An Early Eocene bee (Hymenoptera: Halictidae) from Quilchena, British Columbia

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Abstract—A fossil halictine bee from Early Eocene, Okanagan Highlands deposits of Quilchena, British Columbia, Canada, is described and figured. *Halictus*? *savenyei* **sp.nov.** is distinguished from other Tertiary halictines as well as modern bees. The specimen is the second oldest body fossil of a bee yet discovered and the first fossil bee from Canada. The antiquity of Halictidae and of bees in general is briefly commented upon.

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Résumé—On trouvera ici la description illustrée d'une abeille halictinée fossile de l'Éocène inférieur provenant des sédiments des Hautes Terres d'Okanagan à Quilchena, Colombie-Britannique, Canada. *Halictus*? *savenyei* **sp.nov.** se distingue des autres Halictinae du Tertiaire et des abeilles modernes. Il s'agit là du deuxième plus vieux fossile du corps d'une abeille jamais trouvé et le premier fossile d'une abeille découvert au Canada. L'ancienneté des Halictidae et des abeilles en général fait l'objet d'un bref commentaire.

[Traduit par la Rédaction]

Introduction

The fossil history of bees has commanded greater focus during the past decade than it has since the work of the late Theodore Cockerell at the beginning of the last century (*e.g.*, Cockerell 1906, 1911). As a result, significant advances have been made toward a general geological history of Apoidea and this increased precision in historical facts may then be incorporated into phylogenetic studies (*e.g.*, Camargo *et al.* 2000; Engel 2000, 2001*a*, 2001*b*, 2003). Most fossil bees have been discovered in isolation (only a single or a few specimens comprise most collections) in deposits scattered worldwide through the Cenozoic. Presently the earliest records of bees are a series of fossil nests from the Cenomanian of North America that are attributed to the family Halictidae (Elliott and Nations 1998) and a body fossil in amber from the Maastrichtian of New Jersey that represents a derived lineage in the family Apidae (Michener and Grimaldi 1988; Engel 2000). Three deposits in particular have yielded considerable apoid paleofaunas: Middle Eocene (Lutetian) Baltic amber (Engel 2001*b*); Late Eocene (latest Priabonian near the boundary with the Oligocene; see Evanoff *et al.* 2001) shale of Florissant, Colorado (Zeuner and Manning 1976; Engel 2001*c*, 2002); and Early

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Miocene amber-bearing mines in the Dominican Republic (reviewed in Engel 1999, 2001*b*).

Herein we report the third oldest record of the bees (second oldest definitive bee record if the Cenomanian nests are erroneously assigned). The specimen is a compression fossil of a female in shale from Early Eocene (Ypresian) strata in British Columbia, Canada. It is a member of the derived halictid subfamily Halictinae, slightly older (approximately 7–10 Ma) than the only other Eocene halictine, *Electrolictus antiquus* Engel, from Middle Eocene (Lutetian) Baltic amber. Morphological terminology follows that of Engel (2001*b*).

Stratigraphy

The Quilchena site is a small road-cut exposure of the "Coldwater beds" in one of several depositional basins in the Merritt region of south-central British Columbia (Cockfield 1948). Regional tectonic uplift beginning in the Early Eocene (about 53 Ma) created a scattered series of grabbens that filled with mudstone, sandstone, coal, and ash from associated volcanism (Ewing 1981). This region, called the "Okanagan Highlands," stretches over approximately 1000 km from Republic, Washington, to Driftwood Canyon, British Columbia, and bears richly fossiliferous (fish, insects, plants, and other biota) lacustrine shales. U–Pb dating of zircons suggests that Quilchena may be the oldest of the known Okanagan Highland sites (RW Mathewes and M Villeneueve, personal communication; cited in Archibald and Mathewes 2000). The sediment at Quilchena ranges from thinly splitting fine-grained shale (as in the matrix of the present fossil), interpreted as offshore facies, to more massive and sandy nearshore facies (Guthrie 1995).

Materials and methods

The fossil, part and counterpart, is on two small chips of shale recovered by hand prospecting. Minor preparation with pins and with light, sharpened probes, was done at Simon Fraser University. Distilled water was, at times, applied to clarify detail. Drawings were done with a camera lucida.

Systematic paleontology

Halictus? *savenyei* sp.nov.

