

A Honey Bee from the Miocene of Nevada and the Biogeography of *Apis* (Hymenoptera: Apidae: Apini)

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The first fossil honey bee (Apini: *Apis* Linnaeus) from the New World is described and figured, expanding the former native range of the tribe Apini into the Western Hemisphere. *Apis nearctica* sp. nov., is represented by a single female worker preserved in paper shale from the Middle Miocene of Stewart Valley, Nevada. The species belongs to the *armbrusteri* species group (= *Cascapis* Engel) and is most similar to the extinct species *A. armbrusteri* Zeuner from the Miocene of southwestern Germany. The species is described and its affinities discussed, as well as its implications for our understanding of honey bee and corbiculate bee biogeography and evolution.

KEYWORDS: *Apis*, honey bees, Nearctic, Nevada, Tertiary, taxonomy, biogeography

The honey bees (Apini: *Apis* Linnaeus) are the most famous of all bees, and among the most familiar of all invertebrates, particularly the nearly ubiquitous western honey bee, *Apis mellifera* Linnaeus. This conspicuous lineage of social pollinators has had a long and intimate history with man, depicted in Late Paleolithic cave paintings such as Cuevas de la Araña of the Spanish Levant (near Valencia, Spain) in which men are portrayed collecting honey combs. Early religions of all variety sought inspiration from honey bees and venerated colonies for the sweet substance they produced. Not surprisingly, early on in human history domestication of *Apis* was achieved, usually housing the vertical, waxen combs within wooden boxes or more commonly cylinders made of clay or mud (e.g., Crane 1983, 1999). By the time of the Minoan Civilization there are documents in the ancient script “Linear B” of major honey stores indicative of significant beekeeping operations and honey trade, and Egyptian beekeeping operations are depicted on tomb paintings from even earlier eras, similarly within the ancient Near East such as Sumeria, Assyria, Babylonia, and the Hittite Kingdom centered at Bogazköy. Indeed, ancient Talmudic laws compiled by Jewish scribes during their captivity in Babylon (“The Exile”, 597–539 B.C.) discuss topics ranging from the harvesting of honey on the Sabbath to the proper placement of hives in relation to human domiciles. Early man found that honey bees were not present in some regions, such as Australia, most Oceanic Islands (e.g., Micronesia, Polynesia), and the New World. For some cultures such isolation from the fruit of honey bee labors was of little consequence, but for nearly all of those who developed alongside one or more species of *Apis* this insulation was intolerable. Accordingly, nearly everywhere humans spread, domesticated colonies of honey bees shortly followed such that

today species of *Apis*, particularly *A. mellifera*, can be found feral or domesticated in nearly any region of the World.

In 1622 the first hives of *A. mellifera mellifera* were introduced into the eastern United States, followed shortly thereafter by hives of *A. mellifera ligustica* Spinola and other subspecies. Early reports of honey bees in the Central American regions of the New World were based on misidentifications with stingless bees of the genus *Melipona* Illiger (e.g., Hernandez 1648), with authors of the era rightly noting that honey bees had been transported with colonists to the New World (Josselyn 1674). More than a century later this history apparently had been forgotten and debates began to rage over the nativity of honey bees in the Americas, with some authors considering the feral North American populations as specifically distinct from their native European counterparts (e.g., Belknap 1792) although most correctly recognized them as merely introduced (e.g., Barton 1793). Indeed, U.S. President Thomas Jefferson even noted in his *Notes on the State of Virginia* that the Native American populace referred to honey bees as the “white man’s fly” and that this unfamiliar insect served as an advance signal of encroaching European settlements (Jefferson 1787). Despite the error of Belknap and some of his contemporaries regarding the nativity of *A. mellifera* in the nascent United States, these authors were unwittingly correct in believing the genus *Apis* to have been otherwise native in the Americas. Although all native records of living and fossil honey bees have hitherto come from Europe, Africa, or Asia, and all evolutionary hypotheses based strictly within this Old World framework (e.g., Ruttner 1988; Engel 1998), a recent discovery from the western United States dramatically rewrites the history of *Apis* and our understanding of honey bee biogeography. Herein we describe the first fossil honey bee from North America, the first of its tribe for the Western Hemisphere and allied to a species previously known from roughly contemporaneous deposits in southwestern Germany. All previous fossils of *Apis* have come from within the range of the modern species; either from the Oligocene-Miocene of Europe or the Miocene of Asia (Engel 1998, 1999, 2006), with Late Quaternary records of modern *A. mellifera* in East African copal (Zeuner and Manning 1976) and putative *A. cerana* combs in caves from Malaysia (Stauffer 1979). Lastly, we provide a brief overview of honey bee and corbiculate bee evolution and biogeography from the perspective of this revised geological history.

MATERIAL AND METHODS

The specimen described and discussed herein was recovered from the Late Barstovian (*ca.* 14–14.5 Ma) paper shales of the Stewart Valley Basin in west-central Nevada. A total of 117 Hymenoptera recovered from the site are in the California Academy of Sciences collection. Most are ants (Formicidae, 80 specimens), followed by ichneumonids (14), braconids (9), diapiroids (7), and vespids (2), with single specimens of Proctotrupidae, Tiphidae, Aculeata indeterminate, Parasitica indeterminate, and the *Apis* reported herein. Overall the hymenopteran diversity is consistent with other Neogene localities, and the large number of diapiroids suggests a well forested environment.

