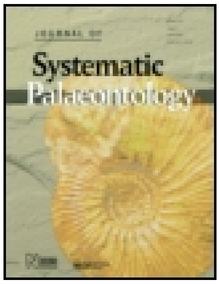

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Lower Cretaceous origin of long-distance mate finding behaviour in Hymenoptera (Insecta)

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Lower Cretaceous origin of long-distance mate finding behaviour in Hymenoptera (Insecta)

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Flabellate antennae have evolved numerous times in males of several insect groups where they carry olfactory receptor neurons enabling the individuals to locate females over long distances. In Recent Hymenoptera, one of the largest species radiations among the Animalia, flabellate antennae are relatively uncommon. Here we describe *Atefia rasnitsyni* gen. et sp. nov. from the Lower Cretaceous Crato Formation of Brazil, representing the first fossil hymenopteran with a biflabellate antenna. The fossil indicates that long-distance mate finding behaviour in Hymenoptera was already well established in the Lower Cretaceous. The new fossil is taxonomically challenging and shares morphological characters with Recent Pergidae and Diprionidae. However, it lacks definite diagnostic features of either family and is here left unplaced as an early lineage of Tenthredinoidea. The occurrence and structural diversity of flabellate antennae in Recent Tenthredinoidea is discussed in a phylogenetic framework.

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Keywords: antennal morphology; sex pheromones; mate recognition; Tenthredinoidea; Crato Formation; Brazil

Introduction

Flabellate antennae have evolved numerous times in the males of several endopterygote insect groups (e.g. Coleoptera, Diptera, Hymenoptera, Lepidoptera, Strepsiptera), where they carry olfactory receptor neurons which enable males to find their female counterparts over long distances (e.g. Steinbrecht 1973; Bergström *et al*. 1995; Batelka *et al*. 2011). In Hymenoptera this character is relatively uncommon (Alekseyev 2010) and in the earliest lineages, the 'Symphyta', flabellate antennae are restricted to a few taxa within Tenthredinoidea (*s. str.*) (*vide* Discussion, *infra*). Here we describe a peculiar new genus of sawflies with uncertain affinities to Recent families of Tenthredinoidea (*s. str.*). The male specimen is characterized by biflabellate antennae, a feature not previously found in the fossil record of Hymenoptera. The structural diversity of flabellate antennae in Recent Tenthredinoidea is compared with the condition found in the new fossil and discussed in a phylogenetic framework.

The Crato Formation of Brazil is one of the most important sources of Cretaceous insects and has already yielded many tens of thousands of excellently preserved specimens, with about 375 species representing most insect orders (Martill *et al*. 2007). However, only three species of non-apocritan hymenopterans had previously been found in the Crato Formation, namely *Prosyntexis gouleti* Sharkey (Sepulcidae), *Cratoenigma articulata* (unassigned to family), and an unnamed species of Siricidae (Darling & Sharkey 1990; Martins-Neto *et al*. 2007; Osten 2007; Jattiot *et al*. 2011; Krogmann & Nel 2012).

Material and methods

The fossil specimen described here is deposited in the Fossil Insect Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, USA. Morphological terminology follows that of Goulet & Huber (1993). Images of the fossil were taken with a Leica DFC490 digital camera attached to a Leica Z16 APO microscope, and processed for focus stacking with Leica Application Suite 3.8.0 software. The antennae of males of the Recent species *Monoctenus juniperi* (L.) and *Macrodiprion nemoralis* (Enslin) were studied and photographed under a Zeiss Evo LS 15 SEM. Uncoated specimens were used which are deposited in the insect collection of the State Museum of Natural History, Stuttgart, Germany. All images

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were edited with Adobe Photoshop CS3 and figure plates assembled with Adobe Illustrator CS3.

Systematic palaeontology

Superfamily **Tenthredinoidea** *s. str.* Latreille, 1802
Family **Incertae sedis**

Genus ***Atefia*** gen. nov.

Type species. *Atefia rasnitsyni* sp. nov.

Diagnosis. As for type species.

Etymology. The new genus-group name is derived from Atef, the crown of the Egyptian Deity Osiris, which is flanked by two ostrich feathers. These feathers resemble the shape of the biflabellate antennae of the new fossil (Fig. 1B). The name is feminine.

