
An aulacid wasp in the Lowermost Eocene amber from the Paris Basin (Hymenoptera: Aulacidae)

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ABSTRACT

Aulacus eocenicus n. sp. is described from the Lowermost Eocene amber of the Paris basin. It is apparently similar to the Australian modern (sub)-genus *Micraulacinus* KIEFFER 1910. We propose a commented list of the fossil species that have been attributed to the Aulacidae. In particular, the attributions to Aulacidae of the Lower Cretaceous subfamilies Baissinae (incl. 'Manlayinae') and Kotujellinae remain weakly supported. A complete phylogenetic revision of the family is urgently needed.

KEYWORDS | Insecta. Hymenoptera. Aulacidae. Eocene French amber. Commented list of fossils.

INTRODUCTION

Aulacidae are rare in the fossil record with about 20 described species. The oldest wasps attributed to this family are from the Lower Cretaceous but these attributions remain somewhat questionable (see appendix below). The Cenozoic record of this group comprises species from the Upper Eocene of the Isle of Wight and Baltic amber and from the Oligocene of North America. One of the main difficulties with the attribution of a fossil to the Aulacidae is the great similarity between this family and the Gasteruptiidae. Rasnitsyn (1988) synonymized the Aulacidae Schuckard, 1841 with the Gasteruptiidae Kirby, 1837. He is followed by Ronquist et al. (1999) who tested Rasnitsyn's hypothesis, but not by Pagliano and Scaramozzino (1990) and other entomologists working on modern faunas (Madl, 1990; Gauld, 1995; Quicke and Fitton, 1995). Basibuyuk et al. (2002) proposed a first attempt of analysis of the phylogenetic relationships between Gasteruptiidae and Aulacidae, but the relative autapomorphies of the Aulacidae remain unknown. The present fossil is the oldest Cenozoic record for this family.

We follow the standard conventions for wing veins proposed by Mason (1986) and the wing venational terminology of Goulet and Huber (1993).

SYSTEMATIC PALAEONTOLOGY

Order: Hymenoptera LINNAEUS, 1758

Family: Aulacidae SHUCKARD, 1841

GENUS *Aulacus* JURINE 1807

Aulacus eocenicus n. sp.

Figures 1 to 3

Diagnosis: Wasp of small size; body only 2.6 mm long; probable absence of occipital carina; petiole inserted on a conical propodeum; absence of ventral lobe of hind coxa; tarsal claws simple; a tooth on the outer apical margin of middle tibia; presence of 3 cubital cells in fore wing, i.e. cells 1R1, 1Rs and 2Rs separated; fore wing cells 1Rs and 2Rs imperfectly closed by nebulous veins

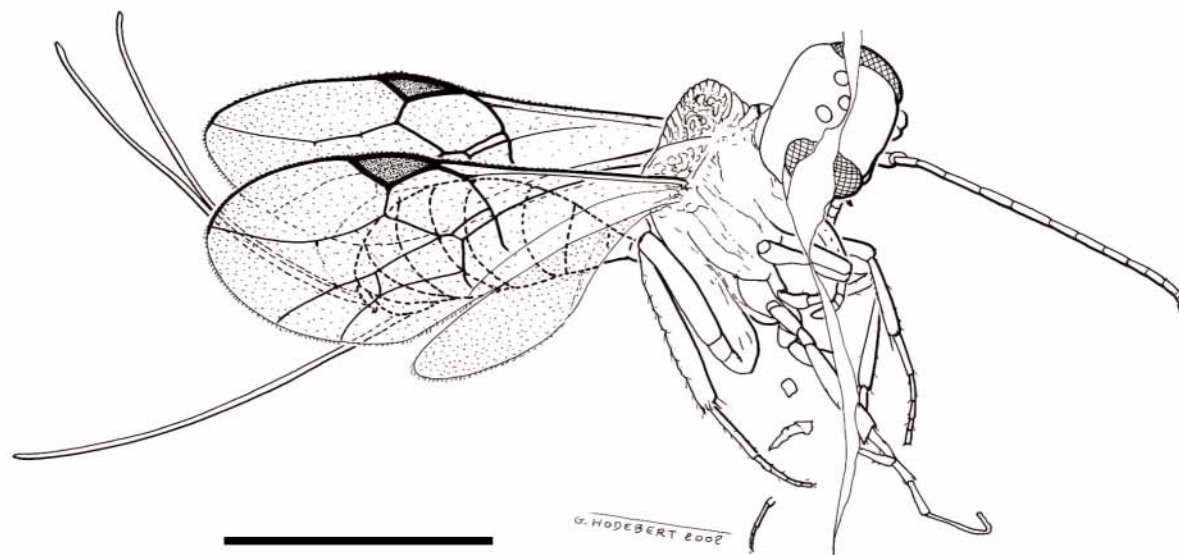


FIGURE 1 | *Aulacus eocenicus* n. sp., holotype specimen PA 2523, general habitus (dorso-lateral view). Scale bar: 1 mm.