Morphological terminology in the following descriptions follows that used elsewhere for bees (e.g., Engel 2001a; Michener 2007; Tan et al. 2008). The taxonomy of honey bees has been in flux for many years, with numerous superfluous synonyms and subspecific names (e.g., Engel 1999, with some updates provided by Engel 2003, 2006, unpubl. data; Radloff et al., in review) and anywhere from four to 24 species recognized in as many as three separate genera (e.g., Gerstäcker 1862, 1863; Smith 1865; Ashmead 1904; Buttel-Reepen 1906; Enderlein 1906; Skorikov 1929a, 1929b; Maa 1953; Ruttner 1988; Engel 1999). The system and characters used herein follows that of Engel (1998, 1999, 2006), which recognizes seven modern species (Fig. 1).



FIGURE 1. Modern honey bee diversity – a) *Apis (Apis) mellifera* Linnaeus; b) *A. (A.) koschevnikovi* Enderlein; c) *A. (A.) nigrocincta* Smith; d) *A. (A.) cerana* Fabricius; e) *A. (Megapis) dorsata* Fabricius; f) *A. (Micrapis) florea* Fabricius; g) *A. (M.) andreniformis* Smith. All specimens to same scale.

SYSTEMATIC PALEONTOLOGY

Tribe Apini Latreille

Genus *Apis* Linnaeus

Subgenus *Cascapis* Engel

Hauffapis Armbruster, 1938a: 37. *Nomen invalidum*.

Cascapis Engel, 1999: 187. Type species: *Apis armbrusteri* Zeuner, 1931, by original designation.

DIAGNOSIS.— Honey bees of average size (forewing lengths about 9 mm, similar in proportion to modern *A. mellifera* or *A. cerana* Fabricius) with the derived condition of the basal vein distad cu-a by distance equivalent to about cu-a length or more, but retaining the ancestral condition of a relatively large third submarginal cell in which the anterior border (along the marginal cell) is wide and the posterior-apical angle is relatively broad (ranging from slightly so in the new species to more dramatically so in *A. armbrusteri*). The hind wing primitively possesses the distal abscissa of M (independently lost in *Micrapis* and *A. mellifera*).

INCLUDED SPECIES.— *Apis armbrusteri* Zeuner, 1931 (Miocene of Europe: Böttingen Marmors and Randecker Maars, Württemberg, southwestern Germany) and *A. nearctica* sp. nov. (Middle Miocene of North America: Stewart Valley, Mineral County, central western Nevada).

Key to Species of *Cascapis*

1. Metabasitarsus about 1.6 times as long as wide; mesoscutellum very light brown (perhaps reddish brown in life), contrasting with dark brown mesoscutum (Fig. 2); pleura light brown; labrum yellow; second free abscissa of Rs strongly arched [western North America, Middle Miocene] *A. nearctica* sp. nov.
Metabasitarsus about twice as long as wide (1.9–2.2 times as long as wide); mesoscutellum concolorous with mesoscutum (apparently dark brown); pleura dark brown; labrum dark brown; second free abscissa of Rs weakly curved or nearly straight [northern Europe, Early to Middle Miocene] *A. armbrusteri* Zeuner

***Apis* (*Cascapis*) *nearctica*, Engel, Hinojosa-Díaz, and Rasnitsyn, sp. nov.**

Figures 2–6

DIAGNOSIS.— Similar to *A. armbrusteri* but can be separated by the shorter metabasitarsus, the contrasting integumental coloration of the mesoscutum and mesoscutellum, the light brown pleura, the yellow labrum, and the strongly arched second free abscissa of Rs (a feature that also differs from many modern *Apis*) (*vide* Key, *supra*). The species can be further distinguished from all other honey bees by the apparent reduction of the supraclypeal area in which the antennal toruli abut the basal clypeal margin, without evidence of the short, subantennal sulci in modern *Apis* species (admittedly this condition has not been documented for other fossil honey bees and is not easily visible in the specimens of *A. armbrusteri* seen, it may also be the same condition, or at least similar, in *A. henshawi*). The hind wings of *A. nearctica* and *A. armbrusteri* are virtually identical.

DESCRIPTION.— **Female (worker).** Head length (as measured from top of vertex to median clypeal apex) 3.38 mm, head width 3.33 mm; scape length 1.48 mm; mandible length 1.33 mm, apical width 0.54 mm; mesoscutal length 3.00 mm, width 2.75 mm; mesoscutellar length 0.67 mm; forewing length (as preserved, apicalmost portion missing) 7.83 mm (perhaps 9.0–9.2 mm in total length in life), maximum preserved width 2.83 mm; hind wing length (as preserved, apicalmost portion missing) 4.17 mm; mesobasitarsus length 1.58 mm, width 0.75 mm; metatibia (corbicula) length 2.88 mm, maximal width 1.08 mm; metabasitarsus length 2.08 mm, width 1.25 mm; first metasomal tergum length 1.75 mm, width 4.00 mm (perhaps distorted from being flattened as it appears somewhat outstretched). Head slightly longer than wide, dark brown except as indicated; scape elongate and dark brown; malar space elongate, nearly as long as clypeal medial length; antennal toruli apparently abutting clypeal basal margin. Compound eyes oblong, with inner margin concave, densely covered in elongate setae (most easily visible under thin layer of distilled water to increase contrast). Clypeus broader than long, widest at tangent of mandibular articulation, apical margin gently concave, dark brown in color. Labrum much broader than long, apical margin gently concave, yellow in color (Figs. 3a, 5a). Mandible spatulate (with broad basal articulation, narrow mid-region, and apically expanded distal third), margins obliquely truncate, without dentition, inner surface with evident median and posterior keels (*sensu* Maa 1953) (Figs. 3b, 5b), outer surface apparently without sculpturing; basal half brown, apical half yellow. Pleura apparently light brown; mesoscutum dark brown, contrasting with relatively bulbous and light brown mesoscutellum; metanotum and propodeum not evident. Legs light brown; metatibia with corbicula developed on outer surface (corbicula *sensu* Engel 2001a, not the broader concept of Michener 1999), with well-defined rastellum present (rastellar comb setae on inner apical margin of metatibia evident in dorsal view extending beyond apex) (Figs. 4c, 5c), apical spurs absent; metabasitarsus with well-defined auricle present on basal margin (Figs. 4b, 5d), at least four pollen brush rows evident on inner surface (Fig. 5d), metabasitarsus about 1.6 times as long as wide, about 0.72 times length of

