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The oldest trigonalid wasp in the Late Albian amber of Charente-Maritime (SW France) (Hymenoptera: Trigonalidae)

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Key words: Insecta, Hymenoptera, Trigonalidae, *Albiogonaly elongatus* gen. n., sp. n., amber, Late Albian, Charente-Maritime, France

ABSTRACT

Albiogonaly elongatus gen. n., sp. n., oldest known representative of the family Trigonalidae, is described from the Late Albian amber of France. It could be placed in a very basal position, as sister group of the modern representatives of the family. The positions of the fossil taxa currently attributed to this family are discussed. Except for *Cretogonaly taimyricus* RASNITSYN 1977, almost all of these taxa are too poorly preserved or described for accurate attributions to this family.

RESUME

Albiotrigonalis elongatus gen. n., sp. n., plus ancien représentant connu de la famille Trigonalidae, est décrit de l'ambre de l'Albien supérieur de France. Il est dans une position basale, comme groupe frère des représentants modernes de la famille. Les positions des taxons fossiles attribués à cette famille sont discutées. Mis à part *Cretogonaly taimyricus* Rasnitsyn, 1977, presque tous ces taxons sont trop mal conservés ou décrits pour une attribution correcte à cette famille.

1. Introduction

The Trigonalidae is a small hymenopteran family that comprises 88 species in sixteen recent genera (Carmean & Kimsey 1998). Very few fossils have been attributed to this group, ranging from the Lower Cretaceous to the Oligocene: *Turgonaly cooperi* RASNITSYN & JARZEMBOWSKI 1998, described from the Lower Barremian of England (Rasnitsyn et al. 1998); *Darbigonaly capitatus* RASNITSYN 1986, from the Early Cretaceous of Gurvaneren Formation, West Mongolia (Rasnitsyn 1986); *Cretogonaly taimyricus* RASNITSYN 1977, from the Cenomanian amber of the Taimyr Peninsula, Russia (Rasnitsyn 1977); *Turgonaly minor* RASNITSYN 1990, from the Cretaceous of Transbaikalia, Russia (Rasnitsyn 1990); '*Trigonalys*' *bischoffii* STATZ 1938, from the Oligocene of Rott, Germany (Statz 1938). In addition, Martínez-Delclòs et al. (1999) listed undescribed specimens of the family 'Trigonalidae' in the Aptian/Albian Spanish amber of Alava. Furthermore, Cockerell (1917) described *Trigonalys pervetus* and (1920) listed the family 'Trigonalidae' in the Albian Burmese amber (recent Albian datation by Cruickshank & Ko 2003), although Antropov

(2000) transferred it in the Sphecidae. However, nearly all these fossils are too poorly preserved for really accurate systematic attributions. Thus, the present discovery of a fossil wasp belonging to this family in the Upper Albian amber of Archingeay (Charente-Maritime, France) is of great interest to estimate the age and origin of this family.

2. Material and methods

The specimen studied here was discovered in a piece of amber together with four other insects (see the list of taxa in the systematic palaeontology section below). This lump, as the most of the amber lumps from the outcrop of Archingeay-Les Nouillers, is honey-coloured to clear brown and rather dusty. It was thus impossible to study this inclusion without preparing the specimen. First, each inclusion was separated from others, and the surrounding amber was removed in order to get as close as possible to the inclusion and to view its entire habitus. These operations were realized under a stereomicroscope using shaving blades transformed into micro-saws. Then, the separated specimens were embedded in Canada balsam be-