(Figs. 1–4)

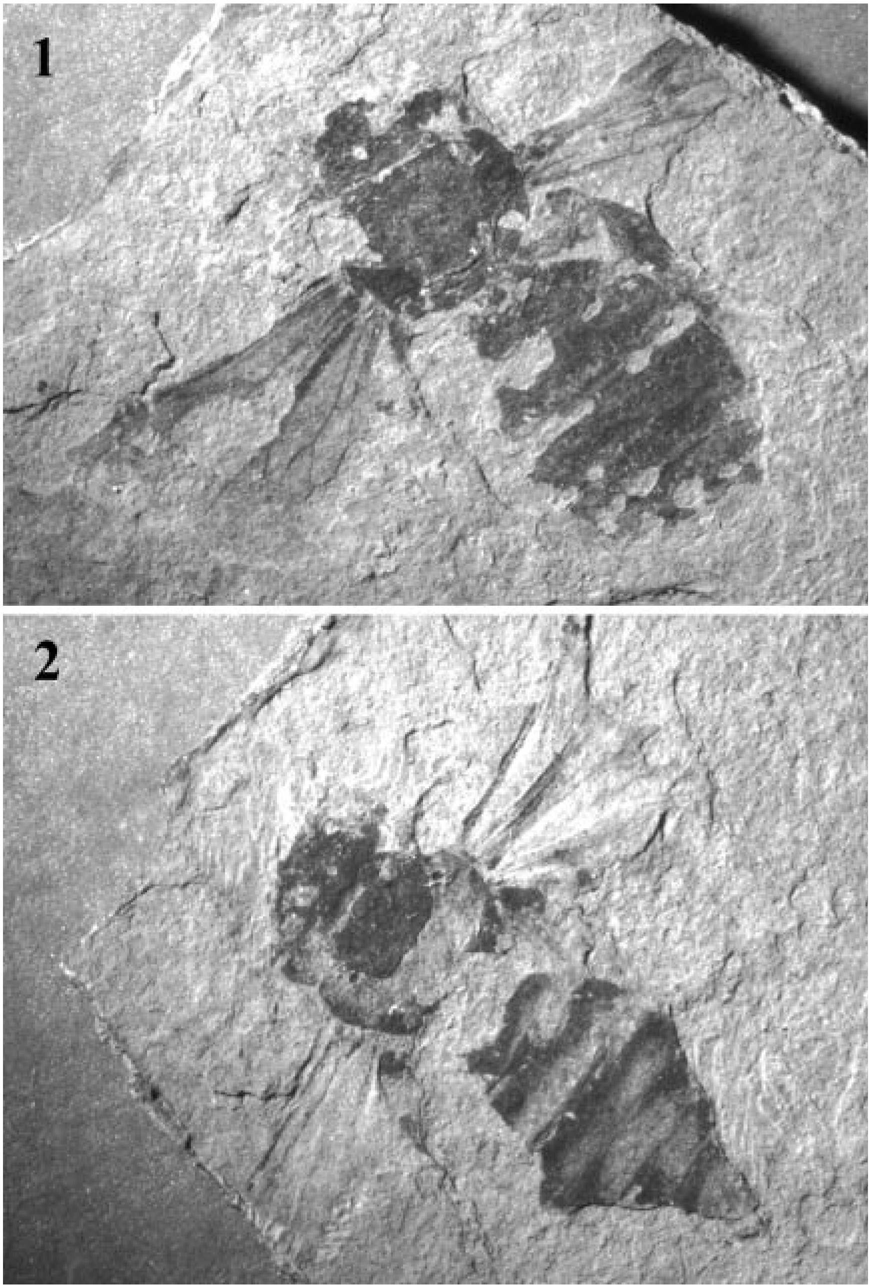
Halictidae sp.; Archibald and Mathewes 2000: 1453.

Type material

Holotype: Q-0424a&b [part and counterpart], female: **CANADA. British Columbia:** Quilchena: Okanagan Highlands, Coldwater beds of the Princeton Group (Read 2000); Early Eocene (52–54.5 Ma); Rene Savenye collector. Labelled "HOLOTYPE: *Halictus*? *savenyei* Engel & Archibald." Deposited in the fossil collection of Simon Fraser University, Burnaby, British Columbia, Canada.