2r-m and 3r-m; hind wing without any defined vein, except Sc+R; only 2 hamuli.

Description: Body about 2.6 mm long. Head 0.44 mm long from above, about 0.60 mm wide, as broad and high as the pronotum, slightly flattened, hypognathous, flattened; eyes large; entire head smooth; 3 large ocelli in a moderately high triangle; antennae inserted on the forehead at the half of the eye; toruli not joined; 13 visible antennomeres; scape broad and twice as long as pedicel; flagellomeres progressively longer from first to apex, but second flagellomere (third segment of antenna) slightly shorter than third; antenna not broadened in any part; occipital carina not visible, probably absent.

Thorax + propodeum 0.72 mm long; brown; propleura long and neck-like; mesoscutum strongly humped anteriorly, 0.26 mm high, covered with small punctures and transverse striae; notauli not visible; propodeum 0.16 mm high; an angle less than 90° between the top and front face of median lobe of the mesoscutum.

Fore wing hyaline, 1.80 mm long, 0.78 mm wide; pterostigma triangular, sclerotized, dark brown, 0.28 mm long, 0.16 mm wide, at the three fourths of the wing length from the base; base of free part of Rs arising from R+Sc 0.1 mm from the pterostigma; nearly all veins tubular, except for basal third of M+Cu and cross-veins 2r-m and 3r-m which are evanescent and nebulous; cells C, R, 1Cu, 2Cu, 1M, 1R1, 2M, and 2R1 closed by tubular veins (Fig. 3); all wing surface densely covered by short setae; cell 1R1 distinctly large, but smaller than 2R1; smallest cell of the wing is 1M, longitudinal, elongate and narrow.

Hind wing 1.10 mm long, 0.28 mm wide; the wing is covered by short setae; 2 hamuli at its two thirds; no visible veins or cells, except for the presence of Sc+R and a fold in the position of vein Cu; no separated posterior lobe.

Legs moderately long and thin; all tarsal claws with only one visible apical tooth; hind tibia only slightly widened toward apex; first anterior tarsomere with a strigil (or antennal cleaning notch) corresponding to a specialized apical tibial spur or calcar, which is apically very weakly bifurcate; 2 apical strong spines on median and posterior tibiae; a small tooth on the outer apical margin of median tibia; no small spines along the posterior tibia and tarsi; spur of the posterior tibia two fifths as long as basitarsus; 5 tarsomeres on each leg; basal tarsomeres longer than others, posterior basal tarsomere as long as the 4 apical tarsomeres combined; posterior tarsus not broadened; no ventral lobe on hind coxa; no longitudinal carina on the ventral part of hind coxa but apparently a longitudinal groove; base of median coxa separated from base of hind coxa by the length of median coxa; a small arolium between the tarsal claws.

Metasoma attached high on the propodeum, but distinctly separated from metanotum by a wide dorsal band of propodeum; metasomal segment 1 ('petiole') conical, short, inserted on a conical propodeum; metasoma elongated, 1.26 mm long and 0.50 mm high, finely punctured; ovipositor and ovipositor sheath longer than propodeum, about 1.60 mm long; ovipositor distinctly bowed up.