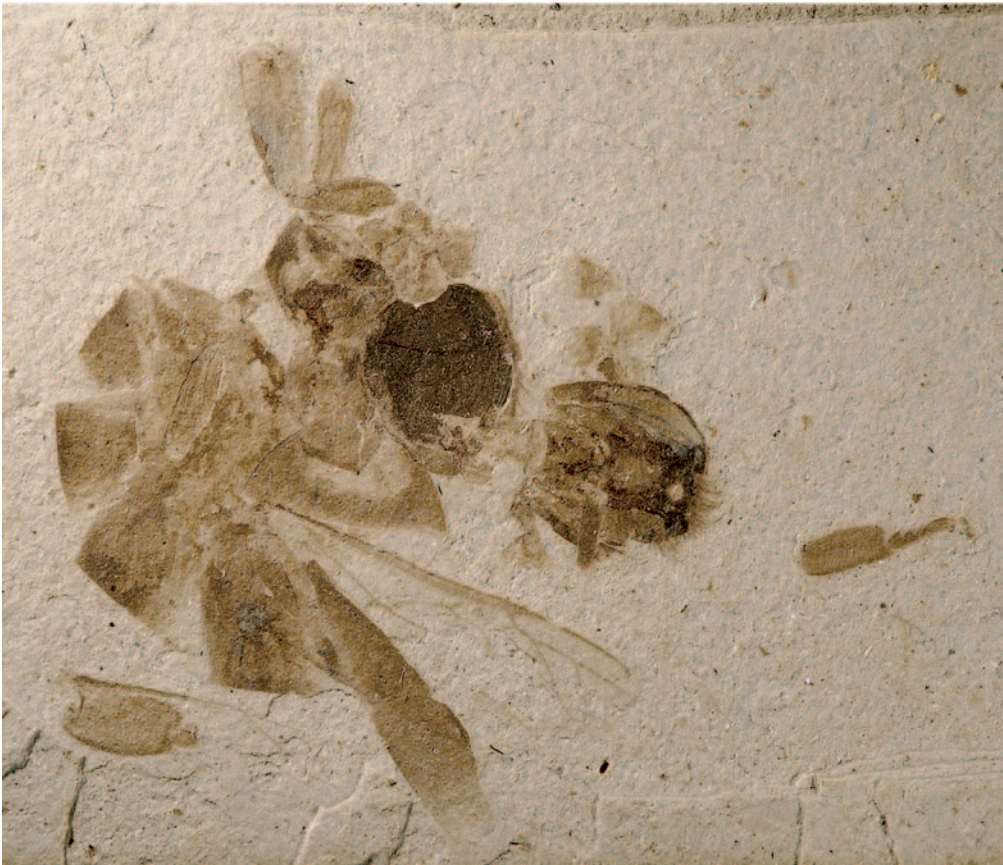


FIGURE 2. Holotype worker of *Apis (Cascapis) nearctica* sp. nov. (CAS #236) as preserved.

metatibia (*versus* about twice as long as wide and 0.67 times length of metatibia in *A. armbrusteri*); pretarsal ungues stout, simple; arolium present and large (Fig. 4a). Metasoma typical for worker honey bee; apical margins of terga relatively straight, terga uniformly colored and brown except medioapical surface of first metasomal tergum lighter and apparently slightly concave; sting evident and straight, with at least a few distinct barbs or serrations along one lancet (Fig. 5e). Forewing with venation typical of *Apis* and subgenus *Cascapis*; basal vein separated from 1cu-a by distance nearly equivalent to 1cu-a length; first submarginal cell smallest, with first free abscissa Rs sinuate (rather than relatively straight); r-rs shorter than anterior margin of second submarginal cell; second submarginal cell trapezoidal in overall shape, with 1rs-m relatively straight and strongly slanted apically such that posterior border of cell is slightly more than three times length of anterior border; third submarginal cell relatively broad anteriorly, with 2rs-m relatively straight for nearly its entirely length before distinctly curving to meet M (Figs. 3, 6), lacking aRs₂ (*sensu* Tan et al. 2008). Hind wing with typical *Apis* venation, with distal abscissa M present (Fig. 6).

HOLOTYPE.— Female (worker); #236, USA: Nevada, Mineral County, Stewart Valley, Cal State Site, UTMG [Universal Transverse Mercator Grid]: Zone 11, 418.170 E × 4271.640 N, 38°35'29"N × 117°56'24"W, Middle Miocene, Late Barstovian (ca. 14–14.5 Ma) paper shales; deposited in the Department of Entomology, California Academy of Sciences, San Francisco, California.

