compares the Ocydromiinae, *Trichinites* (the family's common ancestor), and some characters distinguishing the individual tribes.

The family Hybotidae may be characterised by the following groundplan characters that are apomorphic (all of these are characteristic of the Ocydromiinae and present in *Alavesia* and *Trichinites*).

1. C runs to just below apex of wing, ending at distal end of M_2.
2. Sc does not reach the wing margin. It is incomplete, and ends freely in wing membrane.
3. R_{4+5} is not forked.

Other characteristics *Alavesia* shares with those typical of the subfamily are that cell cup is shorter than cell bm. Also the outer angle is slightly obtuse (a derived feature) and the branches of M are distinct and not evanescent.

The following characteristics of *Alavesia* are at variance with hybotid groups:

1. The anal cell of *Alavesia* is larger than that seen in the groundplan of the Ocydromiinae. The smaller, more reduced anal cell of the Ocydromiinae is, however, a character seen less commonly; in *Trichinites* and the other subfamilies (and in the Hybotidae in general) the anal cell is larger.
2. In the *Alavesia* specimen M_1 is absent (only two veins emitting from cell dm). Although not a feature characteristic of the Ocydromiinae groundplan, which has three emitting veins, this apomorphic state is seen in the sole tribe Ocydromiini (but not in the other two tribes) as well as in the other two subfamilies, Hybotinae and Tachydromiinae. *Trichinites* also has three veins emitting from the discal cell.
3. *Alavesia* has a very small dm cell. The absence of cell dm is apomorphic (Tachydromiinae), its presence is plesiomorphic. It is large in most extant members of the Ocydromiinae and in *Trichinites*.
4. R_1 and R_{2+3} curve anteriorly sooner, therefore veins are shorter as in *Trichinites* but not in extant Ocydromiinae.
5. Femora are slightly thickened and legs originate close together. This is not so in the Ocydromiinae nor *Trichinites*, but this feature did arise independently a few times, also in other groups (eg. subfamily Hybotinae).

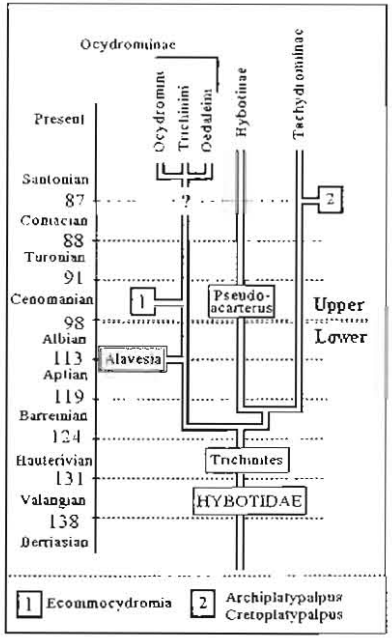

Fig. 4 Phylogeny of Hybotidae

The antennal morphology of *Alavesia* poses a problem because the antennae are similar to those of the tribe Oedaleini, which posses a short antennal style (a plesiomorphic feature seen also in *Trichinites*). The members of the above tribe, however, have three veins emitting from the discal cell (a feature differing with *Alavesia*). *Alavesia* shares the latter characteristic with the tribe Ocydromiini as mentioned above, but this tribe possesses an antennal style which is lengthened into a filiform arista. So *Alavesia* cannot be placed into either tribe with these contradictory elements.

It thus appears that *Alavesia* is not a direct ancestor to any one tribe, but belongs to the Ocydromiinae or perhaps represents its own

group. We propose it existed before the tribes separated from one another. The differentiation into defined tribes would have occurred at some later stage in the history of the Ocydromiinae. Alternatively, one could erect another tribe, the three existing tribes could be rearranged to accommodate the two important characters, which are the shortened antennal style (presently tribe Oedaleini) and the reduction or entire loss of vein M_1 (presently tribe Ocydromiini).

Conclusions

The three subfamilies (Ocydromiinae, Hybotinae, Tachydromiinae) of the Hybotidae had already differentiated by the early Cretaceous (perhaps as early as the Barremian, 119-124 Ma). However *Alavesia*, the new hybotid from the Lower Cretaceous and the earliest known Ocydromid, does not appear to be a direct ancestor to any one of the three tribes (Ocydromiini, Trichiniini, Oedaleini) as it possesses a combination of their characteristics. This indicates that these three tribes had not become differentiated by the Lower Cretaceous, but appear to have emerged later in the evolution of the subfamily.

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