Atefia rasnitsyni sp. nov.
(Figs 1, 2)

Holotype. Male (Figs. 1, 2), deposited in the Fossil Insect Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, USA.

Diagnosis. Male with biflabellate antennae and 40(?) antennomeres; antennae elongate, 0.7 times as long as body; tarsi distinctly elongate, metatarsus 1.4 times as long as metatibia.

Type locality. Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Type horizon. Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation (Martill 2007).

Etymology. The specific epithet is a patronym honouring Prof. Alexandr P. Rasnitsyn (Paleontological Institute, Russian Academy of Sciences, Moscow, Russia), in recognition of his numerous contributions to palaeoentomology that have greatly expanded our understanding of hymenopteran evolution.

Description. Male, total body length 9.1 mm. **Head.** Head preserved in ventral aspect, length 1.7 mm, width 2.7 mm; compound eyes as seen from ventral large, length 1.4 mm, width 0.8 mm; slender apices of incurved mandibles discernible; antennal length ∼6.5 mm, with 40(?) antennomeres, antennae biflabellate, flabellar processes long and slender, each pair of flabellar processes equal in length (Fig. 1B). **Thorax.** Thoracic sclerites not well preserved, ventral portion completely lost, pro- and mesonotum visible from inner surfaces but boundaries obscured; pronotum apparently very short, as indicated by forewing attachment; metanotum short, length about 0.3 mm, width 1.6 mm. **Legs** (Fig. 1D). Forelegs preserved only by fragments; right midleg missing, left mesotibia partly preserved, mesotibial spurs about equal in length, 0.13 times as long as mesobasitarsus; mesotarsus distinctly elongate, length 4.8 mm, length of mesotarsomeres 1.9, 0.9, 0.7, 0.5 and 0.6 mm; metatibial length 3.1 mm, metatibial spurs about equal in length, 0.23 times as long as metabasitarsus; metatarsus distinctly elongate, length 4.2 mm, 1.4 times as long as metatibia; length of metatarsomeres 1.9, 0.8, 0.6, 0.5 and 0.5 mm. **Wings** (Figs 1C, 2). Forewing length 11.6 mm, width 3.1 mm; pterostigma dark, rather broad but exact dimensions not discernible as preserved; costal margin thickened(?), remainder of forewing venation not preserved, only traces of wing folds visible; hind wing scarcely discernible, length probably 7.8 mm, width 2.3 mm; no venational details preserved. **Abdomen.** Abdominal length 5.1 mm, maximum width 2.4 mm; inner surface of eight abdominal terga (T) visible, with the following median lengths: T1 0.6 mm, T2 0.3 mm, T3 0.5 mm, T4 0.6 mm, T5 0.7 mm, T6 0.8 mm, T7 0.9 mm, T8 0.8 mm; male genitalia not visible but sex clearly indicated by the slender metasoma, its blunt apex and the absence of any ovipositor structures.

Discussion

Flabellate antennae in Tenthredinoidea

The flabellate antennae in *Atefia rasnitsyni* represent a character state that is of scattered occurrence within the basal grade of hymenopteran families, i.e. the ‘Symphyta’. Uniflabellate antennae are restricted to males of some Megalodontesidae, where the flabellar processes are always broadly flattened (pers. obs.), to the genus *Cladius* (Tenthredinidae; Smith 1974), some Pergidae (Pterygophorinae), and to all members of the subfamily Monocteninae (Diprionidae) (Benson 1939, 1954; see Fig. 3A). Biflabellate antennae, such as in *A. rasnitsyni*, are present in males of *Cladiucha* (Tenthredinidae; Xiao 1994), some genera of Pergidae (within the subfamilies Perreyiinae, Styracotechyinae and Syzygoniinae) (Smith 1990; Schmidt & Smith 2006), and in all members of the diprionid subfamily Diprioninae (Benson 1939, 1946; see Fig. 3B).