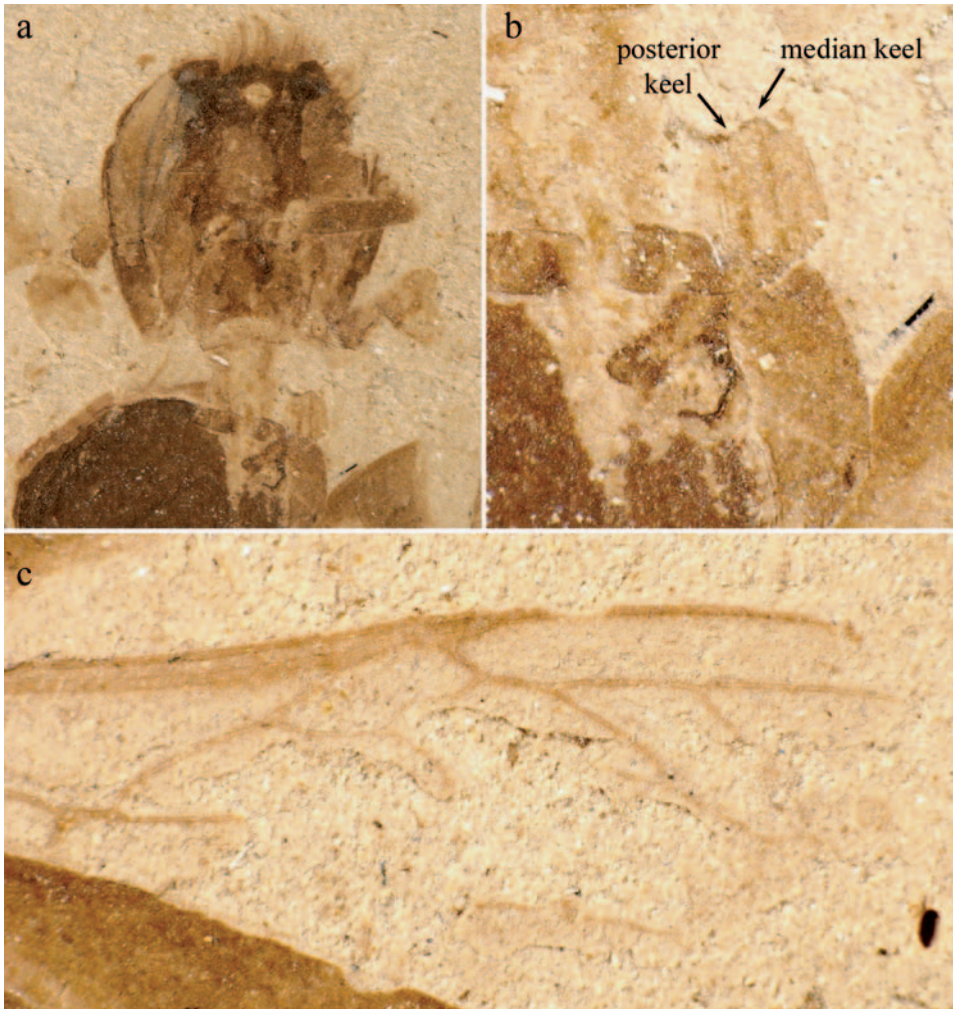


FIGURE 3. Details of holotype worker of *Apis* (*Cascapis*) *nearctica* sp. nov. (CAS #236) – a) head; b) detail of right mandible; c) forewing.

ETYMOLOGY.— The specific epithet is based on the native geographic location of the species in the Nearctic region.

REMARKS.— Although the bee itself is largely disarticulated (Fig. 2), the structures are preserved with remarkable fidelity and nearly every sclerite can be found on the small slab. The head has become entirely dislodged from the body, with the right antenna missing and the left preserved only by the scape. The mandibles have been pulled widely open and the right has become disarticulated and lies partly overlapping the mesosoma (Fig. 3b). The left mandible is twisted in position but remains somewhat attached to the head capsule but is directed upward and away at an oblique angle (Fig. 3a). The labiomaxillary complex is partly extended. The mesosoma can only be seen in dorsal aspect and is directed away from the head such that the right mandible and apex of the glosa overlap the enlarged mesoscutellum and the posterior border of the mesoscutum. The left tegula can be discerned but the other is apparently missing. The pronotum can only be barely seen and the metanotum and propodeum are entirely obscured from view by the mesoscutellum. Some dam-

