A Miocene Halictine Bee from Rubielos de Mora Basin, Spain (Hymenoptera: Halictidae)

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A Miocene Halictine Bee from Rubielos de Mora Basin, Spain (Hymenoptera: Halictidae)

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ABSTRACT

A new species of halictine bee (Apoidea: Anthophila: Halictidae) is described and figured from laminated mudstones of Early Miocene age from Rubielos de Mora Basin, Teruel, Spain. *Halictus petrefactus*, new species, is the first bee from these deposits to be formally described. The geological history of the Halictidae and of the bees as a whole is briefly reviewed.

INTRODUCTION

The Lower Miocene (Lower Aragonian = Orleanian in the Neogene mammal age) lacustrine deposits of the Rubielos de Mora (Province of Teruel) in eastern Spain are known to have an abundance of fossil insects (Martínez-Delclòs et al., 1991; Peñalver and Seilacher, 1995; Montoya et al., 1996; Peñalver, 1998a), and of articulated amphibians and plant remains (Montoya et al., 1996; Anadón et al., 2003). These deposits are located in a lacustrine basin of the Iberian Range with an asymmetrical form elongating in a NNE-SSW direction and with a surface of approximately 15 km^2 (Anadón et al., 1988a, 1988b, 1989).

The basin-fill sequence of the Rubielos de Mora is over 800 m thick and contains three main stratigraphic units that correspond to three evolutionary stages of basin fill (Anadón et al., 2003): **(1)** Lower unit of sandstones with interbedded mudstones and conglomerates, **(2)** Middle unit of lacustrine limestones with interbedded mudstones and sandstones, and **(3)** Upper unit with alluvial-deltaic, marginal lacustrine, and open lacustrine facies. The insect remains are located

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in the laminated grey mudstones (oil shales) and interbedded rhythmite beds of the open lacustrine facies' upper unit. The taphonomic characteristics of Rubielos de Mora indicate that this site corresponds to a Konservat-Lagerstätte as the level of preservation is relatively high. For example, soft tissues are preserved in the amphibians (e.g., eyes, gill impressions, skin, and digestive track in salamanders) and color patterns are still present in insect wings (Peñalver, 1998a, 1998b; Peñalver and Martínez-Delclòs, 2003).

One of the most important areas with fossil insect outcrops, named Río Rubielos, is located less than a kilometer to the east of the village of Rubielos de Mora (fig. 1A). To date, four outcrops have been investigated and these have been named Río Rubielos 1 (RR 1) to Río Rubielos 4 (RR 4). In 1994 an excavation was undertaken in the RR 2 outcrop that is constituted of oil shales with intercalated iron microlevels (fig. 1B). The excavation resulted in more than 820 specimens, principally insects and plants. The fossil insect association in RR 2 is constituted by the orders Diptera, Hymenoptera, Thysanoptera, Hemiptera (Heteroptera and ''Homoptera''), Coleoptera, Orthoptera, and Trichoptera, in order of minor abundance (Peñalver, 1998a). Thus far, the order Hymenoptera is represented by 11 families—Ichneumonidae, Braconidae, Torymidae, Trichogrammatidae, Proctotrupidae, Diapriidae, Bethylidae, Megaspilidae, Apidae, Formicidae, and Halictidae. The Halictidae, like the Torymidae, Trichogrammatidae, and Megaspilidae, are represented only by a single specimen found in RR 2. The halictid material is the focus of the present contribution.

With over 3,460 described species, the Halictidae ranks as one of the most diverse lineages of bees, second only to the Apidae. However, the ubiquitous halictids remain one of the more taxonomically understudied groups and most surveys indicate that the family will surpass in diversity all other lineages of bees (e.g., Gonzalez and Engel, 2004). More than one-third of halictid diversity resides within the derived subfamily Halictinae, which is famous for genera such as *Halictus*, *Lasioglossum*, *Sphecodes*, *Agapostemon*, *Augochlora*, and *Augochlorella*. It is from this subfamily that the only records of fossil halictids are presently documented and despite the modern diversity, the geological history of the family is exceptionally sparse. The first description of a fossil halictid was made by Cockerell in 1906, and only eight records existed for the family by 1980. During the last quarter century the number of records has more than doubled (table 1), most coming about in the last decade, but these are still meager for a family of such diversity and are confined to a relatively few deposits (e.g., all records of Augochlorini and Caenohalictini come from a single deposit and nearly half of those of Halictini are from Florissant). Thus, the recovery of halictid remains from new deposits is of significance.