Atefia rasnitsyni is characterized by a very high number of antennomeres (40?), a character state that comes closest to the condition found in the sawfly family Diprionidae. According to Schedl (1991), Diprionidae is characterized by having 14–32 antennomeres, which he regarded as a “very ancestral” condition. In contrast to Schedl (1991), Schulmeister (2003, p. 258) regarded the high number of antennomeres (i.e. “the antennae being divided into more than 15 segments”) as apomorphic for Dipri-

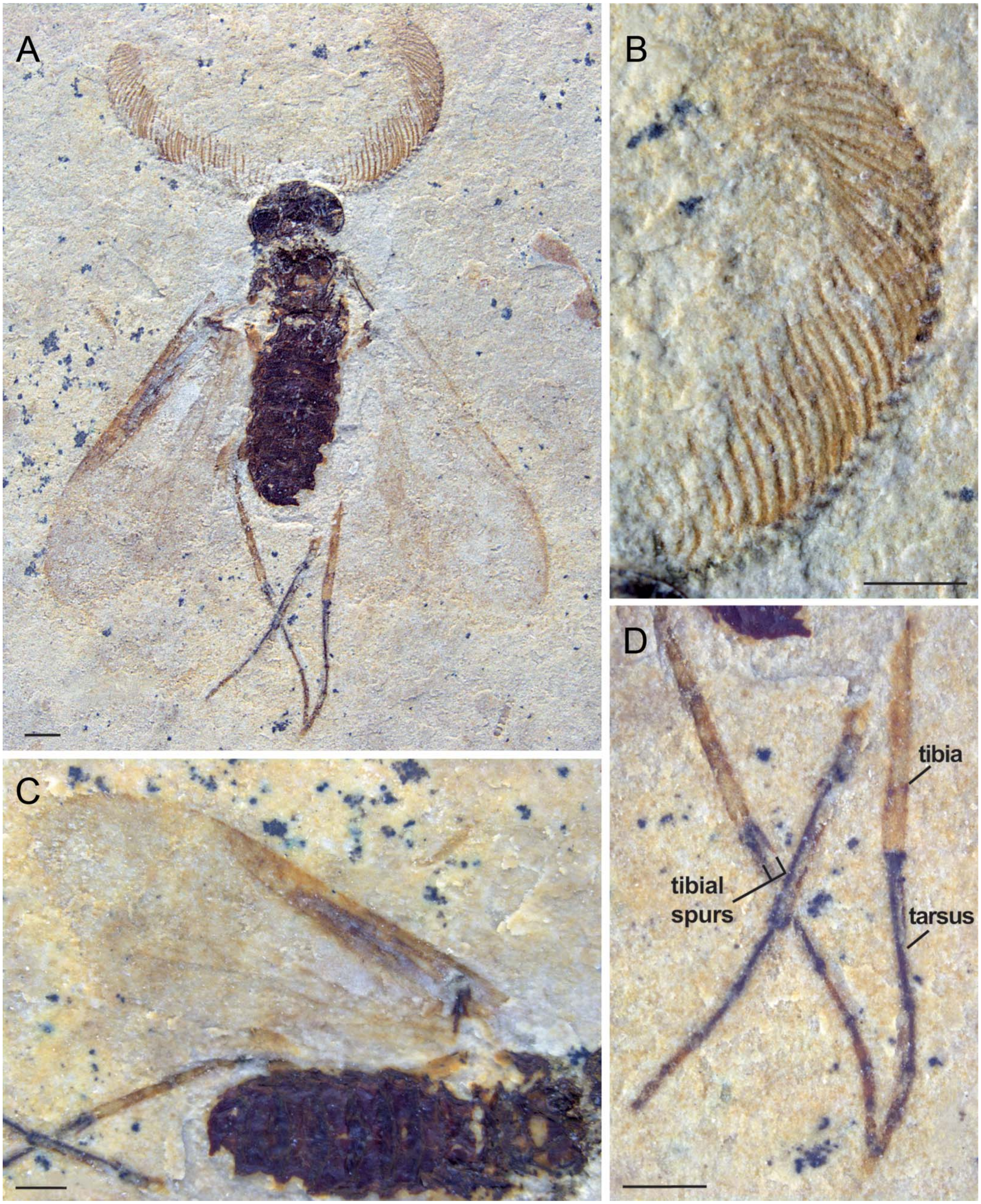

Figure 1. Holotype male of *Atefia rasnitsyni* gen. et sp. nov., ventral view (scale bars = 1 mm); **A,** habitus; **B,** left antenna; **C,** right forewing and hind wing; **D,** left midleg and hind legs.