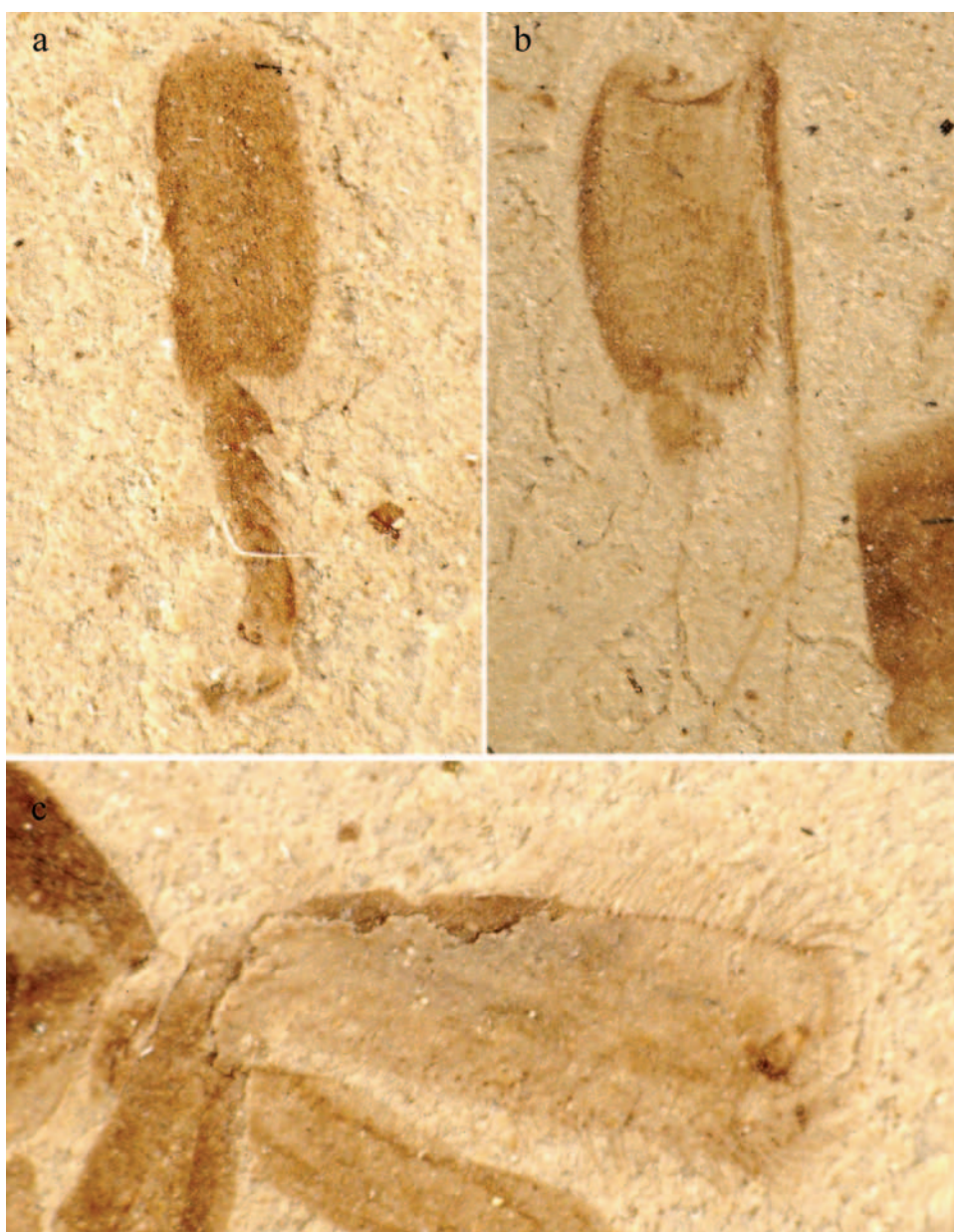


FIGURE 4. Details of holotype worker of *Apis (Cascapis) nearctica* sp. nov. (CAS #236) – a) mesotarsus and meso-pre-tarsus; b) metabasitarsus and first article of metamediotarsus, portion of hind wing can be seen preserved beneath the metabasitarsus; c) corbicula.

aged sclerites that are difficult to interpret to the left of the mesosoma may represent fragments of pleural sclerites. The abdomen is entirely exploded with the dorsal and anterior-facing surfaces of the first metasomal tergum slightly offset to the left of the posterior of the mesosoma (Fig. 2). The remainder of the abdomen is twisted in lateral position and pulled away from the first metasomal segment, while simultaneously twisted back anteriorly such that the successive segments curl back

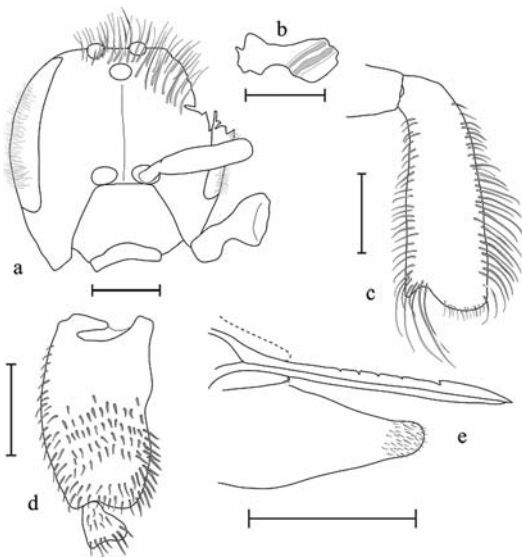


FIGURE 5. Line illustrations of holotype worker of *Apis* (*Cascapis*) *nearctica* sp. nov. (CAS #236) – a) head and left mandible; b) right mandible; c) metabasitarsus; d) corbicula; e) sting. Scale bars = 1 mm.

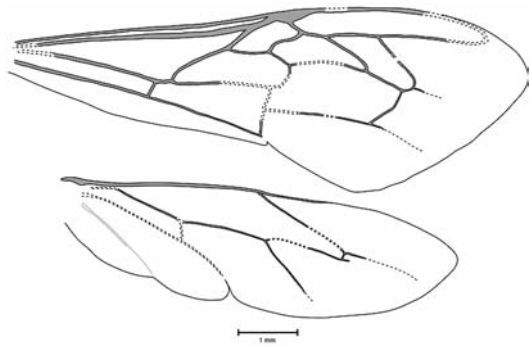


FIGURE 6. Wing venation of *Apis* (*Cascapis*) *nearctica* sp. nov. (CAS #236); forewing above, hind wing below.

toward the anterior of the mesosoma (Fig. 2). The sting is faintly preserved but can be discerned at the apex of the abdominal sclerites. Legs components are scattered over the slab as are the wings. A relatively complete forewing lies between the first metasomal tergum and the second abdominal segment (Figs. 2, 3c), while a hind wing, very faintly impressed, is preserved in line with, and partly underneath, an isolated metabasitarsus and second metatarsomere alongside the second and third abdominal segments (Figs. 2, 4b). A metatibia and metafemur lie disarticulated alongside the anterior of the mesosoma (Figs. 2, 4c). Other leg fragments lay further away from the concentration of body components (e.g., Fig. 4a). All in all, the specimen is remarkably complete, albeit not in one piece nor as the bee clearly functioned in life.

The third submarginal cell is a bit more elongate posteriorly in *A. nearctica* than that seen in *A. armbrusteri*, resulting in 2rs-m being distinctly arched at its posterior-apical corner, while this is very weakly curved in the latter species. This might indicate more affinity with the crown-group honey bees, but in the absence of more corroborating characters we cannot definitively place *A. nearctica* closer to the *Micrapis* + *Megapis* + *Apis s.str.* clade and have accordingly retained it within *Cascapis*.