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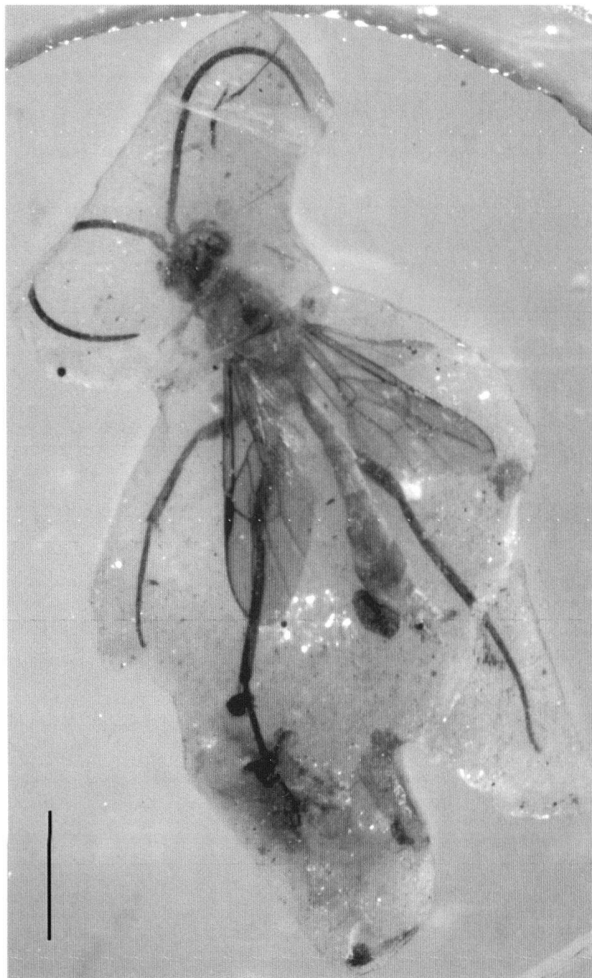


Fig. 1. – *Albiogonalyx elongatus* gen. n., sp. n., holotype ARC 205.1; photography of general habitus. Scale bar represents 2 mm.

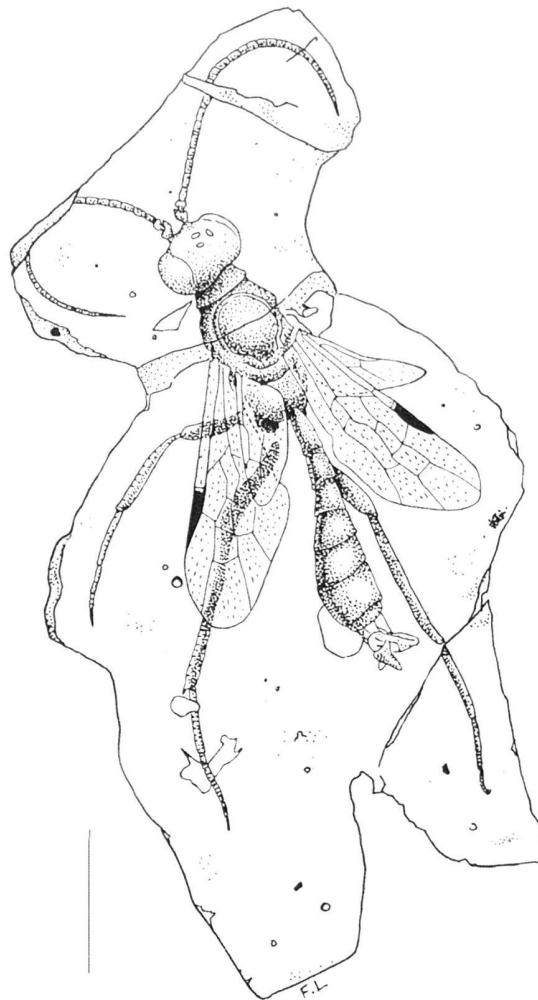


Fig. 2. – *Albiogonalyx elongatus* gen. n., sp. n., holotype ARC 205.1; reconstruction of general habitus. Scale bar represents 2 mm.

tween cover glasses, allowing an easier view of all sides of the insect during its study. We follow the terminology of Huber & Sharkey (1993) for the systematic description.

3. Systematic palaeontology

Superfamily Trigonaloidea CRESSON 1887
Family Trigonalidae CRESSON 1887

Genus *Albiogonalyx* gen. n.

Type species. – *Albiogonalyx elongatus* sp. n.

Gender. – Masculine.

Etymology. – After the Albian age of this fossil, and ‘gonalyx’ derived from the genus *Trigonalys*.