Morphological terminology follows that of Engel (2001). All metrics are of the bee as it is preserved and, thus, for some (e.g., head length) should be considered approximate given the slightly oblique position of certain tagmata in the stone (vide Preservation, infra).

SYSTEMATIC PALEONTOLOGY

Halictus petrefactus, new species
Figures 2–3

Halictus sp. Peñalver, 1998a: 67.
Halictus sp. Grimaldi and Engel, 2005: 465.

DIAGNOSIS: The new species is most similar to the unnamed halictine described by Arillo et al. (1996) from the Early Miocene of Izarra, Spain (vide Barrón et al., 1997, for dating). The new species can be distinguished by minute differences in wing venation (e.g., 1m-cu is positioned more distally in the Izarra bee, the second submarginal cell is more parallel-sided with its posterior border less extended: owing to the degree of variation possible in some venational traits and the roughly contemporaneous age and geographic region, it is a viable hypothesis that the Izarra bee, although less perfectly preserved, is conspecific with *H. petrefactus*). In addition the species is noteworthy for the following combination of traits: black and shining integument; mesoscutum sparsely and faintly punctured, integument otherwise smooth; hyaline wing membrane; sparsely pubescent metasoma.

DESCRIPTION: **Female.** Total body length

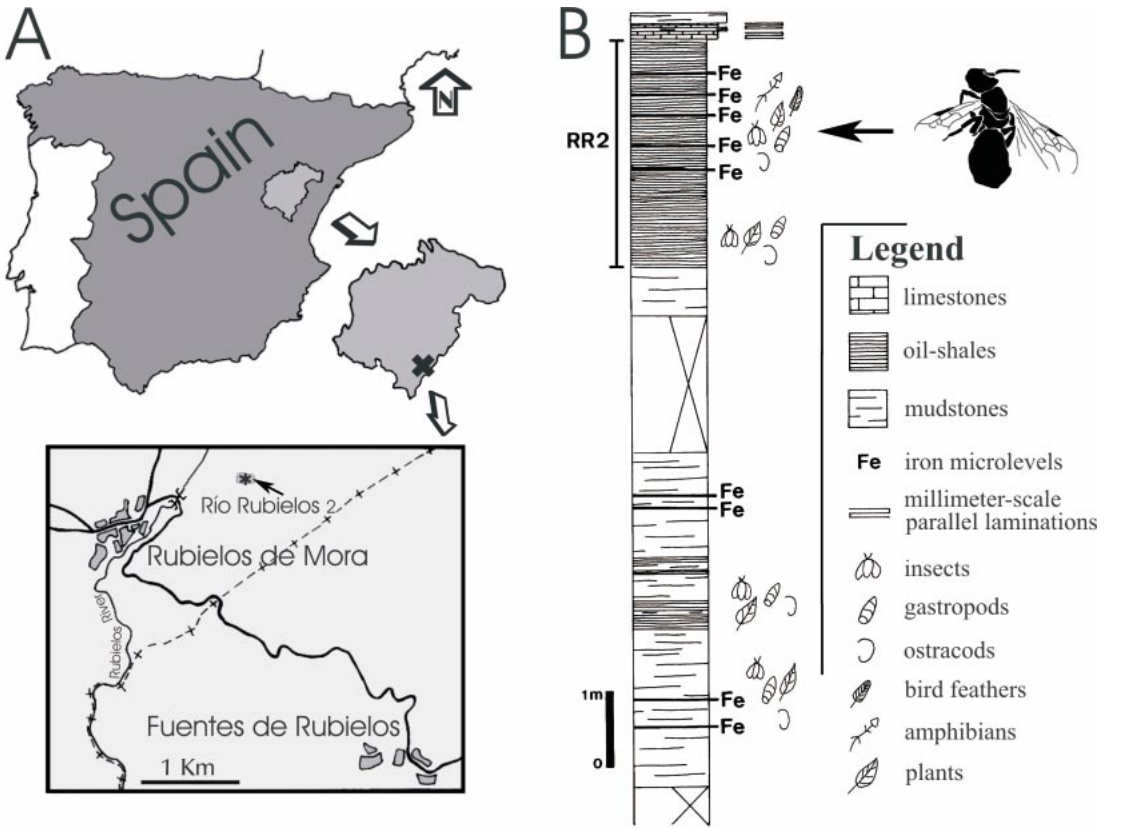

Fig. 1. The Rubielos de Mora locality. **A.** Geographic location of the Rubielos de Mora Basin and Río Rubielos site in the Teruel Province (eastern Spain). **B.** Stratigraphic column of the Río Rubielos 2 site (Rubielos de Mora Basin) with indication of the approximate stratigraphic position where the halictine bee was discovered. RR2 = Río Rubielos 2.