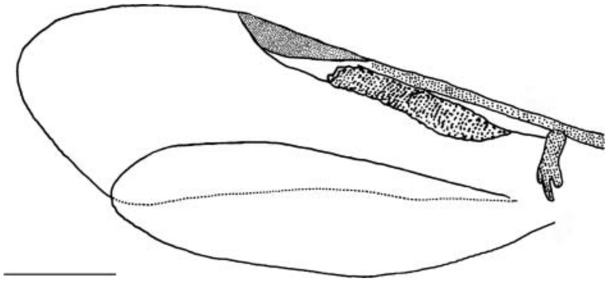

Figure 2. Drawing of the holotype male of *Atefia rasnitsyni* gen. et sp. nov., right forewing and hind wing as preserved, ventral view (scale bar = 2 mm).

onidae. However, a high number of antennomeres is not restricted to Diprionidae but also occurs in some Pergidae (∼6–26 antennomeres) and Tenthredinidae (∼7–27 antennomeres) (D. R. Smith pers. comm.). In fact, the number of antennomeres varies so significantly within Tenthredinoidea, even within genera, that this character seems unsuitable for determining familial placement of the fossil in the absence of other corroborating traits. Furthermore, there is no phylogeny available for the families of Tenthredinoidea such that the polarity of this character remains speculative.

In summary, flabellate antennae can only be found in those families of Tenthredinoidea in which a high number of antennomeres occur, i.e. Tenthredinidae, Pergidae and Diprionidae. In most cases the presence of flabellate antennae is directly correlated with an increased number of antennomeres, which undoubtedly enhances the overall function of the antennae as receptor organs for olfactory signals, i.e. female sex pheromones (see below). Diprionidae as a whole are characterized by a higher number of antennomeres and here all males have flabellate antennae. In Tenthredinidae most species are characterized by ∼8–11 antennomeres, while males of the exceptional species *Cladius pectini-*