Diagnosis. – Easily distinguishable from modern taxa by the following characters: antennae with 25 cylindrical flagellomeres; in hind wing, part of M distal of r-m present and part of A

distal of cu-a present as a nebulous vein, metasoma very elongate and narrow, about ten times as long as broad, tergite VII with two rather long lobes.

Albiogonalyx elongatus sp. n. (Figs. 1–6)

Holotype. – Female specimen ARC 205.1, in the same piece of amber with two Coleoptera, one Hymenoptera: Proctotrupoidea, and one larva of Neuroptera: Myrmeleontoidea: Ascalaphidae? Deposited in the Laboratoire de Paléontologie, Muséum National d’Histoire Naturelle, Paris, France.

Type locality. – Archingeay, Charente-Maritime, SW France.

Stratigraphic horizon. – Lower Cretaceous, Uppermost Albian (Néraudeau et al. 2002).

Etymology. – After its very elongate and narrow metasoma.

Diagnosis. – That of the genus.

Description. – Body 5.4 mm long.

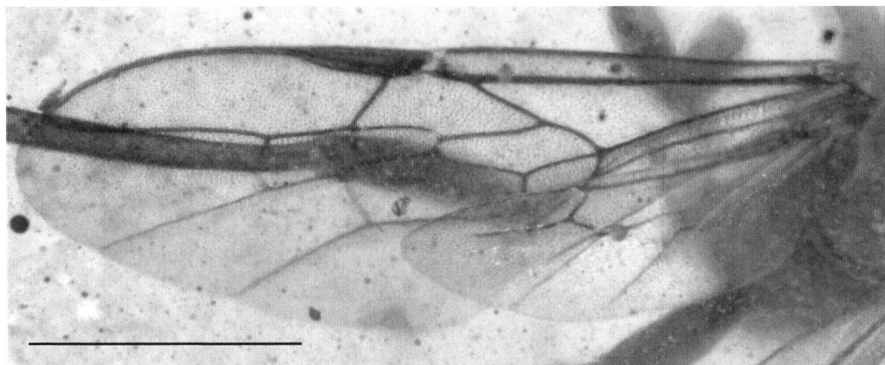


Fig. 3. – *Albiogonalyx elongatus* gen. n., sp. n., holotype ARC 205.1; photography of left wings. Scale bar represents 1 mm.

Head 0.6 mm long, 1.0 mm wide, ratio length/width 0.6; labrum narrow elongate; right mandible strong, with four teeth, left mandible not visible; other mouthparts not or very poorly visible; three ocelli; a slight supra-antennal elevation above the torulus; antennae inserted on frons, 3.8 mm long, with a short scape, 0.2 mm long, ratio length of scape/length of antenna 0.05, pedicel 0.08 mm long, ratio length of pedicel/length of scape 0.4, 25 cylindrical flagellomeres, the apical one being conical; numerous sparse white scales on middle flagellomeres; malar space without a deep depression for reception of scape; eyes oval, large, well separated, 0.4 mm apart.

Mesosoma 1.88 mm long, 0.88 mm wide, ratio length/width 2.14; no triangular axilla and median groove on mesoscutum; propodeum broader than long, 0.4 mm long, 0.52 mm wide, ratio length/width 0.77, without any visible sculpturing ornamentation.

Legs. Only middle and hind legs are preserved, with five tarsomeres; tarsomeres 1–4 each with plantar lobe, 0.02 mm long; mid femur about 1 mm long, 0.2 mm wide, ratio length/width 5.0; tibia 1.12 mm long, 0.12 mm wide, ratio length/width 9.3, tarsus 1.48 mm long; hind femur about 1.2 mm long, 0.24 mm wide, ratio length/width 5; tibia 1.72 mm long, 0.16 mm wide, ratio length/width 10.75, tarsus 1.84 mm long; coxae, trochanters and trochantelli not preserved; tarsal claws with a preapical small tooth.