Apis (*Cascapis*) *armbrusteri* Zeuner

Apis armbrusteri Zeuner, 1931:292; Statz, 1934:7; Armbruster, 1938a:12, 45; Statz, 1941:102; Roussy, 1937:65; Statz, 1944:65; Maa, 1953:631, 633; Kelner-Pillault, 1969a:89; Kelner-Pillault, 1969b:525; Zeuner and Manning, 1976:244; Culliney, 1983:34; Ruttner et al., 1986:348–350; Ruttner, 1988:26–30; Zhang, 1990:87; Petrov, 1992:361; Ruttner, 1992:138–140; Michener, 1990:140; Hong and Miao, 1992:2; Lutz, 1993:183–184, 188, 191, 192; Michener, 1997:28; Engel, 1998:266, 276–279; Engel, 1999:187; Nel et al., 1999:261; Engel, 2000:224; Michener, 2000:807; Engel, 2001b:115; Engel, 2002:5; Kotthoff, 2005:4, 17–18, 24–25; Engel, 2006:3, 6, 7; Michener, 2007:831; Tan et al., 2008:680.

Hauffapis scheuthlei Armbruster, 1938a:43; Maa, 1953:632; Culliney, 1983:34.

Hauffapis scheeri Armbruster, 1938a:43; Maa, 1953:632; Culliney, 1983:34.

Hauffapis scharmanni Armbruster, 1938a:44; Maa, 1953:632; Culliney, 1983:34.

Hauffapis scheeri variety *gallauni* Armbruster, 1938a:45; Maa, 1953:632.

Hauffapis scheeri variety *rahdei* Armbruster, 1938a:45; Maa, 1953:632.

Hauffapis scheuthlei variety *seemanni* Armbruster, 1938a:45; Maa, 1953:632.

- Hauffapis scheuthlei* variety *zeuneri* Armbruster, 1938a:45; Maa, 1953:632.
- Apis (Apis) armbrusteri armbrusteri* Zeuner; Zeuner and Manning, 1976:245; Burnham, 1978:123; Culliney, 1983:34; Zhang, 1990:87; Hong and Miao, 1992:2; Nel et al., 1999:261.
- Apis (Apis) armbrusteri scharmanni* (Armbruster); Zeuner and Manning, 1976:246; Burnham, 1978:123; Culliney, 1983:34; Zhang, 1990:88; Hong and Miao, 1992:2; Nel et al., 1999:261.
- Apis (Apis) armbrusteri scheeri* (Armbruster); Zeuner and Manning, 1976:247; Burnham, 1978:123; Culliney, 1983:34; Zhang, 1990:88; Hong and Miao, 1992:2; Nel et al., 1999:261.
- Apis (Apis) armbrusteri scheuthlei* (Armbruster); Zeuner and Manning, 1976:247; Burnham, 1978:123; Culliney, 1983:34; Zhang, 1990:88; Nel et al., 1999:261.
- Apis armbrusteri cheuthlei* Hong and Miao, 1992:2. *Lapsus calami*.
- Apis scheeri* (Armbruster); Schweigert and Bechly, 2001:4.
- Apis scheuthlei* (Armbruster); Schweigert and Bechly, 2001:4.
- Apis scharmanni* (Armbruster); Schweigert and Bechly, 2001:4.

DIAGNOSIS.— Refer to key and diagnosis for *A. nearctica* (*vide supra*).

REMARKS.— *Apis armbrusteri* was described by Frederick E. Zeuner (1931) based on a “swarm” of worker bees preserved on a slab of thermal limestone from near Böttingen in the Swabian Alb, Württemberg, Germany. This area bordered a Miocene volcanic crater and which apparently had hot springs formed within fissures releasing carbon dioxide, into which the bees had apparently fallen and perished. In the same area and time period of Württemberg was a somewhat larger crater which formed a lake, the Randecker Maar. Shales of the Randecker Maar have preserved a wide diversity of fossils, including an abundance of insects (e.g., Schweigert and Bechly 2001; Kotthoff 2005). Wilhelm Scheuthle initially discovered bees at the Randecker Maar in 1926 and was joined in the hunt for more by Ludwig Armbruster in 1928. A large number of specimens were accumulated and in 1938 Armbruster published an account of their material, describing three separate species and several subspecies for each minor variation in size and shape which they had discovered such that nearly everyone who participated in their digs was honored with a patronym. The variation described by Armbruster (1938a, 1938b, 1938c) certainly falls well within the range seen within modern honey bee species (sometimes even within a single population or colony!) and there can be no justification for the fine distinctions Armbruster drew for recognizing so many, nearly identical species from an area of less than 50 square miles (including the Böttingen material and locality). Unfortunately, Armbruster’s account of the honey bees from Randecker Maar is fraught with errors and cannot be relied upon. Despite the assertions of Zeuner (1931) and Armbruster (1938a, 1938b, 1938c), unfortunately perpetuated by Maa (1953), the compound eyes are not bare, the mouthparts are not weakly developed, and the mesoscutum does not overlap the mesoscutellum. Zeuner and Manning (1976) rightly synonymized the various species of Armbruster but unfortunately retained some of his taxa as subspecies. These were later synonymized by Engel (1999). The Lower Miocene *Apis* from the Most Basin, Czech Republic reported by Prokop and Nel (2003) appears to be a specimen of *A. armbrusteri*, as do “species” D, E, F, and H of Nel et al. (1999).