Etymology

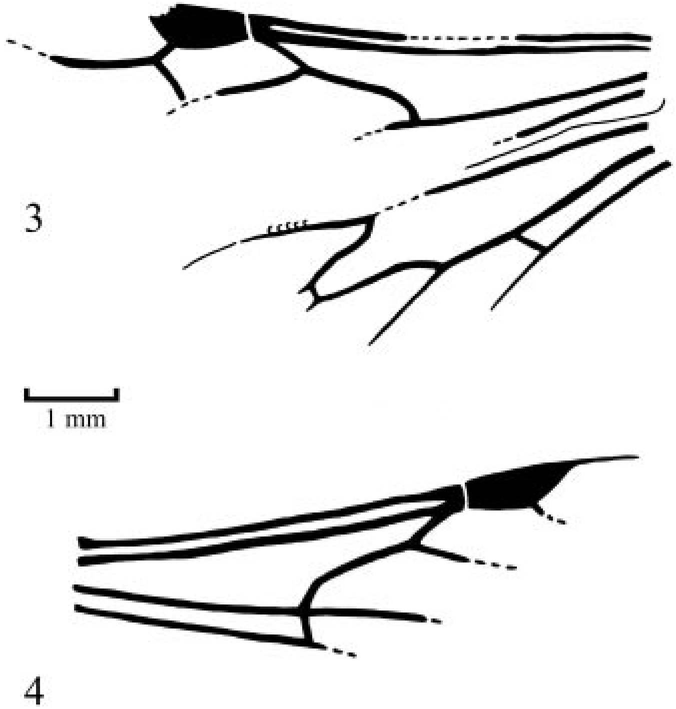
The specific epithet is a patronymic honouring the late Rene Savenye, who collected and generously donated the specimen to Simon Fraser University.



Figures 1–2. Photomicrographs of holotype female of *Halictus*? *savenyei* sp.nov.: 1, part (Q-0424a); 2, counterpart (Q-0424b).

Diagnosis

Although the apex of the metasoma is poorly preserved, the weak indication of a short pygidial plate on the fifth metasomal tergum bordered by setae is diagnostic of Halictinae. Among halictines, the absence of a medial cleft in the fifth tergum is further



FIGURES 3–4. Line illustrations of preserved wing venation of *Halictus*? *savenyei* sp.nov.: 3, forewing and hind wing of part (Q-0424a) as preserved; 4, forewing of counterpart (Q-0424b) as preserved.

indicative of the Halictini. The presence of apical bands of tomentum or minute plumose setae is indicative of the genus *Halictus* and can immediately distinguish the fossil from other Tertiary, North American halictines (*i.e.*, those from Florissant, which lack setal bands on the metasoma; Engel 2002). Although some African halictines also have apical bands (*e.g.*, some subgenera of *Patellapis*; see Michener 2000), these all have broad pallid translucent tergal margins, features not present in the genus *Halictus* and clearly not present in the fossil. Thus the suite of characters indicate a placement in the genus *Halictus*; however, this is done here with some hesitation, owing to the absence of information regarding the clypeal and genitalic structure of males, which are features rarely preserved in compression fossils and are particularly important for determination within the Halictini. Furthermore, the pterostigma is somewhat small for many halictines. If indeed the specimen is a true *Halictus*, as we strongly suspect, then this is the oldest record of the genus. Hopefully the discovery of additional material will refine our understanding of this ancient bee.