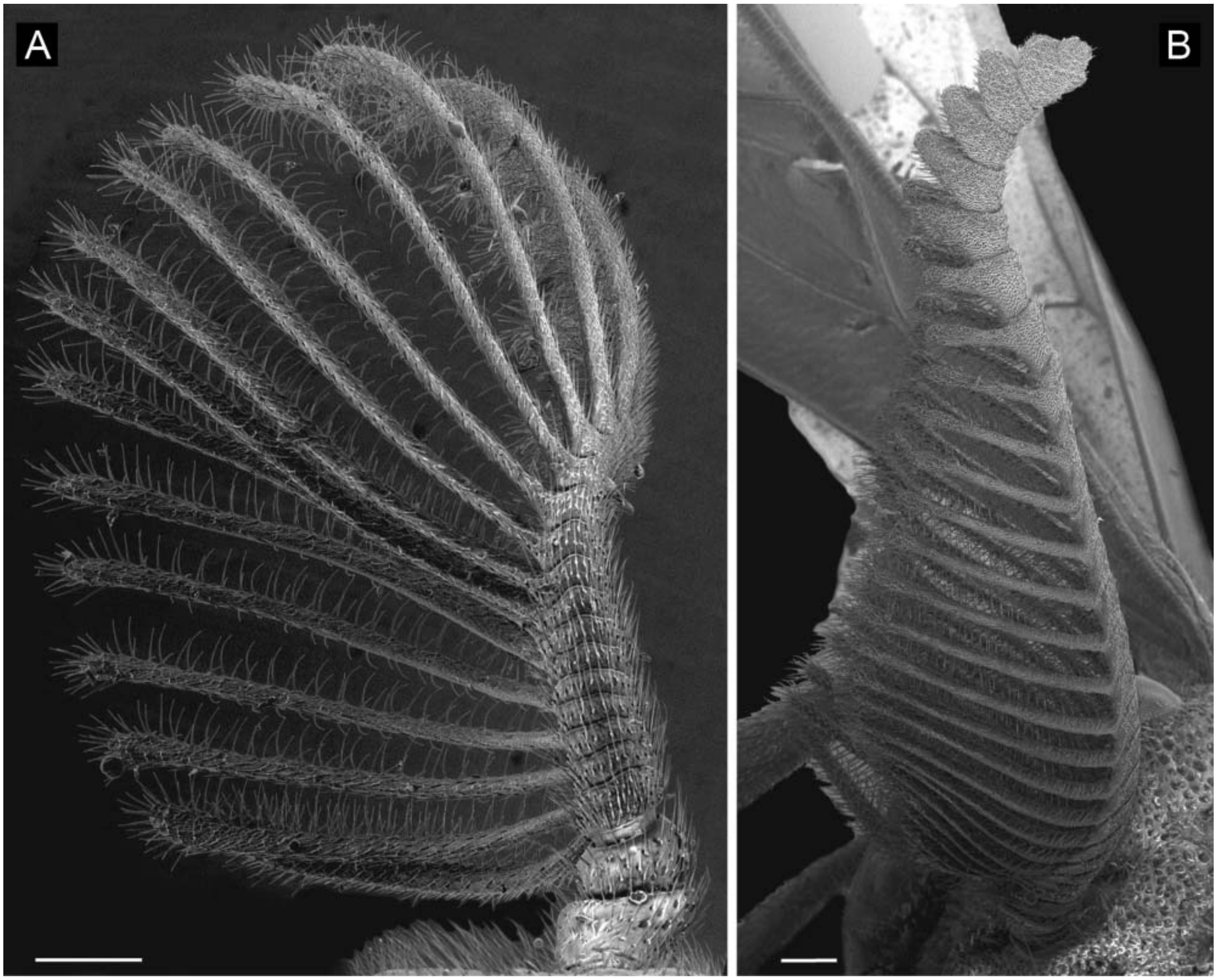

Figure 3. Male antennae in Diprionidae (scale bars = 200 μm). **A,** *Monoctenus juniperi* (L.), dorsal view; **B,** *Macrodiprion nemoralis* (Enslin), dorsolateral view.

cornis are characterized by 27 antennomeres and flabellate antennae. The same pattern can be found in Pergidae, where the genera in which flabellate antennae occur are characterized by relatively high numbers of antennomeres (e.g. *Perreyia* 10–20, *Perreyiella* 15–24, *Cladomacra* 18; D. R. Smith pers. comm.).

As the internal phylogenies of the families of Tenthredinoidea similarly are unresolved, the polarity of the flabellate antennal condition cannot be determined. It is also unclear whether uniflabellate antennae are derived from the biflabellate condition, or vice versa. It is similarly possible that they are derived independently from ancestrally unmodified antennae. This is not likely to be the case at least within Diprionidae, the only sawfly family in which males are exclusively characterized by flabellate antennae. Here, one subfamily (Monocteninae) is characterized by uniflabellate antennae (Fig. 3A) and the other subfamily (Diprioninae) by biflabellate antennae (Fig. 3B). It is most parsimonious to consider that uni- or biflabellate antennae represent the groundplan condition of Diprionidae. A different situation can be observed in Pergidae. Here, the most parsimonious explanation for the scattered occurrence of uni- and biflabellate antennae is that these character states are secondarily derived within the family and neither represents the groundplan condition of Pergidae. To our knowledge, the occurrence of flabellate antennae in Tenthredinidae is restricted to the genera *Cladius* (uniflabellate) and *Cladiucha* (biflabellate) (Smith 1974; Xiao 1994), and it is most likely that these features evolved secondarily and independently from each other. The antennal morphology of *Cladius pectinicornis* (= *C. difformis*) greatly differs from the condition found in the fossil because it is uniflabellate, the antennomeres are reduced to nine, and only the first three flagellomeres bear the flabellate processes (Smith 1974, fig. 2). In *Cladiucha* the flabellar processes are short (Xiao 1994), which differs from the condition found in *A. rasnitsyni*.

Functional morphology and significance

The flabellar processes on the antennae of male Hymenoptera have evolved as crucial elements in mate finding over long distances (see Schmidt *et al*. 2006). The flabellar processes carry olfactory receptor neurons which help the male to identify sex pheromones released as attractants from its female counterpart (Bergström *et al*. 1995). However, it seems puzzling that within Pergidae (e.g. within Pterygophorinae) there are a few taxa in which females have also evolved short flabellar processes. In female pergids the antennae obviously have a different function which may include locating of potential host plants (S. Schmidt pers. comm.). A putative function of the antennal chemoreceptors in host locating has already been suggested by Crook *et al*. (2008) for female Siricidae.