DISCUSSION

Honey bees comprise one of four remarkably apomorphic, living tribes of corbiculate apine bees (Engel 2001a; Michener 2007), the others being the highly eusocial Meliponini (stingless bees), the primitively eusocial Bombini (bumble bees), and the communal or solitary Euglossini (orchid bees). A further three tribes — Melikertini, Electrapini, and Electrobombini — are known only from as recently as the Eocene (Engel 2001a). Apini are most closely related to the stingless bees (Meliponini) and melikertine bees (Engel 2001a; Schultz et al. 1999, 2001; Cardinal and Packer 2007). Like each of the corbiculate tribes, numerous apomorphies support the monophyly

of Apini and nearly all of those observable in the worker caste are readily visible in the fossil discussed herein — compound eye covered in dense, long setae; worker mandible lacking dentition; metatibia without spurs or penicillum; inner surface of metabasitarsus with brush combs rows of setae; forewing marginal cell elongate, with rounded apex set off from wing margin, 1rs-m and 2rs-m strongly angled respective to M; sting straight and barbed. Thus, despite the overall fragmentary nature of the specimen, a remarkable diversity of features are finely preserved permitting a confident attribution of the specimen not only to genus but permitting diagnosis of the species. Nonetheless, it is greatly hoped that further and more

complete, or at least fully articulated, specimens will be recovered in time. Among living *Apis* the wing venation of the giant honey bees (*Megapis* Ashmead) retain the most plesiomorphies, hence it is little wonder why the venation of *A. dorsata* Fabricius and *A. lithohermaea* Engel are reminiscent in some respects to those of *A. armbrusteri* and *A. nearctica* in regard to the width of the anterior border of the third submarginal cell in the forewing and the presence of the distal abscissa of M in the hind wing.

The presence of *Apis* in North America during the Tertiary highlights the futility of building historical biogeographic hypotheses in the absence of a fossil record (Rasnitsyn 2006). The vast majority of life is extinct and to surmise that we have adequately sampled a group when looking only at modern members is naïve, even in the absence of a fossil record for that particular lineage. Every taxon or clade represents an unbroken genetic lineage back through time and what we have seen in every group with a preserved record is that there have been false starts and evolutionary experimentations that eventually gave rise to the modern diversity. Some of these fossils are intercalated among the crown or surviving species of a clade, while others form grades (stem groups) or natural sister groups to a lineage otherwise characterized on the basis of a suite of attributes seen in crown-group taxa. Changing historical environments, abiotic historical events, or even past differences in biology may result in fossil species that do not occur in the same region or habitat in which modern counterparts live. Fossil insects have redefined biogeographic hypotheses of various lineages of insects otherwise believed to have modern restricted distributions resulting from various vicariant events (e.g., Rasnitsyn 2006; Grimaldi and Engel 2005, 2006; Engel 2008; Engel and Grimaldi 2007, 2008; Engel et al. 2007; Azar and Engel 2008). Elaborate hypotheses have been constructed for the tribes of corbiculate bees, as well as many other insect lineages, that *a priori*

TABLE 1: Classification of living and fossil honey bees (Apini: *Apis*).

—Tribe APINI Latreille—
Genus *Apis* Linnaeus (*s. lato*)
henshawi species group (†*Priorapis* Engel, †*Synapis* Cockerell)
‡*A. vetusta* Engel
‡*A. henshawi* Cockerell
‡*A. petrefacta* (Říha)
‡*A. miocenica* Hong
‡*A. “longtibia”* Zhang
‡*A. “Miocene 1”*
armbrusteri species group (†*Cascapis* Engel)
‡*A. armbrusteri* Zeuner
‡*A. nearctica*, sp. nov.
floreana species group (*Micrapis* Ashmead)
A. florea Fabricius
A. andreniformis Smith
dorsata species group (*Megapis* Ashmead)
‡*A. lithohermaea* Engel
A. dorsata Fabricius
mellifera species group (*Apis* Linnaeus *s. stricto*)
mellifera subgroup
A. mellifera Linnaeus (*Apis* Linnaeus *s. strictissimo*)
cerana subgroup (*Sigmatapis* Maa)
A. cerana Fabricius
A. nigrocincta Smith
A. koschevnikovi Enderlein