Fore wing hyaline, 3.28 mm long, 1.12 mm wide, ratio length/width 2.93; veins C and Sc+R distinct; pterostigma black, 0.52 mm long, 0.12 mm wide, ratio length/width 4.33; Rs separating from Sc+R distinctly basal of pterostigma (0.16 mm); basal part of Rs straight, relatively (0.28 mm) long before its fusion with M; basal part of vein M moderately curved, 0.24 mm long; base of M 0.96 mm from wing base, aligned with cross-vein 1cu-a; Rs+M rather long (0.4 mm long); distal free part of M, before its contact with 1m-cu short (0.08 mm long); distal free part of Rs, before its contact with r-rs longer (0.32 mm long); cross-vein 2r-m aligned with r-rs; 2m-cu ending in cell [2Rs]; 3r-m present but with its median part nebulous; distal part of vein Cu strongly bent posteriorly; 2cu-a very short (0.04 mm long), distinctly shorter than 1cu-a; 1m-cu ending in M distal of fork of Rs+M; 2m-cu well defined but with a short nebulous part near its anterior end; distal ends of

M and Cu well defined and reaching wing margin; no vein 2A+3A and cross-vein a; all cells [1M], [2M], [1R1], [1Rs], [2Rs], and [2R1] closed; [2R1] longer than other distal cells, 1.24 mm long, 0.32 mm wide, ratio length/width 3.87; [1R1] 0.72 mm long, 0.24 mm wide, ratio length/width 3.0; [1Rs] 0.32 mm long, 0.12 mm wide, ratio length/width 2.66; [2Rs] 0.36 mm long, 0.16 mm wide, ratio length/width 2.25; [1M] 0.6 mm long, 0.2 mm wide, ratio length/width 3.0; [2M] 0.68 mm long, 0.24 mm wide, ratio length/width 2.83.

Hind wing hyaline, 1.6 mm long, 0.56 mm wide, ratio length/width 2.85; distal part of Rs 0.36 mm long, not reaching wing margin; cross-vein r-m long and oblique, 0.12 mm long; distal parts of M and Cu reaching wing margin; a distinct angle between cu-a and vein A; distal part of vein A present but nebulous; vein cu-a 0.08 mm long; vein C present at wing base but only 0.2 mm long; no visible posterior lobe at wing base; five strong distal hamuli.

Metasoma pedunculate, very elongate, higher than broad, 3.44 mm long, 0.32 mm wide in broadest part, ratio length/width 10.75, sterna hard, convex; no metasomal armature on sternum II or III; spiracles not visible, probably absent, ovipositor very reduced, not surpassing apex of metasoma, sternite VII with two broad and long lobes, 0.4 mm long, 0.28 mm wide, ratio length/length of metasoma 0.11; cerci visible, 0.08 mm long.

4. Discussion

If we follow the key to modern wasp families proposed in Mason (1993), *Albiogonalyx* gen. n. falls in the Trigonalidae. There is still no real consensus on the phylogenetic relationships of the Trigonalidae. Among other papers, Dowton et al. (1997) considered the Trigonalidae, in their molecular phylogeny of the Apocrita, as the sister group of the Megalyridae, in the clade Evaniomorpha. Ronquist et al. (1999: figs 5–9) proposed several other phylogenetic hypotheses, depending on the method to obtain them. Lastly, Rasnitsyn (2002: fig. 331), following Rasnitsyn (1988), considered the Trigonalidae as a ‘sister group’ of a paraphyletic lineage Megalyridae (+ Stephanidae). He characterized the group Megalyridae+ Stephanidae+ Trigonalidae by the hind wing vein A lost beyond cu-a. In *Albiogonalyx* gen. n., the vein

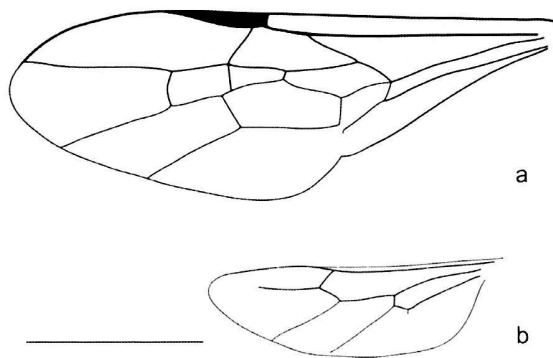


Fig. 4. – *Albiogonalyx elongatus* gen. n., sp. n., holotype ARC 205.1; reconstruction of wings: a. left fore wing, b. left hind wing. Scale bar represents 1 mm.

