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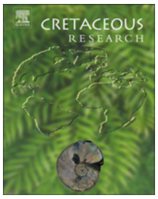

Review paper

Hymenoptera in Canadian Cretaceous amber (Insecta)

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ABSTRACT

An overview of the hymenopteran (sawflies, wasps, ants, and bees) taxa known from Canadian Late Cretaceous (Campanian) amber is presented. These taxa are discussed in the context of hymenopteran phylogeny and the fossil assemblages within other well-known Cretaceous ambers. This provides some insight into the taxa present in the region subsequent to the Mesozoic diversification of the order, and just prior to the Cretaceous-Tertiary extinction event. Fossil records of Hymenoptera within Canadian amber are revised, and future work and expectations for hymenopterans within the deposit are also outlined.

1. Introduction

The Hymenoptera are a hyperdiverse insect order consisting of approximately 145,000 described species, with an estimated 0.5 to 1.2 million modern species (Gaston, 1991; Grimaldi and Engel, 2005; Huber, 2009). Some consider that Hymenoptera may rival Coleoptera as the most diverse insect order if undescribed species are included (Grissell, 1999; Sharkey, 2007; Huber, 2009). The order is commonly known for its social members, such as some wasps or bees, the latter of which are important pollinators (Michener, 2007); or ants, which constitute a sizeable part of terrestrial biomass (Hölldobler and Wilson, 1990). However, these taxa constitute only a fraction of total hymenopteran diversity. The vast majority of hymenopterans are actually parasitoids: internal or external parasites that kill their hosts (Quicke, 1997; Grimaldi and Engel, 2005; Huber, 2009). Parasitoids are key members of many ecosystems and often limit populations of other insects groups (LaSalle and Gauld, 1993). Because of their host selectivity, they are employed extensively as biological control agents for pest management. Although stinging hymenoptera (Aculeata) and agricultural pests, such as sawflies (symphytans), are conspicuous members of modern ecosystems and are familiar to most people, the parasitic Hymenoptera, not surprisingly, comprise the majority of Cretaceous fossils for the order, and are the main focus of this review.

The relationships between Hymenoptera and other holometabolous insect orders, as well as the arrangement and composition of many of the taxa within the Hymenoptera are somewhat unresolved. Sharkey (2007) and Heraty et al. (2011) have recently provided reviews of hymenopteran phylogeny, so little additional detail remains to be presented here. Although there is strong support for the monophyly of the order (e.g., Vilhelmsen, 1997, 2001; Grimaldi and Engel, 2005; Sharkey, 2007), many internal relationships are disputed, so we have adhered to a relatively conservative taxonomy (Table 1). Historically, the order has been divided into the grades 'Symphyta' (sawflies, wood wasps, and orussids), and 'Parasitica' (the numerous parasitoid lineages within the Apocrita), leading to the Aculeata (ants, bees, and wasps).

Symphytans are almost unknown from Mesozoic amber, with the exception of a single member of Anaxyelidae from Early Cretaceous Spanish amber (Ortega-Blanco et al., 2008) and isolated orussid specimens from Late Cretaceous Siberian and New Jersey amber (Vilhelmsen, 2004). Therefore, the portions of the hymenopteran phylogeny most pertinent to our discussion are within the suborder Apocrita, and to a limited extent, the parvorder Aculeata. The composition of the Canadian amber hymenopteran assemblage is presented in this context, with a strong focus on the non-aculeate Apocrita, and with superfamilies forming the major units for most of the discussion. Relationships

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Table 1
Classification and list of extant families of Hymenoptera (adapted from Huber, 2009).