8.2 mm; forewing length 6.3 mm. Head slightly longer than wide (length 1.9 mm, width 1.7 mm); integument black and shining, apparently smooth with scattered, shallow, minute punctures except pedicel and flagellum dark brown. Compound eyes with inner margins slightly emarginate in upper third, compound eyes slightly converging below, strongly converging above owing to emargination; ocelli not preserved. Malar space linear. Antennal toruli just below emargination of compound eyes, at about head length midpoint, apparently separated from basal margin of clypeus by more than 1.5 times torulus diameter; scape slender, length 0.7 mm; flagellum length 1.6 mm; second flagellomere subequal in length to first flagellomere, tenth flagellomere longest, 10 flagellomeres of typical female form (vide Preservation, infra). Mesosoma integument black and shining, apparently smooth between scattered, faint, minute punctures; mesoscutal length 1.7 mm, anterior border broadly rounded; scutellum length 0.5 mm; metanotum length 0.26 mm; dorsal-facing surface of propodeum apparently exceedingly short (less than length of metanotum), integument apparently minutely and faintly roughened. Forewing with all veins strong (i.e., distal veins not weakened as in *Lasioglossum*); basal vein strongly arched in basal half, distad cu-a by 2.5 times vein width; cu-a strongly oblique, about as long as anterior border of second submarginal cell; r-rs forms acute angle with pterostigma in marginal cell, slightly shorter than first free abscissa of Rs; 1m-cu basad 1rs-m by nearly three times vein width; 2m-cu basad 2rs-m by three

TABLE 1
Geological Records of Halictidae
(updated from Engel, 1996, 2002)

Taxon	Fossil type	Epoch	Locality	References
Tribe Halictini Thomson				
Cyrtapis anomala Cockerell	Compression	Eocene-Oligocene	Florissant, CO	Cockerell, 1908; Engle, 2002
Dialictus coeruleus Robertson[a]	Subfossil	Holocene (postglacial)	Lockport, NY	Miller and Morgan, 1982
Dialictus sp.[a]	Subfossil	Holocene (postglacial)	Lockport, NY	Miller and Morgan, 1982
Electrolictus antiquus Engel	Inclusion	Mid-Eocene	Baltic	Engel, 2001
Halictus petrefactus Engel and Peñalver	Compression	Early Miocene	Teruel, Spain	present contribution
''Halictus'' ruissatelensis Timon-David[b]	Compression	Late Oligocene	Marseilles, France	Timon-David, 1943, 1944
''Halictus'' savenyei Engel and Archibald	Compression	Early Eocene	Quilchena, Canada	Engel and Archibald, 2003
''Halictus'' schemppi (Armbruster)	Compression	Late Miocene	Randeck, Germany	Armbruster, 1938; Zeuner and Manning, 1976
''Halictus'' sp.[c]	Inclusion	Mid-Eocene	Baltic	Bachofen-Echt, 1949
''Halictus'' sp.	Compression	Early Miocene	Euboea, Greece	Bachmayer et al., 1971
Kronolictus scudderiellus (Cockerell)	Compression	Eocene-Oligocene	Florissant, CO	Cockerell, 1906; Engel, 2002
Kronolictus vulcanus Engel	Compression	Eocene-Oligocene	Florissant, CO	Engel, 2002
Lasioglossum celinae Nel and Petrulevičius	Compression	Late Oligocene	Bois d'Asson, France	Nel and Petrulevičius, 2003
Ocymoromelitta florissantella (Cockerell)	Compression	Eocene-Oligocene	Florissant, CO	Cockerell, 1906; Engel, 2002
Ocymoromelitta miocenica (Cockerell)	Compression	Eocene-Oligocene	Florissant, CO	Cockerell, 1909; Engel, 2002
Ocymoromelitta sorella Engel	Compression	Eocene-Oligocene	Florissant, CO	Engel, 2002
Halictinae sp.[d]	Compression	Early Miocene[e]	Izarra, Spain	Arillo et al., 1996
Tribe Caenohalictini Michener				
Eickwortapis dominicana Michener and Poinar	Inclusion	Early Miocene	Dominican Republic	Michener and Poinar, 1996
Tribe Augochlorini Beebe				
Augochlora leptoloba Engel	Inclusion	Early Miocene	Dominican Republic	Engel, 2000a
''Augochloropsis'' sp.[f]	Inclusion	Early Miocene	Dominican Republic	Poinar, 2004
Neocorynura electra Engel	Inclusion	Early Miocene	Dominican Republic	Engel, 1995
Oligochlora eickworti Engel	Inclusion	Early Miocene	Dominican Republic	Engel, 1996
Oligochlora grimaldii Engel	Inclusion	Early Miocene	Dominican Republic	Engel, 1997
Oligochlora marquettorum Engel and Rightmyer	Inclusion	Early Miocene	Dominican Republic	Engel and Rightmyer, 2000
Oligochlora micheneri Engel	Inclusion	Early Miocene	Dominican Republic	Engel, 1996
Oligochlora rozeni Engel	Inclusion	Early Miocene	Dominican Republic	Engel, 2000a
Trace fossils (Ichnotaxa)				
Cellicalichnus chubutensis Genise	Trace	Maastrichtian	Chubut, Argentina	Genise, 2000
Cellicalichnus dakotensis (Elliott and Nations)	Trace	Late Cenomanian	Arizona	Elliott and Nations, 1998; Genise, 2000