Material: Holotype specimen PA 2523, mounted in Canada balsam, in collection De Ploëg and Indivision

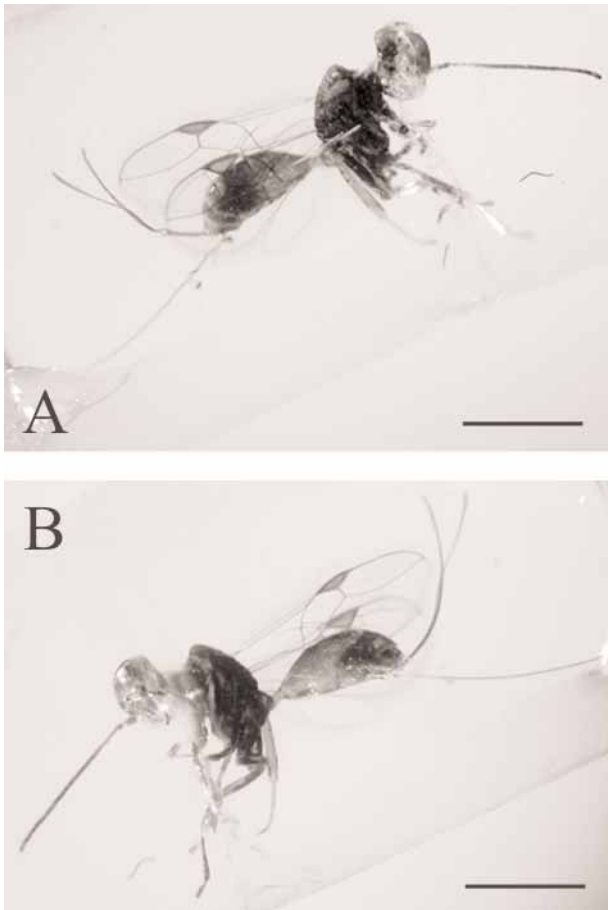


FIGURE 2 | *Aulacus eocenicus* n. sp., holotype specimen PA 2523. A) Photograph of the dorso-lateral view. B) photograph of the ventro-lateral view. Scale bar: 1 mm.

Langlois-Meurine, deposited in Muséum National d'Histoire Naturelle, Paris. Specimens collected in Le Quesnoy all bear the letter PA for Paris (meaning Paris Basin).

Locality deposit: Le Quesnoy, Chevrière, region of Creil, Oise department, France.

Geological age: Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. The amber is autochthonous and very different from the Baltic amber in age, chemical composition and origin (Feugueur, 1963; De Ploëg et al., 1998; Nel et al., 1999).

Etymology of the specific epithet: After Eocene.

Discussion: After the key of the evanioid families of Mason (1993, pp. 510-511), the present fossil specimen falls in the Aulacidae because of its anterior margin of metasomal segment 1 ('petiole') distinctly separated from metanotum, and its metatibia only slightly widened toward apex. Its calcar apically very weakly bifurcate is typical of the Aulacidae and Gasteruptiidae (Basibuyuk

and Quicke, 1995). The presence of two hamuli would also exclude this fossil from the Gasteruptiidae, which have three hamuli (Basibuyuk and Quicke, 1997). The present fossil does not share the synapomorphies of the aulacid sister group, i.e. the Kotujellitinae + Gasteruptiinae which are fore wing vein 3r-m at most spectral with not sign of meeting with Rs and M and fore wing vein 2m-cu absent, but rather displays the groundplan features of Evanioidea (Basibuyuk et al., 2002).

Kieffer (1911) listed and keyed 13 recent aulacid genera. Hedicke (1939) maintained all of them except *Psilaulacus* KIEFFER 1910 that he synonymized with *Pristaulacus* KIEFFER 1899. Townes (1950) considered all these genera as 'species groups or as subgenera' of *Pristaulacus* (under the name *Aulacostethus* PHILIPPI 1873) or *Aulacus* oehlke 1983; Pagliano and Scaramozzino (1990), Konishi (1990), Madl (1990), and Gauld (1995) followed Townes (1950) and recognized only the 3 genera *Aulacus*, *Pristaulacus* and *Panaulix* BENOIT 1984. Nevertheless, Mason (1993) indicated that the family comprises 13 recent genera. Thus, he probably considered the 12 genera listed by Hedicke (1939) to be valid. Lastly, He et al. (2002) recognized 13 genera. Thus, the whole family clearly needs a complete revision and phylogenetic analysis.

