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An Eocene Bee in Rovno Amber, Ukraine (Hymenoptera: Megachilidae)

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ABSTRACT

A new species of fossil bee is described and figured in Late Eocene amber from the Rovno region of the Ukraine. ***Ctenoplectrella zherikhini*** n.sp. (Megachilinae: Ctenoplectrellini), is similar to those species known from the slightly older Baltic amber (middle Eocene). This is the first bee discovered in the Rovno amber and the fourth species for its genus. The presently known megachilid bee fossils are summarized and the geological history of the family reviewed.

INTRODUCTION

Bees are among the most recognizable insects and have endeared themselves to humans owing to their diligent pollination services (agricultural and otherwise) and, in the case of the honey bees, the honey and wax they produce. Those species of the family Megachilidae are most familiar for the leafcutter bees, whose semicircular swaths from petals and leaves are the frustration of gardeners. Although our knowledge of the bees is advanced by comparison to most other lineages of Hymenoptera, understanding of their evolutionary history is compromised by the paucity of information from the fossil record. Whereas wasps and ants are frequently plentiful in Cenozoic or Cretaceous deposits, bees are scarcely recovered despite their almost assured presence and perhaps abundance in the same paleo-habitats. The history of bees is partially compromised by the poor preservation of organisms in arid habitats, since it is in such environments that bees, particularly basal bee lineages, flourish. This rarity makes the discovery of any bee fossil of importance and excitement. Herein we provide the description of an Eocene bee preserved as an amber inclusion from the Rovno region of the Ukraine. This is the first bee recovered from these deposits (Klesov and Dubrovitsa deposits of the Obukhov Formation) and was found in the collection of Rovno amber inclusions acquired by the Institute of Zoology of the National Academy of Sciences of Ukraine in Kiev. The fossil is a representative of *Ctenoplectrella*, an extinct genus of megachiline bees previously known only from Baltic amber (Engel, 2001). To the description we have appended an account of the geological history of the Megachilidae (*vide etiam* Engel, 1999) and an updated checklist of the known fossils for the family.

Structurally, the region of the amber-bearing deposits is referred to the northwestern margin of the Ukrainian Crystalline Shield. Here terrestrial and shallow, marine, Paleogene sediments along with terrestrial (mainly bog-lacustrine) Neogene and predominantly Anthropogene glacial formations overlie the Pre-Cambrian layers and their weathering surface. The Paleogene deposits in the most complete sections contain the Buchak (Lutetian), Kiev (Bartonian), Obukhov (Priabonian), Mezhigorje (Rupelian), and Berek (Chattian) Formations. Amber occurs in almost all stratigraphic units of the sedimentary cover, although it has not been found in the Buchak deposits and is extremely rare in those of the Kiev. However, even in the part of the section where amber occurrences are abundant, its content in the rock is substantially different between layers. The richest placers are associated with the Obukhov (Late Eocene) and Mezhigorje (Early Oligocene) Formations. The Obukhov and Mezhigorje Formations seem to have been formed in shallow water zones of marine basins, with deep water areas situated in the Pripyat and Dnieper-Donetsk depressions. The shorelines of these basins lay within the Ukrainian Shield. The zone of littoral shallow waters in this shield was apparently the area where the formation of amber placers in the sea was simultaneous with the accumulation of primary sediment material of latter formations. The Klesov deposit is often misinterpreted as of Oligocene age (e.g., Tutskij and Stepanjuk, 1999; Weitschat and Wichard, 2002). The source of this confusion stems from Maidanovich and Makarenko (1988) wherein in one section the Klesov and Dubrovitsa are referred to the Oligocene whereas in all other sections of the same paper they are correctly assigned to the Late Eocene.

Most inclusions from the Institute of Zoology are from the Klesov deposit. A list of

Fig. 1. Photomicrograph of ***Ctenoplectrella zherikhini*** n.sp. (holotype female, UA-1748). Specimen length 5.2 mm.

the 16 insect orders and 97 families reported from Rovno amber was provided by Perkovsky et al. (2003, to which can be added the Aleyrodidae and Megachilidae). Although roughly contemporaneous with the more historically studied Baltic amber, the fauna of Rovno amber is quite distinct. More than 26% of the ants represent genera and species not found in Baltic amber (Dlussky and Perkovsky, 2002) and all of the more than 50 species of gall midges are unique to Rovno amber (Fedotova and Perkovsky, 2004, 2005; Perkovsky and Fedotova, 2004). In particular, the Rovno amber fauna differs from that of the Baltic by the dominance of Sciaridae and other forest litter Diptera, whereas Chironomidae and other aquatic insects are underrepresented (Perkovsky et al., in prep.).