TABLE 1
(*Continued*)

Taxon	Fossil type	Epoch	Locality	References
Cellicalichnus ficoides (Retallack)	Trace	Late Oligocene	South Dakota	Retallack, 1984, Genise, 2000
Cellicalichnus habari (Thackray)	Trace	Early Miocene	Rusinga Island, Kenya	Thackray, 1994; Genise, 2000
Celliforma germanica Brown	Trace	Oligocene	Württemberg, Germany	Brown, 1935; Retallack, 1984
Corimbatichnus fernandezi Genise and Verde	Trace	Maastrichtian	Nueva Palmira, Uruguay	Genise and Verde, 2000
Ellipsoideichnus meyeri Roselli	Trace	Maastrichtian	Nueva Palmira, Uruguay	Roselli, 1987
Rosellichnus arabicus Genise and Bown	Trace	Late Pleistocene	Abu Dhabi, U.A.E.	Genise and Bown, 1996
Rosellichnus sp.	Trace	?	?	Genise, 2000
Uruguay auroranormae Roselli	Trace	Maastrichtian	Nueva Palmira, Uruguay	Roselli, 1938; Genise and Bown, 1996; Genise, 2000; Cilla, 2001
Uruguay rivasi (Roselli)	Trace	Maastrichtian	Nueva Palmira, Uruguay	Roselli, 1987; Genise, 2000; Cilla, 2001

[a] This is a modern species recorded as a subfossil from postglacial sediments (Miller and Morgan, 1982).

[b] Timon-Daivd (1943) referred to this material as "*Sphecodes*" but left the species unnamed until 1944, when he then placed it in *Halictus*.

[c] As noted by Engel (1996, 2002) the identity of this missing specimen is of some suspicion and it may be that the specimen referred to by Bachofen-Echt (1949) is the holotype of *E. antiquus* in the Museum für Naturkunde.

[d] Although formally unassigned, this fossil is assuredly of the tribe Halictini and is very likely conspecific with *H. petrefactus*, new species (*vide* Diagnosis).

[e] The Izarra outcrop was considered as of Late Oligocene age but is currently dated as Early Miocene (*vide* Barrón et al., 1997).

[f] It must be noted that the published photograph of this specimen, which resides in the private collection of G. Poinar, resembles very little a species of *Augochloropsis* and instead shows characters suggesting *Neocorynura* (indeed, it may very well be a specimen of *N. electra*).

Fig. 2. Photomicrograph of holotype of *Halictus petrefactus*, new species (MPZ-98/423). Total length of specimen = 8.2 mm.

times vein width (i.e., 1m-cu and 2m-cu [recurrent veins] enter separate submarginal cells); 2rs-m arcuate; pterostigma elongate, length about three times width, border inside marginal cell convex; apex of marginal cell acute, minutely separated from wing margin; first submarginal cell elongate, nearly as long as combined lengths of second and third submarginal cells; second submarginal cell shorter than third submarginal cell, trapezoidal shape, posterior and anterior borders not parallel, posterior border diverging apically toward 1m-cu, anterior border slightly shorter than that of anterior border of third submarginal cell; third submarginal cell with posterior border nearly 1.5 times length of anterior border. Hind wing as depicted in figure 3; only a few hamuli observable (three just distad separation of R, two near termination of costa). Wing veins black, membrane hyaline. Legs black except tarsi (where preserved and evident) apparently dark brown; metafemoral scopa present (setae faintly preserved but distinctly present). Metasoma length 3.7 mm (as preserved); maximal width 2.7 mm. Integument shining, apparently smooth to finely imbricate, black except apical margins of terga dark brown. Apical tomentose bands apparently absent, but setation of metasoma not well preserved (some setae weakly evident along apical margins). **Male.** Unknown.