Aulacus eocenicus n. sp. shares tarsal claws simple and probable absence of an occipital carina with *Aulacus* (Townes, 1950; Gauld, 1995). But it shares with *Pristaulacus* the presence of a tooth on the outer apical margin of middle tibia (but also present in some *Aulacus*, after Townes, 1950). Presence of an angle less than 90° between the top and front face of median lobe of its mesos-

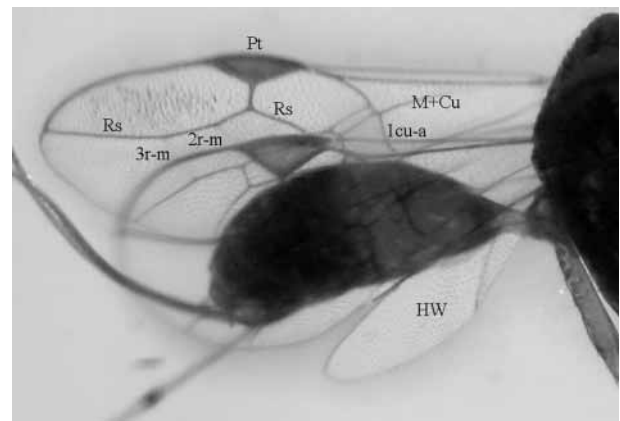


FIGURE 3 | *Aulacus eocenicus* n. sp., holotype specimen PA 2523, photograph of the wings. HW: hind wing; Pt: pterostigma; 2r-m: second radial-median cross-vein; 3r-m: third radial-median cross-vein; 1cu-a: first cubito-anal cross-sector; M+Cu: common stem median+cubitus; Rs: radial sector.

cutum, suggests more affinities with *Pristaulacus* than that of *Aulacus* (Townes, 1950). However, some *Aulacus* species also have this character (Townes, 1950). *A. eocenicus* n. sp. would also share the absence of a ventral lobe of the hind coxa with *Pristaulacus* (Konishi, 1990), but the value of this character for the Aulacidae world wide remains uncertain.

Using the key of Kieffer (1911), this fossil would fall near the Australian modern *Micraulacinus* KIEFFER 1910 (maintained as valid genus in Hedicke, 1939, but junior synonym of *Aulacus*, in Pagliano and Scaramozzino, 1990), because of the following characters: (1) presence of 3 'cubital cells' in fore wing, i.e. cells 1R1, 1Rs and 2Rs separated; (2) tarsal claws simple; (3) petiole inserted on a conical propodeum; (4) hind wing without any defined vein, except Sc+R; (5) fore wing cells 1Rs and 2Rs imperfectly closed by the nebulous veins 2r-m and 3r-m. *A. eocenicus* n. sp. differs from the type species *Aulacus* (*Micraulacinus*) *elegans* (KIEFFER 1911) in the presence of only two hamuli instead of three. Kieffer (1910) only gave the diagnosis of the (sub?)-genus *Micraulacinus* and described the type species in 1911.

A. eocenicus n. sp. differs from *Panaulix* in the characters (1), (2) and (4) listed just above. It also differs from the Oligocene species *Alaucus bradleyi* BRUES 1910, *Pristaulacus rohweri* BRUES 1910, the Upper Cretaceous genera *Protofoenus* COCKERELL 1917, *Hyptiogastrites* COCKERELL 1917, *Electrofoenus* COCKERELL 1917 and the Eocene genus *Vectevania* COCKERELL 1922 in the presence of three cubital cells (Brues, 1910; Cockerell, 1917a, b, 1922). All these taxa cannot be correctly compared with the modern Aulacidae and should be redescribed.

A. eocenicus n. sp. differs from the Baltic amber species *Pristaulacus* (*Oleisoprister*) *praevolans* and *Pristaulacus mandibularis* in its distinctly smaller size (2.6 mm long instead of 12 mm and 10 mm, respectively) (Brues, 1923, 1932). It is also distinctly smaller than *Aulacus* (*Micraulacinus*) *prisculus* and *Aulacus* (*Micraulacinus*) *fritschii* (6 mm and 4.3 mm, respectively). Unlike *A. eocenicus* n. sp., the third joint of antenna is longer than fourth in *A. (M.) prisculus* and the fore wing cell is distally close by a tubular vein in *A. (M.) fritschii*, (BRUES 1932). *A. eocenicus* n. sp. is also distinctly smaller than the Cretaceous species of *Baissa*, *Kotujella* and *Manlaya*.

The exact affinities of *A. eocenicus* n. sp. within the Aulacidae remain uncertain. Because it has some characters that are associated with *Pristaulacus*, it could correspond to a new genus. But the establishment of such a genus has to wait after a revision and a phylogenetic analysis of the whole family.