MATERIAL AND METHODS

Morphological terminology and format for the description follow that of Engel (2001). The abbreviations F, S, and T are employed for flagellomere, metasomal sternum, and metasomal tergum, respectively. Measurements were made with an ocular micrometer on an Olympus SZX12 stereomicroscope. All metrics should be considered approximate since the optimal visual angle was not always achievable owing to the state of preservation. Photomicrographs were prepared using a Microptics ML-1000 Digital Imaging System. Comparative material of Baltic amber species of *Ctenoplectrella* was studied by the senior author in the collections of the American Museum of Natural History (New York) and the University of Kansas Natural History Museum (Lawrence).

SYSTEMATIC PALEONTOLOGY

Ctenoplectrella zherikhini, new species

Figure 1

DIAGNOSIS: The new species is most similar to *C. grimaldii* Engel in Baltic amber as both have the pleura impunctate and the imbricate propodeum and metasoma. *Ctenoplectrella zherikhini*, however, differs by the fuscous setae on the inner surfaces of the tarsi; long, branched setae of the propodeum; and tapering gena.

DESCRIPTION: **Female.** Total body length approximately 5.2 mm. Head apparently slightly wider than long; face relatively flat; gena much narrower than compound eye in lateral view, gena tapering slightly in width (widest dorsally, narrower ventrally). Basal vein confluent with cu-a; second abscissa Rs basad 1m-cu by approximately six times vein width; other forewing venational details unobservable (forewing is obliquely torn); eight distal hamuli, arranged in a single, evenly spaced series.

Outer surface of mandible impunctate and smooth. Clypeus with small punctures separated by a puncture width or less, integument between smooth. Supraclypeal area apparently sculptured as on clypeus. Integument of face mostly obscured by thin layer of Schimmel and debris toward vertex. Gena with minute punctures separated by about a puncture width or less, integument between smooth. Notal integument obscured by debris. Pleura impunctate and smooth. Lateral surface of propodeum (basal and posterior surfaces obscured) impunctate and faintly imbricate. Metasomal terga and sterna faintly imbricate and impunctate.

Integument dark brown, without maculations. Wing membrane hyaline; veins strong and black. Pubescence generally white or off-white, except setae on inner surfaces of tarsi fuscous (dark brown to black).

Mandible with minute, simple, appressed setae. Clypeus with minute, appressed, simple setae not obscuring integument; similar setae also on face below level of antennal sockets, intermixed with scattered, longer, erect setae on face, clypeus, supraclypeal area, gena, and postgena. Pleura with scattered, short, simple setae, setae becoming gradually longer ventrally. Lateral surface of propodeum with abundant moderate length to long, branched setae. Pubescence of legs generally simple and of moderate length although becoming long on outer surfaces of tibiae and tarsi; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with moderate length, branched setae; metatibia with abundant, moderate length to long setae, setae with short branches. Terga with sparse, short, simple, appressed or suberect setae, setae longer and suberect to erect on lateral borders (some setae laterally with a few, minute branches); sternal scopa composed of dense, long, erect, simple setae.

HOLOTYPE: Female, Rovno amber, UA-1748 (fig. 1), labeled ‘‘Holotype, *Ctenoplectrella zherikhini* Engel & Perkovsky [red label]’’. Deposited in the Institute of Zoology, National Academy of Sciences of Ukraine, Kiev.

ETYMOLOGY: The specific epithet is a patronymic for the late Dr. Vladimir V. Zherikhin (1945–2001). Dr. Zherikhin was a prominent coleopterist and paleoentomologist whose untimely death has deprived us of his unrivaled scholarship and warm humor.

KEY TO SPECIES OF *CTENOPLECTRELLA*
(modified from Engel, 2001)

1. Crossvein 2rs-m strongly and doubly arcuate, thus second submarginal cell more strongly produced toward wing apex along its posterior margin; medioapical margin of clypeus straight 2

— Crossvein 2rs-m relatively straight and therefore second submarginal cell not more strongly produced toward wing apex along its posterior margin; medioapical margin of clypeus gently convex . . . . *C. viridiceps* Cockerell

2. Pleura impunctate; metasomal terga faintly imbricate 3

— Pleura with coarse, faint punctures; metasomal terga with small, scattered punctures . . . . *C. cockerelli* Engel