A, although nebulous, is not absent. Rasnitsyn (1988, 2002) also characterized the Trigonaliidae by the following characters: (1) mandibular dentition asymmetrical (four teeth in right mandible and three in left, unlike three in Megalyridae). Carmean & Kimsey (1998) noted that this character is secondarily lost in three modern genera. The presence of four teeth in the right mandible of *Albiogonalyx* gen. n. strongly suggests that it might be of the trigonalid type; (2) median mesoscutal sulcus absent, as in *Albiogonalyx* gen. n. but also in the modern megalyrid genus *Carminator* SHAW 1988 (Shaw 1988: 107); (3) metasomal sterna hard, convex, as in *Albiogonalyx* gen. n.; (4) ovipositor internalised, as in *Albiogonalyx* gen. n. Furthermore, after the diagnosis of the Trigonaliidae of Carmean & Kimsey (1998), *Albiogonalyx* gen. n. has the following further derived characters: (5) presence of sparse white scales on the female flagellomeres ('feature unique to all members of this family'); (6) presence of a supra-antennal elevation. It also has the following other, plesiomorphic characters: (7) tarsi with plantar lobes; (8) fore wing with complete venation; (9) hind wing with two closed cells; (10) numerous antennomeres (25 in *Albiogonalyx* gen. n.). *Albiogonalyx* gen. n. has not the 'metasomal armature' proper to some modern Trigonaliidae.

If we follow Shaw (1988) in his redefinition of the Megalyridae as a monophyletic group, *Albiogonalyx* gen. n. does not fit in it because it has not the main apomorphic character of the family, i.e. hind wing venation greatly reduced. It can also be separated from this family after the following key characters (but some are either plesiomorphies or of more uncertain polarity): median mesoscutal sulcus present, long ovipositor, mandibles symmetrical, twelve antennal flagellomeres, fore wing venation reduced, broad metasoma, presence of a subantennal groove in the malar space. Thus there is no argument supporting a close relationship between *Albiogonalyx* gen. n. and the modern Megalyridae.

Rasnitsyn (2002) considered the Megalyridae as a paraphyletic group. All the other Ceraphronoidea *sensu* Rasnitsyn and more especially the Stephanidae and Trigonaliidae are supposed to be derived from it. We prefer to reject this confusing

point of view and to use monophyletic groups. In particular, Rasnitsyn (1975) created the Mesozoic subfamily Cleistogastrinae for several genera with complete fore wing venation very similar to those of the modern Trigonaliidae. As Shaw (1988) already noted, the main body characters necessary for a family attribution are not preserved in all these fossils (bases of antennae, mandibles, thoracic ornamentation, structure of tarsi, structure of metasomal sterna). Thus, their attribution to the Megalyridae is not demonstrated. Nevertheless, many of these Cleistogastrinae have long ovipositors, unlike the modern Trigonaliidae. Their trigonalid-like wing venation is not sufficient alone for their attribution to this family or its stem group. Their positions are uncertain. All these Cleistogastrinae can be easily distinguished from *Albiogonalyx* gen. n. after their rounder metasoma.

Carmean & Kimsey (1998) separated the Trigonaliidae in the two subfamilies Orthogonalinae CARMEAN & KIMSEY 1998 and Trigonaliinae on the basis of the presence of tyloids on the male antennae as a synapomorphy of the former subfamily. These structures are not available in *Albiogonalyx* gen. n. This fossil genus differs from *Orthogonalys* SCHULZ 1905, unique genus of the Orthogonalinae and most basal modern genus, in the absence of areolate-rugose propodeal sculpturing ornamentation. *Albiogonalyx* gen. n. differs from all modern Trigonaliidae in its very narrow elongate metasoma and the presence of a hind wing vein A (Schulz 1907; Yamane & Kojima 1982; Carmean & Kimsey 1998). This last character state is supposed to be plesiomorphic for the Trigonaliidae after Rasnitsyn (2002), thus it would suggest a very basal position for *Albiogonalyx* gen. n. in the trigonalid lineage.