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Appendix. List of fossil taxa attributed in the past to the Aulacidae

Jurassic

- *Mesaulacinus oviformis* MARTYNOV 1925 (Upper Jurassic, Kazakhstan). Originally attributed to the Aulacinae, Tillyard (1927) doubted this attribution. It is considered as a Megalyridae: Cleistogastrinae by Pagliano and Scaramozzino (1990).

Cretaceous

- *Kotujella crucis* RASNITSYN 1975 (Upper Cretaceous, Taymir amber, C.E.S.). It is the type species of the fossil subfamily Kotujellinae Rasnitsyn, 1975. Originally as a family, the Kotujellidae (in Evanioidea) is now included in the Aulacidae (Rasnitsyn, 1980; Pagliano and Scaramozzino, 1990).
- *Baissa anomala* RASNITSYN 1975 (Lower Cretaceous, Neocomian or Barremian-Aptian, Mostovski and Martínez-Delclòs, 2000). Baissa, Vitim river, Transbaikalia, C.E.S., type species of the fossil subfamily Baissinae Rasnitsyn, 1975). Originally as a family, the Baissidae (in Evanioidea) is now included into the Aulacidae (Rasnitsyn, 1980; Pagliano and Scaramozzino, 1990) or ‘Gasteruptiidae’ as basal sister group of the [Aulacidae + (Gasteruptiinae + Kotujellitinae)] (Basibuyuk et al., 2002). The same authors proposed two synapomorphies for the clade Baissinae + [Aulacidae + (Gasteruptiinae + Kotujellitinae)], i.e. 14 antennal segments in female; number of antennal segments dimorphic.
- *Manlaya mongolica* RASNITSYN 1980 (Lower Cretaceous, Neocomian, Manlay, Mongolia, type genus and species of the fossil subfamily Manlayinae Rasnitsyn, 1986, which was synonymized with Baissinae by Rasnitsyn (1991), followed by Basibuyuk et al. (2002). One genus with 17 species, all described on relatively poorly preserved impressions, after the original figures of Rasnitsyn, 1980, 1986, etc.). As for the previous fossils, the structure of the metasomal segment 1 is not known, thus the main family diagnostic character remains dubious (Goulet and Huber, 1993). Apparently, *Baissa* and all the ‘Manlayinae’ have a more or less rounded metasoma, a long narrow cell 2R1 and apparently no cells 1Rs and 2Rs separated and closed by veins 2r-m and 3r-m. Nothing is known about the tarsal claws (simple or not) or the hind wing structures. The exclusion of relationships between Baissinae, ‘Manlayinae’ and the Gasteruptiinae *sensu stricto* would be based only on the general shape of the metasoma, not elongated but rounded (note that the metasoma of *Kotujella* is rather elongate). The fore wing venation is very similar in the Aulacidae and Gasteruptiidae. Nevertheless, *Baissa*, *Manlaya* and the modern Aulacidae differ from the modern Gasteruptiinae *sensu stricto* in the presence of a closed cell 2M (character observable in fossils, apparently unknown in *Kotujella*, after Rasnitsyn, 1975). Nevertheless, the exact relationships between these three ‘subfamilies’ and the Aulacidae: Aulacinae remains dubious, because of the lack of information concerning very important structures (tarsal claws, propodeum, etc.).
- *Manlaya ventricosa* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya pinguis* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya laevinota* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya gurvanica* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya corrugata* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya obscura* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya caudata* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya pallida* RASNITSYN 1986 (Lower Cretaceous, Mongolia).
- *Manlaya undurgensis* (RASNITSYN 1975) (Lower Cretaceous, Mongolia).
- *Manlaya pachyura* RASNITSYN 1990 (Lower Cretaceous, Transbaikalia).
- *Manlaya ghidarina* RASNITSYN 1990 (Lower Cretaceous, Transbaikalia).
- *Manlaya anglica* RASNITSYN et al. 1998 (Lower Cretaceous, England).
- *Manlaya occulatissima* RASNITSYN et al. 1998 (Lower Cretaceous, England).
- *Manlaya ockleyensis* RASNITSYN et al. 1998 (Lower Cretaceous, England).
- *Manlaya capelensis* RASNITSYN et al. 1998 (Lower Cretaceous, England).
- *Manlaya lacabrua* RASNITSYN and ANSORGE 2000 (Lower Cretaceous, Spain).
- *Manlaya ansorgei* RASNITSYN and MARTÍNEZ-DELCLÒS 2000 (Lower Cretaceous, Spain).