3. Propodeal setae long, erect, and branched; tarsal setae fuscous; gena tapering . . . . *C. zherikhini* n.sp.

— Propodeal setae scattered, short, and simple; tarsal setae white or off-white; gena of relatively equal width along its length . . . . *C. grimaldii* Engel

DISCUSSION

The historical record of Megachilidae is relatively good, with the amount of material being second only to that of the Apidae. From more recent history are Bronze Age remains of burrows perhaps originating from the activity of osmiines in Israel (Buxton, 1932). True fossil material of the family (i.e., Pre-Quaternary) is presently confined to the

Cenozoic and to deposits of the Northern Hemisphere (appendix 1). However, the zoogeography of the modern lineages coupled with the temporal and phylogenetic distribution of known fossils (and trace fossils) is quite revealing, suggesting at least a preliminary outline of megachilid evolutionary history.

The almost complete lack of fossils from the Cretaceous limits any discussion of early bee evolution. The oldest fossil of a bee is *Cretotrigona prisca* (Michener and Grimaldi) from the Late Cretaceous of eastern North America (Michener and Grimaldi, 1988; Engel, 2000). Although *Cretotrigona* is, quite unfortunately, a singular fossil, it reveals much owing to its derived position in a derived family (Apidae), implying that significant stages of bee evolution had already occurred by the Late Cretaceous. Earlier evidence of bee activity is suggested by presumed halictine nests of Cenomanian age from Arizona (Elliott and Nations, 1998), again indicating that bees are older than this epoch, perhaps as old as late in the Early Cretaceous to early in the middle Cretaceous (Engel, 2001, 2004c). Even in the absence of any fossil megachilids, the simple presence of an apid (the sister-group of Megachilidae) in the Late Cretaceous indicates that the megachilid lineage was also present during this period. Indeed, most clades today considered as families of the Apoidea were likely established during the middle Cretaceous (Engel, 2001, 2004c; Grimaldi and Engel, 2005). By the middle of the Eocene epoch, the period from which most bee lineages are first known, representatives of the principal families are already present and are apparently not basal (Engel, 2001).

Certainly origins of the family Megachilidae are, like the beginnings of all bee families, obscure. The family is organized into four subfamilies (vide Engel, 2005); the Pararhophitinae, Fideliinae, Lithurginae, and Megachilinae. Among the numerous characters supporting the family, the most noteworthy is the development and use of a metasomal scopa for pollen transport. Phylogenetic studies support the notion that pararhophitines and fideliines are basal to a Lithurginae + Megachilinae clade (e.g., Roig-Alsina and Michener, 1993; fig. 2). The Pararhophitinae, consisting of a single genus with three species, are restricted to the deserts of Central Asia, Asia Minor, Arabia, and northeastern Africa. The species of *Pararhophites* are small, sparsely setose, mostly yellowish bees that are not commonly encountered. The genus is clearly relic and united to the Fideliinae by a unique cocoon construction by the mature larvae (in both subfamilies the larvae ingest sand and then defecate in thin strips running from the poles of the cocoon). The fideliines are generally robust bees and atypical for the family in the densely setose legs, termination of the subantennal sulci on the ventral margin of the antennal sockets, and three submarginal cells (symplesiomorphies for the family), among other traits. Species nest in the ground and are restricted to xeric regions mostly in southern Africa but with isolated representatives in Chile (i.e., *Neofidelia*) and Morocco (i.e., *Fidelia ulrikei* Warncke). Modern Fideliinae are likely relictual, and the subfamily perhaps once had a much broader distribution with surviving remnants in the regions where it is found today (Engel, 2002, 2004a). This would be in general accord with patterns for other hymenopteran groups with similar ‘‘Gondwanan’’ distributions but which were in fact distributed widely in the Northern Hemisphere during the Cretaceous and until the early Neogene (e.g., Scolebythidae, Megalyridae). Unfortunately, pararhophitines and fideliines do not occur in habitats that produce amber (i.e., subtropical to tropical environments) and compression fossils would likely be almost impossible to distinguish from other large bees (in the case of the fideliines) or small, sparsely setose apoids (in the case of the pararhophitines). Although a fossil fideliine or pararhophitine would indeed be significant, particularly if from some northern deposit for the fideliines, such material is unlikely to be recovered.