Description

Total body length approximately 7.4 mm as preserved (owing to possible postmortem factors, such as swelling from bacterial action, disarticulation, incompletely preserved margins, or suboptimal position of structures, this measure should be considered approximate); forewing length (preserved) approximately 4.8 mm. Integument preserved as dark brown [description of colouration is as preserved; fossil insects from the Okanagan Highlands tend to have colour patterns (value, or relative lightness) preserved, not original colour (hue, or particular wavelength); all colours are diagenetically altered to values of brown, from off-white to practically black; therefore description of colouration is useful between fossils or when comparing with hueless values of extant insects]; setae (where preserved) black; tomentum [observable on counterpart, *i.e.*, Q-0424b (Fig. 2)] pale brown to off-white; dark brown fimbrial setae weakly observable on part [*i.e.*, Q-0424a (Fig. 1)]. Head slightly narrower than mesosoma; median ocellus separated from posterior border of vertex by twice ocellar diameter. Basal area of propodeum approximately one-half length of scutellum and only slightly longer than length of metanotum. Metafemur, metatibia, and metabasitarsus with dense scopa. First metasomal tergum broader than long; tomentum present apically on terga 1–5; weak divided fimbria present on tergum 5 [visible in part, *i.e.*, Q-0424a (Fig. 1)]; tergum 6 without tomentum. Basal vein confluent with cu-a [observable in right forewing on part, *i.e.*, Q-0424a (Fig. 1)]; basal vein strongly arcuate near stem of M + Cu, then straight until meeting Rs (Figs. 3, 4); prestigma short, wider than long; margin of pterostigma inside of marginal cell weakly convex; r-rs originating slightly distad pterostigmal midpoint; wing veins dark brown to black; wing membrane fuscous, infuscation darkest near Sc + R and C of forewing and costal area in hind wing, membrane with scattered setae [observable on counterpart, *i.e.*, Q-0424b (Fig. 2)]; five, evenly spaced distal hamuli visible along leading edge of hind wing [observable in left hind wing of part, *i.e.*, Q-0424a (Fig. 1)].

Discussion

The significance of the present specimen is immediately evident. Not only is this bee the first Tertiary fossil of Apoidea from Canada but it is currently the second oldest bee described. *Halictus*? *savenyei* is also the oldest body fossil of any halictid lineage presently known, being slightly older (perhaps 7–10 Ma) than *Electrolictus* from Europe. The bee family Halictidae comprises three subfamilies of which only the most derived (Michener 2000; Engel 2001*b*) is presently known from the fossil record, *i.e.*, the Halictinae. Halictine fossils are uncommon, with presently 22 specimens from deposits around the world and ranging from the early Miocene to the earliest Eocene (Engel 2002). Owing to the derived phylogenetic position of these taxa with respect to the other subfamilies, the family as a whole must be considerably older (Engel 2001*b*, 2003). The relatively modern character of the fossil described herein, as well as those from the middle Eocene of northern Europe (Engel 2001*b*) and latest Eocene of North America (Engel 2002), further supports the notion that the deeper cladogenetic events in halictid phylogeny occurred much earlier, as concluded by Engel (1996, 2001*b*) and further supported by the derived position for *Halictus* found by Danforth (2002). Certainly, with our current understanding of apoid phylogeny (Michener 2000; Engel 2001*b*), the cladogenetic events giving rise to the halictids as a whole occurred before the origination of apids (which includes *Cretotrigona* from the Maastrichtian of New Jersey) and thus must be older than the Late Cretaceous. If the assignment to Halictidae of some North American Cenomanian trace fossils (Elliott and Nations 1998) as well as the Maastrichtian nests from Argentina (Genise *et al.* 2002) is correct, then paleoichnological evidence further supports this conclusion. However, there are no truly diagnostic suites of characters that would allow such precise assignment of these trace fossils and they should, therefore, be considered with some scepticism. A detailed review of the geological history of Halictidae is presented by Engel (2002).

Current phylogenetic and paleontological evidence supports the conclusion that the bees may have originated in the earliest mid-Cretaceous, *after* the origination of flowering plants (Engel 2001*b*, 2003). The earliest evidence of the Apoidea is from the Early Cretaceous, but only on the basis of plesiomorphic spheciform wasps (*i.e.*, the paraphyletic group of apoid wasps from which bees arose) and, in fact, the Aculeata as a whole is unknown until around the Jurassic–Cretaceous boundary (Engel 2001*b*). Thus, all available evidence indicates that bees are younger than the flowering plants. However, the origination and radiation of the bees perhaps coincided with (but may not necessarily have caused) the dramatic increases in angiosperm diversity appearing in the fossil record between 115–90 Ma ago (Lidgard and Crane 1988; Crane and Lidgard 1990). At present, all the earliest known bees are related to or are members of lineages that are polyletic and, therefore, cannot be phylogenetically correlated with the origination and diversification of any particular angiosperm clade. Hopefully, new fossils from Cretaceous deposits (particularly mid-Cretaceous) will clarify the origin and early diversification of bees in the same way that the past decade has seen considerable resolution of their evolution during the Cenozoic.

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