ETYMOLOGY: The specific epithet is a combination of the Latin words *petra* (meaning, ''rock'', and also of Greek origin) and *factus* (meaning, ''made''). The name literally means ''made of stone'' or ''made into stone''.

HOLOTYPE: Female, MPZ-98/423 (RM-RR-253); Rubielos de Mora, Teruel, Spain; Lower Miocene; labeled ''HOLOTYPE, *Halictus petrefactus* Engel & Peñalver''. The holotype is deposited in the Museo de Paleontología de la Universidad de Zaragoza, Zaragoza Province, Spain.

PRESERVATION: The holotype of *H. petre-*

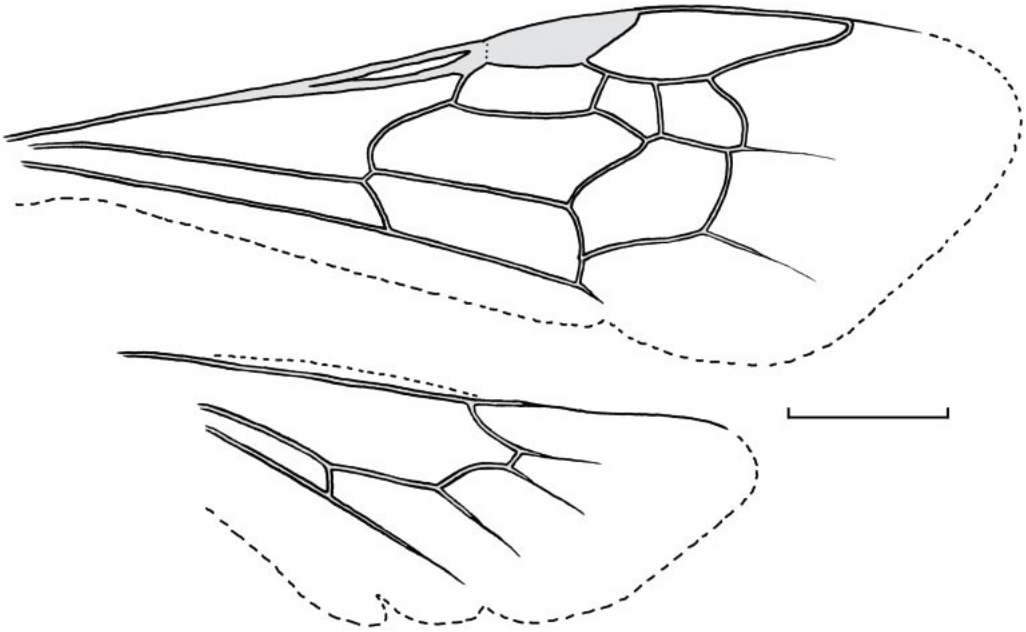

Fig. 3. Line illustration of wing venation of *Halictus petrefactus*, new species (MPZ-98/423); forewing above, hind wing below. Scale bar = 1 mm.

factus, new species, is dorsoventrally compressed in oil shales, the fine sediment resulting in outstanding fidelity in preservation (fig. 2). The specimen is best viewed under ethanol, which permits higher contrast between the bee's integument and the surrounding matrix. The bee is positioned with the mesosoma and metasoma in line, and the head slightly twisted to the left. The head is in a relatively straight frontal view, being thrust forward from the body, although it is at a very slight tilt (the anterior end is minutely tilted downward and to the right). The left antenna is entirely missing (the empty torulus is easily evident in the fossil), but the right antenna is perfectly preserved and entirely within a single plane, making its examination quite simple. The antenna is slightly broken in that the pedicel is slightly pulled out from the scape, its cuticle partly fractured (it almost appears as though the ventral integumental surface of the pedicel was fractured from the remainder). As a result of the dislocation and fragmentation of the pedicel from the apex of the scape, the flagellum may be erroneously assigned 11 flagellomeres (i.e., being male), but closer examination under alcohol clearly shows only 10 flagellomeres. The right legs are positioned mostly alongside and under the body of the bee, with only portions of the mesofemur, mesotibia, metafemur, and metatibia visible. The left forewing is preserved at about an 80° angle from the body, with its lower portion either damaged or obscured; the membrane is torn not far beyond the marginal cell apex and beyond 2m-cu. The right pair of wings is nicely displayed (not overlapping) and they extend at a posterior, oblique angle to the body's axis. The leading edge of the right forewing is slightly twisted proximally such that the costal vein is twisted back and underneath Sc + R (fig. 3), but otherwise the venation is preserved with remarkable fidelity and no distortion of the membrane. The left midleg is tucked alongside and under the body just as described for the right legs. The foreleg, however, is slightly extended from the body, with the protibia and probasitarsus most visible. The left hind leg is extended at about 80° from the body's main axis, and is visible from the apex of the metacoxa through portions of the metadistitarsus, indeed, fragments of what are likely