assume that the current absence of a group from a particular region today means that this group or its predecessors (stem groups) was similarly not present in that same geographical region. Such biogeographic hypotheses have even been used to argue against certain phylogenetic reconstructions that seem otherwise at odds with vicariant models based solely on surviving species. Relationships among the four extant corbiculate tribes (Apini, Bombini, Euglossini and Meliponini) have been examined recurrently in the last three decades. Studies using different sets of characters; either morphological, molecular, behavioral, or combined; have produced nine of the 15 theoretically possible rooted and fully resolved topologies, as noted by Cardinal and Packer (2007), who present a summary of these different hypotheses. The difficulty of analyzing relationships among the corbiculate tribes can be immediately appreciated by this over abundance of purportedly supported hypotheses. Nonetheless, the main point of contention seems to lie between a hypothesis supported by morphological (Prentice 1991; Roig-Alsina and Michener 1993; Schultz et al. 1999, 2001; Engel 2001a, 2001c; Cardinal and Packer 2007), behavioral (Noll 2002), and combined morphological-molecular (e.g., Ascher et al. 2001) studies, in which Euglossini are sister to the other tribes (Euglossini + (Bombini + (Apini + Meliponini))), and several strictly molecular approaches (Cameron 1991, 1993; Mardulyn and Cameron 1999; Cameron and Mardulyn 2001) which produce a sister-group relationship between Bombini and Meliponini. Interestingly enough, of the two cases mentioned, the first hypothesis (Euglossini sister to the other extant tribes, while Apini sister to Meliponini) is strongly supported in studies in which fossil corbiculates are included (Engel 2001a, 2001c), with the addition of three extinct tribes (Euglossini + (Bombini + (Electrobombini + (Electrapini + (Apini + (Meliponini + Melikertini)))))). The current evidence seems to favor strongly this phylogenetic arrangement, as proposed for most of the morphology-based studies. On the other hand, the distribution of the living representatives of the extant corbiculate tribes gives a picture that is not necessarily easily explained by this phylogenetic hypothesis. The Euglossini are restricted to the Neotropical region, while the Bombini are primarily Palearctic (but also Nearctic, Neotropical, and Oriental in distribution), the Apini are Palearctic, Ethiopian, and Oriental, and the Meliponini are Pantropical (e.g., Rebêlo 2001; Michener 2007). As such the restriction of the Euglossini (sister to the remainder of the tribes) to the New World tropics seems to be at odds with a basal placement in the clade. Rebêlo (2001) concluded that if Euglossini and Bombini shared an immediate common ancestor (i.e., were sisters), then this ancestral population likely existed across a combined supercontinent (“Pangea” in his scenario, although true Pangea predated any of these lineages). He further speculated that during the separation of the Northern Hemisphere and Southern Hemisphere vicariant populations were produced, the northern one ancestral to the Bombini and the southern one to Euglossini, so the absence of the latter from other Gondwanan continents (at least from Africa) could imply that they perhaps existed there with subsequent extinction. It should be noted, however, that the initial rifting of these continental plates began much earlier than the time frame by which Rebêlo (2001) speculated making his scenario a less than ideal match. Regardless, the same author (Rebêlo 2001) as well as Michener (2007), interpreted the modern distribution of Euglossini as the result origination in South America after the complete separation of this continent from Africa (around 100 mya), and evolving there. In any case the interpretation of Euglossini existing once in Africa and going extinct, or never existing there at all, is largely hindered by a lack of suitable paleontological information from that region. That crown group Euglossini date from the Paleocene or earlier, with numerous extinct stem groups of widespread distribution, is certainly a distinct possibility. This also indicates that molecular estimates based strictly on modern (i.e., crown group) euglossines would not be capable of successfully estimating the age at which the lineage (stem and crown groups together) diverged from other corbiculates but instead only when the crown group first appeared, which would be much later. Regardless, paleon-

tological discoveries such as the “lost” corbiculate tribes and of Apini in the Nearctic region demonstrate that significant losses in corbiculate diversity have taken place. Attempts to overlap biogeographical information based exclusively on modern species may contradict well supported phylogenies, but at the same time must be taken with extreme caution as extinction is a real and significant factor that is frequently ignored in cladistic biogeographic analyses (Rasnitsyn 2006).

In terms of *Apis* distribution, biotic exchanges between Asia and North America via Beringia are known from the Late Cretaceous and Miocene periods (e.g., Hopkins 1967; Kontrimavichus 1985), well before the more famously studied Pleistocene connection that permitted early humans to disperse into the Americas. It is likely that species of *Cascapis* were widespread across Europe and Asia during the Early and mid-Miocene, perhaps even the latest Oligocene, and were capable of dispersing into western North America like so many other plant and animal species of the time. The closing of this passageway during the latter part of the Miocene would have left species such as *A. nearctica* isolated and the eventual climatic changes that took place later in and by the close of the Miocene, dramatically altering the flora and fauna of Neogene western North America potentially resulting in their demise at that time. Continued climate change from warm-wet to cool-dry conditions following the mid-Miocene may have contributed to an eventual demise of honey bees in northwestern North America, similar to that seen in some mammal and plant groups (Kürschner et al. 2008).

Honey bees are aggressive competitors of stingless bee colonies wherever they are sympatric. Indeed, it has been noted that stingless bee diversity is greatest in regions where honey bees are not native (e.g., meliponine diversity is greatest in South and Central America, but relatively poor in tropical Africa and Asia), and it is likely that this competitive behavior has contributed to the overall shape of meliponine diversity as well as the overall loss of eusocial bee diversity since the Eocene. Expanding the native distribution of Apini into the New World would appear to contradict some details of this observed pattern in that it would appear little would exclude *Apis* from having co-occurred with the radiation of Meliponini in South America during the Tertiary. However, Miocene climate and habitat might indicate that *Apis* was perhaps relatively confined within North America and that the aforementioned scenario for meliponine diversification might remain viable. During the Early Miocene, western North America beyond the Sierras was of a tropical to warm temperate climate, similar to much of the Palearctic during the same period (e.g., Retallack 2004). This region was bounded by a large, strongly arid area running from central Mexico through the center of the United States, effectively representing a major habitat barrier for honey bees. It is likely that while species of *Cascapis* were contiguous from Europe, northern Asia, and the westernmost North America (perhaps only northwestern North America), honey bees were prevented from migrating further in the Americas and from reaching other New World tropical regions like South America. This would have resulted in a natural absence of Apini from the region in which Meliponini experienced its greatest diversification.

Honey bees were likely truly absent from the North American fauna during the Pliocene and Pleistocene, not becoming reintroduced until the major European colonization of the New World in the early 17th century. Certainly extensive exploration of further Miocene and Pliocene deposits must be undertaken in order to further document the extent of *Apis* distribution in North America and to help refine our estimates of when they declined and eventually disappeared from the fauna. Nonetheless, the currently available information on similar faunistic changes in Miocene North America and Neogene biogeography are consistent with the presence of honey bees in the region at that time and their extirpation late in the Miocene or earliest Pliocene at the latest. Regardless, *A. nearctica* highlights how the perceived absence of lineages from major geographic regions must be tempered with evidence from the fossil record. In the case of the honey bees, *A. nearctica* indi-

cates that North America was one of the native regions of *Apis* distribution, where they became extinct sometime subsequent to the Miocene, and the genus, like horses (*Equus caballus* Linnaeus), ginkgos, and the Chinese tree of heaven (*Ailanthus*), was later reintroduced by European colonization of the Americas.

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