- **ARCHIHYMENOPTERA**
    - **Infraorder Xyelomorpha**
        - **Superfamily Xyeloidea**
            - Xyelidae
- **NEOHYMENOPTERA**
    - **Infraorder Tenthredinomorpha**
        - **Superfamily Pamphiloidea**
            - Megalodontesidae
            - Pamphiliidae
        - **Superfamily Tenthredinoidea**
            - Argidae
            - Blasticotomidae
            - Cimbicidae
            - Diprionidae
            - Pergidae
            - Tenthredinidae
    - **Infraorder Cephomorpha**
        - **Superfamily Cephoidea**
            - Cephidae
    - **Infraorder Siricomorpha**
        - **Superfamily Siricoidea**
            - Siricidae
            - Anaxyelidae
    - **Infraorder Xiphydriomorpha**
        - **Superfamily Xiphydrioidea**
            - Xiphydriidae
  - **Euhymenoptera**
    - **Infraorder Orussomorpha**
        - **Superfamily Orussoidea**
            - Orussidae
  - **Suborder Apocrita**
    - **Infraorder Stephanomorpha**
        - **Superfamily Stephanoidea**
            - Stephanidae
    - **Infraorder Evaniomorpha**
        - **Superfamily Trigonalyoidea**
            - Trigonalyidae
        - **Superfamily Megalyroidea**
            - Megalyridae
        - **Superfamily Ceraphronoidea**
            - Megaspilidae
            - Ceraphronidae
        - **Superfamily Evanioidea**
            - Aulacidae
            - Gasteruptiidae
            - Evaniidae
    - **Infraorder Vespomorpha**
        - **Superfamily Ichneumonoidea**
            - Braconidae
            - Ichneumonidae
    - **Parvorder Aculeata**
        - **Superfamily Chrysidoidea**
            - Plumariidae
            - Scolebythidae
            - Sclerogibbidae
            - Dryinidae
            - Embolemidae
            - Bethylidae
            - Rotoitidae
            - Encyrtidae
            - Eucharitidae
            - Agaonidae
            - Perilampidae
            - Ormyridae
            - Chrysididae
        - **Superfamily Vespoidea**
            - Sierolomorphidae
            - Tiphiidae
            - Pompilidae
            - Mutillidae
            - Sapygidae
            - Rhopalosomatidae
            - Bradynobaenidae
            - Formicidae
            - Scoliidae
            - Vespidae
        - **Superfamily Apoidea**
            - Heterogynaidae
            - Ampulicidae
            - Sphecidae
            - Crabronidae
            - Colletidae
            - Halictidae
            - Andrenidae
            - Melittidae
            - Megachilidae
            - Apidae
    - **Infraorder Proctotrupomorpha**
        - **Superfamily Proctotrupoidea**
            - Proctotrupidae
            - Vanhorniidae
            - Roproniidae
            - Austroniidae
            - Peradeniidae
            - Heloridae
            - Pelecinidae
            - Proctorenyxidae
        - **Superfamily Diaprioidea**
            - Monomachidae
            - Diapriidae
            - Maamingidae
        - **Superfamily Cynipoidea**
            - Austrocynipidae
            - Ibaliidae
            - Liopteridae
            - Figitidae
            - Cynipidae
        - **Superfamily Platygastroidea**
            - Nixoniidae
            - Sparasionidae
            - Scelionidae
            - Platygastridae
        - **Superfamily Mymarommatoidea**
            - Mymarommatidae
        - **Superfamily Chalcidoidea**
            - Mymaridae
            - Trichogrammatidae
            - Aphelinidae
            - Signiphoridae
            - Eulophidae
            - Tanaostigmatidae
            - Eupelmidae
            - Torymidae
            - Tetracampidae
            - Eurytomidae
            - Pteromalidae
            - Leucospidae
            - Chalcididae

among the apocritan superfamilies are highly unstable, with the most recent reviews and syntheses (e.g., Sharkey, 2007; Vilhelmsen et al., 2010a; Heraty et al., 2011) still suggesting a largely unresolved or weakly supported topology. We have adopted a relatively conservative outline of proposed superfamily relationships because of this uncertainty (Fig. 1). Finer details regarding the placement and monophyly of each of the families or superfamilies discussed are presented within their respective sections (3.1–3.11).

1.1. Canadian amber perspective on the Hymenoptera

The high diversity and wide range of biology that characterizes modern Hymenoptera appears to have been largely established by the Cretaceous, when the insect-bearing amber deposits first became abundant, and the fossil record of insects was greatly improved (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). Within Canadian amber, the hymenopteran assemblage is composed almost exclusively of parasitoids. These taxa offer insights into the antiquity of parasitoid associations, through comparison to modern relatives with known biology. Additionally, the obligate parasitoid-host relationships of many of these taxa also provide evidence for the presence of other groups within the Cretaceous amber-producing forest, even though these host groups may not be preserved, or have yet to be recovered as inclusions themselves. The reliance of parasitoids on specific hosts may also make them viable as ecological indicators, but this aspect of their ecology remains largely inaccessible in Mesozoic ambers owing to partial representation and the limited study of each assemblage.

Canadian amber offers a unique window on the evolution of the Hymenoptera. This deposit constitutes the last known diverse insect assemblage in the Mesozoic (Grimaldi and Engel, 2005). Its proximity to the end-Cretaceous extinction event makes the deposit an important point for comparisons across the event, as well as to previous assemblages within the Mesozoic. It helps to refine our understanding of the impacts Late Cretaceous and early Tertiary events had on insects, while at the same time establishing the cast of taxa for later developments. Capturing Late Cretaceous diversity is particularly important for Hymenoptera because the group appears to have undergone two major adaptive radiations, one in the Mesozoic (e.g., Rasnitsyn, 2002; Grimaldi and Engel, 2005), followed by the rise of its social members in the Tertiary (e.g., Grimaldi and Agosti, 2000; Engel, 2001). Canadian amber provides a glimpse of the order during the latter part of its Mesozoic radiation (alongside the rise of angiosperms), and indicates which extinct groups were still present near the end of the era. Interestingly, Mesozoic representatives of ‘parasitica’ display some family-level extinctions across the end-Cretaceous boundary. Although the end-Cretaceous extinction is considered to have had little effect on insects (e.g., Labandeira and Sepkoski, 1993; Rasnitsyn, 2002; Grimaldi and Engel, 2005), the loss of some hymenopteran families coupled with a reduction in the diversity of others, suggests that there may be perceptible ecological effects around this time. An improved understanding of the biology of the affected groups (through their modern relatives and amber syninclusions) may provide insights into terrestrial changes associated with this time interval.

There are a number of caveats for the study of Canadian amber that should be considered throughout this work. It should be noted that the record provided from amber is generally biased towards small taxa and those that live within the amber-producing forest or utilize the resin, and may be affected by such factors as temperature fluctuations or other controls on the production and viscosity of resin (e.g., Pike, 1995; Zherikhin, 2002; Martínez-Delclòs et al., 2004). In the case of Canadian amber, the record is strongly biased toward smaller insects, with collected amber pieces typically displaying a length of less than 1 cm and rarely reaching 3.5 cm in length (Pike, 1995; McKellar et al., 2008). Furthermore, Canadian amber does not appear to have been exposed to long distance transport prior to burial, so it may