The Lithurginae have more the habitus of typical megachilid bees and share with the Megachilinae reduced metatibial scopae (except *Protolithurgus*), subantennal sulci meeting the antennal toruli along the outer margins, and the presence of only two submarginal cells (i.e., 1rs-m is absent). Species nest in rotten or dried wood, without brood cell linings. The subfamily is noteworthy for the

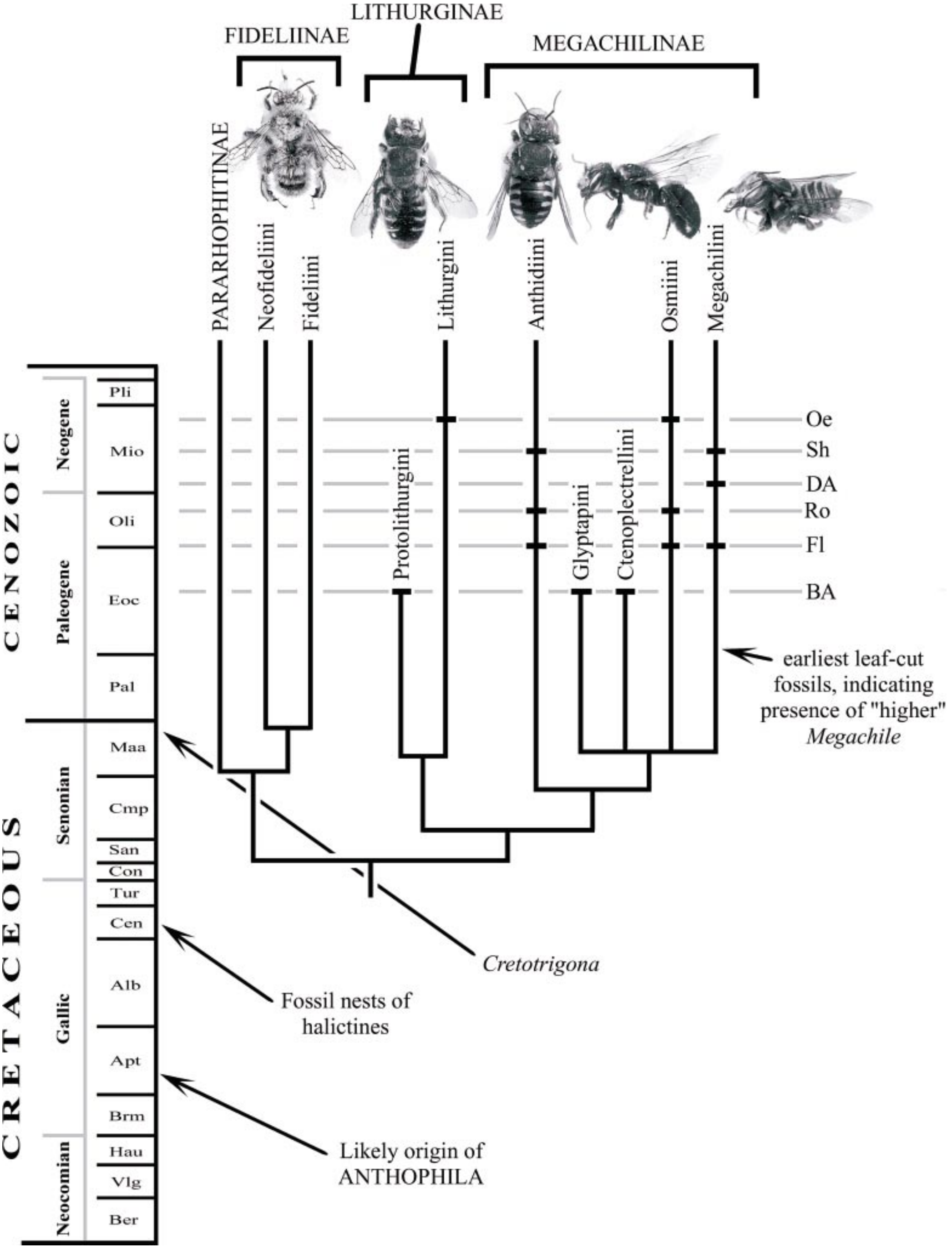

Fig. 2. Phylogeny of Megachilidae, with significant fossils indicated; note that Osmiini is likely paraphyletic and Anthidiini includes Dioxyini. **Oe** = Oeningen; **Sh** = Shandong; **DA** = Dominican amber; **Ro** = Rott; **Fl** = Florissant; **BA** = Baltic amber (including the Ukrainian amber fossil); refer to appendix 1. Arrows indicate the position and age of particularly important fossil records for Anthophila. *Cretotrigona* is currently the oldest body fossil of the lineage sister to Megachilidae (i.e., Apidae) (Michener and Grimaldi, 1988; Engel, 2000). The principal extant lineages are represented by *Neofidelia*