- *Tillywhimia spectra* RASNITSYN et al. 1998 (Lower Cretaceous, England).
- *Sinowestratia communicata* ZHANG and ZHANG 2000 (Lower Cretaceous?, Liaoning Province, China, originally described in Praeaulacidae, transferred in Baissinae by Basibuyuk et al., 2002).
- *Aulacopsis laiyangensis* HONG and WANG 1990 (Lower Cretaceous, Shandong Province, China) (Originally described in Aulacidae, transferred in Baissinae by Rasnitsyn et al., 1990 and Basibuyuk et al., 2002).
- *Humiryssus leucus* LIN 1980 (Lower Cretaceous, China) (Originally described in Paroryssidae, transferred in Baissinae by Rasnitsyn et al., 1990 and Basibuyuk et al., 2002, a very poorly preserved fossil).
- Jell and Duncan (1986) briefly described and figured a female ‘Aulacid indet.’ from the Lower Cretaceous (Late Aptian) Koonwarra bed (Victoria, Australia). It is apparently a very poorly preserved specimen. The 14-segmented antenna (condition occurring in Aulacidae and Gasteruptiidae) and the ‘apparently generalized venation’ support this placement. Thus, its attribution remains very doubtful. Basibuyuk et al. (2002) indicated it is ‘currently considered Apocrita incertae sedis’.
- *Paraulacus sinicus* PING 1928 (Upper Coal series, Lower Cretaceous, Peipiao, Jehol, China). Originally attributed to the Aulacidae, it is considered as a Mesoserphidae in Pagliano and Scaramozzino (1990).
- *Protofoenus swinhoei* COCKERELL 1917 (Upper Cretaceous, Burmese amber). Originally in Evaniidae (Cockerell, 1917a), Spahr (1987) and Pagliano and Scaramozzino (1990) considered it as an Aulacidae. Ross and York (2000) listed it in the Gasteruptiidae (incl. Aulacidae).
- *Electrofoenius gracilipes* COCKERELL 1917 (Upper Cretaceous, Burmese amber). Originally in Evaniidae (Cockerell, 1917b; Keilbach, 1982), Spahr (1987) and Pagliano and Scaramozzino (1990) considered it as an

Aulacidae. Ross and York (2000) put it in the Gasteruptiidae (incl. Aulacidae).

- *Hyptiogastrites electrinus* COCKERELL 1917 (Upper Cretaceous, Burmese amber). Spahr (1987) listed it in the Aulacidae, and Ross and York (2000) in the Gasteruptiidae (incl. Aulacidae).

Eocene

- *Vectevania vetula* COCKERELL 1922 (Bembridge Marls, Gurnet Bay, Isle of Wight, England, Upper Eocene). It was included in the Aulacidae by Pagliano and Scaramozzino (1990).
- *Alaucus bradleyi* BRUES 1910 (Oligocene, Florissant, Colorado, U.S.A., Brues, 1910);
- *Aulacus (Micraulacinus) prisculus* (BRUES 1932) (Upper Eocene, Baltic amber, listed in the Aulacidae by Keilbach, 1982; Spahr, 1987).
- *Aulacus (Micraulacinus) fritschii* (BRUES 1932) (Upper Eocene, Baltic amber, listed in the Aulacidae by Keilbach, 1982; Spahr, 1987).
- *Pristaulacus mandibularis* BRUES 1932 (Upper Eocene, Baltic amber, listed in the Aulacidae by Keilbach, 1982; Spahr, 1987).

Oligocene

- *Pristaulacus rohweri* BRUES 1910 (Oligocene, Florissant, Colorado, U.S.A., Brues, 1910);
- *Pristaulacus (Oleisoprister) praevolans* (BRUES 1923) (Upper Eocene, Baltic amber, listed in the Evaniidae by Keilbach, 1982 and in the Aulacidae by Spahr, 1987).
- *Pristaulacus secundus* (COCKERELL 1916) (Oligocene, Florissant, Colorado, U.S.A.). Originally described in the fossil genus *Aulacites* COCKERELL 1916, later synonymized with *Pristaulacus* (Townes, 1950; Pagliano and Scaramozzino, 1990), in Aulacidae.