The sensory function and efficiency of the antennae can be enhanced by increasing the total number of olfactory receptor neurons on the flabellar processes. In principle, this can be achieved by: (1) elongation of the individual flabellar processes (especially distinct in *Cladomacra*); (2) doubling of antennal processes on each individual flagellomere (in all biflabellate species, see Fig. 3B); or (3) increase in antennomeres (in the majority of flabellate species, *vide supra* and Fig. 3A, B). Recent flabellate Tenthredinoidea (*s. str*.) species display at least one of the above features. In Pergidae, there is a qualitative similarity between the antennal sensilla across the sexes, but males possess more than females, which results from the larger surface of the flabellate male antennae (Schmidt *et al*. 2006). Despite the similarity in shape of the flabellate male antennae in Diprionidae and Pergidae, the sensilla in Pergidae differ from those in Diprionidae (Hallberg 1979; Schmidt *et al*. 2006), which demonstrates that the presence of flabellate antennae clearly is a convergence between these wasp families.

In *A. rasnitsyni* all three features have been combined into a highly modified sensory organ which represents the first fossil record of a biflabellate antenna in the Hymenoptera. The fossil indicates that long-distance mating behaviour was already well established in the Early Cretaceous (~92–108 Ma). The only other known hymenopteran fossil with flabellate antennae is a male of *Eodiprion* sp. (Diprionidae; Schedl 2008), which is characterized by uniflabellate antennae (pers. obs.) and dates from the Middle Eocene (38–54 Ma).

Phylogenetic placement of *Atefia*

The high number of antennomeres and the biflabellate antennae in *Atefia rasnitsyni* do not unequivocally place this fossil into any of the Recent families of Tenthredinoidea (*vide supra*). The antennae of *A. rasnitsyni* differs from Recent Diprionidae in being distinctly elongate (0.7 times as long as the body) and slender. Long and slender antennae can be found in Recent *Cladomacra* species (Pergidae: Perreyiinae), where the antennal length can surpass even the body length, but these species are characterized by uniflabellate antennae (Smith 1980). In *Perreyiella* males, however, the antennae are biflabellate and also long and slender (~0.5 times body length) (D. R. Smith pers. comm.), resembling the condition found in *A. rasnitsyni*.

Atefia rasnitsyni is characterized by elongate tarsomeres as well as a possibly thickened costal margin of the forewing (Fig. 2). Recent Diprionidae have relatively short tarsomeres and a thin costal margin. In Recent Pergidae the costal margin of the forewing resembles the condition possibly found in *A. rasnitsyni* and the tarsi of pergids also are enlarged, but in Pergidae it is only the basitarsus that is distinctly elongate, a condition that differs from that of the present fossil.

From a biogeographical perspective the existence of fossil Diprionidae in the Crato Formation may seem less likely than the existence of fossil Pergidae. In the Western Hemisphere Recent diprionids are distributed mainly throughout the Nearctic and do not extend beyond the northern Neotropical region (e.g. Nicaragua and Cuba), while pergids occur in the Western Hemisphere and Australasia and show the largest species radiation in the Neotropics (Schmidt & Smith 2006). However, the sawfly family Siricidae is today also absent from South America and mainly restricted to the Nearctic, with a single species recorded from Cuba (Morgan 1968), while it is recorded from the Crato Formation and the Cenozoic of Argentina (Fidalgo & Smith 1987; Martill *et al*. 2007). The same situation can be found in the insect order Raphidioptera, which is recorded from the Crato Formation (Jepson *et al*. 2011) but is absent from the Recent Neotropical region.

In summary the current biogeographical and morphological evidence does not allow a conclusive placement of *A. rasnitsyni* into any of the Recent tenthredinoid families, even though there are a number of morphological features that are shared with Pergidae and to a lesser extent with Diprionidae. However, these shared similarities do not necessarily indicate a close relationship (Hennig 1966), and familial assignment must wait until definitive synapomorphies can be identified. It is hoped that more fossils of *Atefia* will become available in the future and that these will allow for a consideration of its wing venation. This information would conclusively place *Atefia* into Pergidae or another Recent family, or perhaps recognize it as a hitherto unknown extinct lineage of Tenthredinoidea.

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