presence of the metabasitibial plate (represented only posteriorly in modern taxa), the pygidial plate, metatibial spicules (in modern taxa), and the shortened first metasomal tergum, which is flattened in profile. The earliest record of lithurgines is *Protolithurgus ditomeus* Engel in Baltic amber, a species that is also sister to all other members of the subfamily (Engel, 2001). Cladistic study has also suggested that the most basal, living members of the subfamily are those species of the genus *Trichothurgus* from southern South America (Engel, 2001). *Trichothurgus* consists of robust, densely setose bees reminiscent of fideliines but otherwise having typical lithurgine-megachiline traits. The derived genus *Lithurgus* consists of two principal lineages: *Lithurgopsis* in the New World (Argentina to the northern United States) and *Lithurgus* proper (native to Eurasia, Africa, and Australia), which should perhaps be distinguished as separate genera (vide Engel, 2001). The enigmatic *Lithurgus rubricatus* Smith from Australia is notable for the occurrence of elongate arolia and should perhaps be transferred to its own subgenus. A putative *Lithurgus* was described from the Miocene of Germany (Cockerell, 1909a: appendix 1) but although certainly a megachilid, the generic assignment is dubious. Thus, *Protolithurgus* is the only definitive fossil of the subfamily. It is likely that the lithurgines originated in the Southern Hemisphere (i.e., of Gondwanan origin), differentiating from Megachilinae sometime in the middle to Late Cretaceous.

Of the megachilids, Megachilinae are the most numerous in the fossil record (appendix 1), with each tribe represented to some extent (fig. 2). Early accounts of ‘‘*Osmia*’’, ‘‘*Chalicodoma*’’, and ‘‘*Megachile*’’ in Baltic amber (e.g., Menge, 1856; Brischke, 1886; Bachofen-Echt, 1949; Scudder, 1885, 1891) were likely specimens of *Ctenoplectrella*, which has the general habitus of an osmiine. Reference to a fossil ’’*Coelioxys*’’ sp. (Lewis et al., 1990; earlier referred to as simply Megachilidae in Lewis, 1969) was tantalizing not only as an early record of this genus but as one of the only parasitic bee fossils. The specimen, however, is preserved solely as a forewing and cannot be assigned to any particular megachiline tribe, let alone to the parasitic genus *Coelioxys* (Engel, 2004b). Cockerell (1909a) referred to a fossil *Osmia* from Germany originally identified by Oswald Heer under the manuscript name ’’*Osmia kirbyana*’’, but subsequently recognized the specimen as a polistine wasp (Cockerell, 1914; Cockerell did not cite the manuscript name in 1909a but did so in 1914). Most of the fossil Megachilinae need to be critically revised.

The famous leaf-cutter bees (*Megachile* group I sensu Michener, 2000, or *Megachile* in the traditional sense, e.g., Michener, 1962; Mitchell, 1980) are a derived group of the Megachilini. This group is certainly older than the middle Eocene. Although the earliest body fossils of this lineage are those from the Eocene–Oligocene boundary of Florissant, Colorado (appendix 1), the distinctive semicircular traces of their activity in fossilized leaves are known from the Early to middle Eocene of various deposits in North American and Europe (e.g., Berry, 1916, 1931; Brooks, 1955; Lewis, 1994; Wappler and Engel, 2002, 2003; Wappler, 2003a, 2003b). Leaves with such cuts are also known from other Tertiary deposits (Cockerell, 1908, 1910; Meyer, 2002), as well as an inclusion in Dominican amber with a specimen of *Sphaerodactylus* (Grimaldi, 1996). Interestingly, the leaf cuts from the Eocene are presently the earliest evidence of the Megachilidae as a whole (fig. 2), being slightly older than the Baltic amber fossils. The presence of derived *Megachile* in the Early Eocene, however, indicates that more basal divergences in the Megachilini must have taken place earlier in the Paleocene or Latest Cretaceous. Similarly, divergences between the tribes of Megachilinae and concomitantly between the subfamilies must

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profuga Moure and Michener (Fideliinae + Pararhophitinae), *Lithurgus chrysurus* (Fonscolombe) (Lithurginae), *Anthidium florentinum* Latreille (Anthidiini), *Hoplitis fulgida* (Cresson) (Osmiini), and *Megachile candida* Smith (Megachilini).

have occurred even earlier (fig. 2). The exploration of Cretaceous and Paleocene fossil locales will be of considerable importance for unraveling the earliest evolution of the Megachilidae, particularly amber sites. Although fossils of bees are admittedly rather uncommon, if not rare, in most places, the remains of leaves are abundant and may continue to provide data on the Cenozoic paleogeographical and temporal distribution of the leaf-cutting clade.