Position of the fossil taxa previously attributed to the Trigonaliidae

The Mesozoic Cleistogastrinae, especially *Cleistogaster* RASNITSYN 1975 have a wing venation very similar to those of the modern Trigonaliidae but they differ from this family in their very long ovipositor. As already indicated above, their position is uncertain. But their existence demonstrates that the wing venational characters are not sufficient for the attribution of a fossil taxon to the Trigonaliidae *sensu stricto*.

The following taxa have been attributed to the Trigonaliidae:

- Cockerell (1917) described *Trigonalys pervetus* and the same author (1920) listed the family 'Trigonaliidae' in the Albian Burmese amber (recently dated as Albian by Cruickshank & Ko 2003). However Antropov (2000) transferred it in the Sphecidae.
- Statz (1938) described '*Trigonalys*' *bischoffii* from the Oligocene of Rott (Germany). The type of this species is stored in the Natural History Museum of Los Angeles County (Sphon 1973). Its wing venation is of the trigonalid-type but there is no body character supporting its attribution to the Trigonaliidae. '*Trigonalys*' *bischoffii* differs from *Albiogonalyx* gen. n. in the following characters of the fore

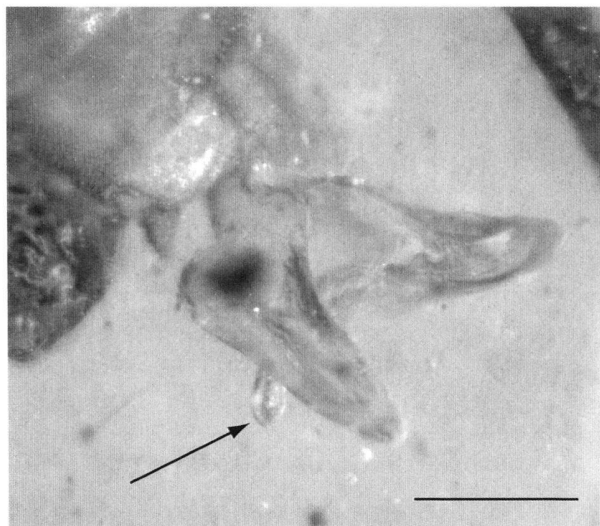


Fig. 5. – *Albiogonalyx elongatus* gen. n., sp. n., holotype ARC 205.1; photograph of ovipositor. Arrow shows the cerci. Scale bar represents 0,25 mm.

wing venation: cross-vein 2r-m reaching Rs well distal to the point of fusion between Rs and r-rs; point of separation between Rs and M is distal to anterior end of 1m-cu.

- Martínez-Delclòs et al. (1999) listed the family 'Trigonalidae' in the Aptian/Albian Spanish amber of Alava.
- Rasnitsyn (1977) described the fossil genus and species *Cretogonalyx taimyricus* from the Cenomanian amber of the Taimyr Peninsula (Russia). He erected the fossil subfamily Cretogonalyxinae RASNITSYN 1977 for this taxon. *Cretogonalyx* shows dissymmetric mandibles, as in modern Trigonalidae. It is the unique argument of Rasnitsyn to include it in this family, but its wing venation strongly differs from those of modern Trigonalidae. It also has areolate-rugose propodeal sculpturing ornamentation, as in 'primitive evaniomorph' and *Orthogonalyx* (Carmean & Kimsey 1998: 53). *Cretogonalyx taimyricus* strongly differs from *Albiogonalyx* gen. n. in the following characters of the fore wing venation: cell [1M] very small, cell [1R1] very large; cell [2R1] small, not elongate; propodeum sculptured.
- Rasnitsyn (1986) described the fossil genus and species *Darbigonalyx capitatus* from the Early Cretaceous of Gurbaneren Formation, West Mongolia. It is a very poorly preserved specimen with the body structures nearly useless and a bad preservation of the wing venation. It is an *incertae sedis*. *Darbigonalyx capitatus* differs from *Albiogonalyx* gen. n. in its rounded metasoma, but also in the shape of its fore wing cell [1R1].
- Rasnitsyn (1990: 189, pl. 15, fig. 1) described the fossil genus and species *Turgonalyx minor* from the Cretaceous of Transbaikalia (Russia). It is based on a rather poorly preserved impression, with no detail in the body structure and a wing venation in bad condition.