the pretarsal claws are also evident. The mesosoma is minutely tilted to the right, but otherwise provides a clear dorsal view. The metasoma is compressed dorsoventrally without any apparent oblique tilt. The integument is in outstanding condition and some aspects of the microsculpture are easily discernable under microscopic examination. All in all, the specimen is one of the most exceptional compressions of any bee.

DISCUSSION

Fossils of bees are uncommon and thus the recovery of any new material is of significance, particularly for a family as diverse as the Halictidae. The bees (Anthophila) are a derived group of the Apoidea that differentiated from the grade of spheciform families sometime in the late Early Cretaceous, or perhaps early mid-Cretaceous (Engel, 2001, 2004; Grimaldi and Engel, 2005). The lineage likely radiated rapidly such that derived bee lineages were already present and well represented by the Late Cretaceous (Engel, 2000b, 2004; Grimaldi and Engel, 2005). During this time bees assumed their role as the most significant pollinators of many angiosperms and indeed derived floral morphologies associated with bee pollination are well documented from the Cretaceous, particularly pollination by apine bees (e.g., Crepet and Nixon, 1998). During the Early Tertiary the bee fauna was composed of a mix of enigmatic, early forms alongside long-lived modern tribes, although the former seem to have given way during the Eocene-Oligocene transition (Engel, 2001, 2004). During the Oligocene the bee fauna seems to have become relatively modern in character, at least at the generic level. Certainly by the latest Oligocene and Miocene, as well as later epochs, the fauna was dominated by living genera or extinct genera closely allied to still extant lineages.

The family Halictidae as a whole stems from the mid-Cretaceous and is one of the more early branching lineages in bee phylogeny (Grimaldi and Engel, 2005). Fossilized nests of halictine origin are recorded from the Cenomanian (ca. 89 mya) of North America (Elliott and Nations, 1998) and from the Maastrichtian (ca. 70 mya) of Uruguay (Genise and Bown, 1996; Genise and Verde, 2000), representing some of the earliest records of bee activity. The preserved body fossils of halictids, however, are all of the derived subfamily Halictinae and from the Tertiary (rather equally distributed between the Paleogene and Neogene). However, by the earliest Eocene derived genera of Halictinae were already present among the fauna (e.g., Engel and Archibald, 2003), indicating that the diversification of halictids, particularly the separation of the subfamilial lineages, must have taken place much earlier. The tribes Augochlorini and Caenohalictini are abundant members of the Neotropical fauna, and it is, therefore, of little wonder why they are found in Tertiary amber of the Dominican Republic (table 1). Species of the Halictini, albeit still diverse, are less dominant in this region, and *Lasioglossum* spp., which most frequently occur here, are less likely to be entrapped by resins owing to their biology. The bias toward Halictini in compression fossils versus amber inclusions would presumably be less pronounced if more Tertiary deposits were explored in the New World, particularly South America, for compressions of Halictidae. Thus, this taphonomic bias is likely the result of poor sampling of New World deposits. Table 1 summarizes the geological records of halictid bees and their nests. The geological history of the bees (Anthophila) is discussed further by Engel (2001, 2002, 2004) and Grimaldi and Engel (2005).

Unfortunately, our understanding of the geological history of bees is ''northern'' biased. Little information is available on fossils from deposits in the Southern Hemisphere. For a group that was undoubtedly of Gondwanan origin (likely originating in the central, xeric regions of Gondwanaland during the early mid-Cretaceous: Engel, 2001, 2004), it will be critical to extensively document the fossil bee fauna from this large region of the globe. Thus, continued paleomelittological investigation in the field must continue before any further conclusions can be made concerning the early evolution, diversification, and historical biogeography of the bees.

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