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APPENDIX 1

FOSSIL MEGACHILIDAE

The following is a checklist of described fossil bees of the family Megachilidae (updated and modified from Engel, 1999). Note that although in some instances assignment to family, subfamily, and tribe may be reasonable, many generic assignments for compression fossils must be taken with caution. *Apiaria dubia* Germar (1849) of the Oligocene of Germany is excluded despite its inclusion in *Osmia* by Giebel (1856; *vide etiam* Scudder, 1891; Handlirsch, 1907) since it is so poorly understood (e.g., Pictet, 1854, considered it similar to *Bombus*!). A specimen of *Heriades* sp. in African copal is also excluded since it is likely of an extant species (Engel, 2001). The record of *Megachile* sp. in Baltic amber by Gerlach (1989) was a misidentification with *Ctenoplectrella* (Engel, 2001). The listing of *Stelis seneciophila* Cockerell as a fossil from the Florissant Fossil Beds (Meyer, 2002) is erroneous as this is, in fact, a living species that was simply described from near modern Florissant, Colorado, and in the same paper with some actual fossil taxa.

Taxa	References
EOCENE	
Baltic Amber (Lutetian)	
Protolithurgus ditomeus Engel	Engel, 2001
Ctenoplectrella cockerelli Engel	Engel, 2001
Ctenoplectrella grimaldii Engel	Engel, 2001
Ctenoplectrella viridiceps Cockerell	Cockerell, 1909a
=*Ctenoplectrella dentata* Salt, 1931	
=*Ctenoplectrella splendens* Kelner-Pillault, 1970	

Taxa	References
Glaesosmia genalis Engel	Engel, 2001
Glyptapis densopunctata Engel	Engel, 2001
Glyptapis disareolata Engel	Engel, 2001
Glyptapis fuscula Cockerell	Cockerell, 1909b
=*Glyptapis reticulata* Cockerell, 1909b	
=*Glyptapis reducta* Cockerell, 1909b	
=*Glyptapis neglectula* Salt, 1931	
=*Dasypoda* sp. Gerlach, 1989 [misident.]	
Glyptapis mirabilis Cockerell	Cockerell, 1909a
Rovno Amber (Bartonian-Priabonian?)	
Ctenoplectrella zherikhini, new species	Present study
EOCENE–OLIGOCENE	
Florissant, Colorado (Priabonian-Rupelian)	
Anthidium exhumatum Cockerell	Cockerell, 1906
Anthidium scudderi Cockerell	Cockerell, 1906
‘‘*Dianthidium*’’ *tertiarium* Cockerell	Cockerell, 1906
Heriades bowditchi Cockerell	Cockerell, 1906
Heriades halictinus Cockerell	Cockerell, 1906
Heriades laminarum Cockerell	Cockerell, 1906
Heriades mersatus Cockerell	Cockerell, 1923
Heriades mildredae Cockerell	Cockerell, 1925a
Heriades priscus Cockerell	Cockerell, 1917
Heriades saxosus Cockerell	Cockerell, 1913
Lithanthidium pertriste Cockerell	Cockerell, 1911
Megachile praedicta Cockerell	Cockerell, 1908
OLIGOCENE	
Rott, Germany (Chattian)	
Anthidium mortuum (Meunier)	Meunier, 1920; Statz, 1936
Osmia carbonum Heyden	Heyden, 1862
MIOCENE	
Dominican Amber (Burdigalian)	
Megachile (*Chalicodomopsis*) *glaesaria* Engel	Engel, 1999
Kudia River, Amagu, Russia (Burdigalian?)[a]	
Megachile amaguensis (Cockerell	Cockerell, 1925b
Shandong, China (Serravallian?)	
Anthidium basalticum Zhang	Zhang, 1989a
Megachile shanwangae Zhang	Zhang, 1989b
Oeningen, Germany (Messinian)	
‘‘*Lithurgus*’’ *adamiticus* (Heer)	Heer, 1865; Cockerell, 1909a
Osmia antiqua Heer	Heer, 1849
Osmia nigra Zeuner and Manning	Zeuner and Manning, 1976

[a] These deposits are often referred to as Early Miocene or Uppermost Oligocene; however, Zherikhin (1998) believed them to be perhaps as old as the Early Oligocene.

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