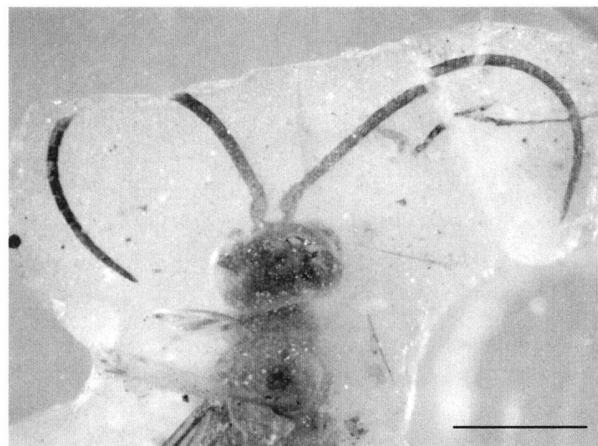


Fig. 6. – *Albiogonalyx elongatus* gen. n., sp. n., holotype ARC 205.1; photograph of head and mesosoma. Scale bar represents 1 mm.

- Rasnitsyn et al. (1998) described an isolated fore wing from the Lower Barremian of England under the name *Turgonalyx cooperi* RASNITSYN & JARZEMBOWSKI, 1998. As indicated above, if this wing venation is of trigonalid-type, it is not sufficient for an attribution to this family *sensu stricto*.

The genus *Turgonalyx* can only be considered as an *incertae sedis* that could be related to the Trigonalidae. It differs from *Albiogonalyx* gen. n. in its rounded metasoma and fore wing venation.

In conclusion, except maybe for *Cretogonalyx taimyricus*, all the fossil taxa that are currently attributed to the Trigonalidae are of uncertain familial affinities. *Albiogonalyx* gen. n. is thus the first and oldest accurate fossil representative of this family.

5. Palaeoecological remarks

Many modern Trigonalidae have a very particular biology, laying their eggs on foliage. These eggs have to be consumed by the host to develop. The reduction of the ovipositor and the metasomal armature are related to this behaviour. However, none of the known hosts, except for sawflies, can be considered ancient. The most widely distributed trigonalid, *Taeniogonalyx*, is a relatively derived genus known to directly parasitize sawflies as well as indirectly tachinids and ichneumonids (Weinstein & Austin 1991). The least derived trigonalid, *Orthogonalyx*, is widely distributed, absent only from Europe and Australia. Host information for the genus is limited to few rearings from Lepidoptera pupae that are believed to be intermediate hosts and a tachinid parasitoid of Lepidoptera. Considering its great antiquity and the lack of metasomal armature, *Albiogonalyx* gen. n. was probably still a direct parasitoid, with sawflies as possible hosts.

Modern Trigonalidae have a nearly cosmopolitan distribution, with the exception of arctic and alpine regions. However, most taxa occur in the intertropical areas, under warm cli-

mates, and only one species is found in Europe. This intertropical distribution is congruent, for *Albiogonaly* gen. n., with the warm palaeoclimate generally admitted in Europe for the Mid-Cretaceous period (Frakes 1979; Jenkyns et al. 1994), as well as with the global temporary view shown by both the arthropod assemblage found in the amber and by the associated palynological remains identified in the outcrop of Archingeay-Les Nouillers thus far (Perrichot, in press; Perrichot et al., in press, 2002; Nel et al., in press; Azar et al. 2003; Néraudeau et al. 2002). The distribution of modern trigonalid genera linking widely separated regions appears to be relictual and supports evidence for the ancient origin of the group, at least Upper Jurassic or Lower Cretaceous, as shown by the present discovery of *Albiogonaly* gen. n.

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