



## **A Giant Honey Bee from the Middle Miocene of Japan (Hymenoptera: Apidae)**

Author: ENGEL, MICHAEL S.

Source: American Museum Novitates, 2006(3504) : 1-12

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2006\)504\[0001:AGHBFT\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)504[0001:AGHBFT]2.0.CO;2)

---

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3504, 12 pp., 4 figures, 1 table

January 12, 2006

## A Giant Honey Bee from the Middle Miocene of Japan (Hymenoptera: Apidae)

MICHAEL S. ENGEL<sup>1</sup>

### CONTENTS

Abstract .....	2
Introduction .....	2
Systematic Paleontology .....	3
<i>Apis lithohermaea</i> , new species .....	3
Discussion .....	5
Acknowledgments .....	8
References .....	8
Appendix 1: Nomenclatorial Notes in <i>Apis</i> .....	10

<sup>1</sup> Division of Invertebrate Zoology, American Museum of Natural History; Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology and Evolutionary Biology, 1460 Jayhawk Boulevard, Snow Hall, University of Kansas, Lawrence, Kansas 66045-7523 (msengel@ku.edu).

## ABSTRACT

A new fossil honey bee is described and figured from middle Miocene deposits of Iki Island, Japan. *Apis lithohermaea* n.sp., is the largest fossil honey bee discovered, rivaling in size the modern giant honey bee, *A. dorsata* Fabricius. *Apis lithohermaea* is the first fossil of the *dorsata* species group recorded. Although the *dorsata* group does not occur farther north than Tibet and southern China and in the Philippines in the Pacific, this lineage occurred near what is today southern Korea and Japan during the Miocene. The geological history of the honey bees is briefly discussed in light of this new discovery. Important notes on the taxonomy of some honey bees (*A. henshawi* Cockerell, *A. aquitaniensis* de Rilly, and subspecies within *A. mellifera* Linnaeus and *A. cerana* Fabricius) are appended.

## INTRODUCTION

The honey bees (genus *Apis* Linnaeus, 1758) are perhaps the most recognizable of all insects. Together with a few other animals (e.g., *Homo sapiens* Linnaeus, *Drosophila melanogaster* Meigen, *Caenorhabditis elegans* [Maupas]), the common honey bee has become one of the most heavily studied of taxa in the animal kingdom. Despite this intense scrutiny, our understanding of honey bee systematics and evolution is remarkably confused and obscured. *Apis* is the only genus in the corbiculate bee tribe Apini (Engel, 1999; Michener, 2000), although some past authors have elevated the subgenera *Megapis*, *Micrapis*, and *Synapis* to generic rank (e.g., Ashmead, 1904; Maa, 1953; Wu and Kuang, 1986, 1987). Species of the corbiculate tribes are more frequently encountered as fossils than any other lineage of bees, particularly when the common Dominican amber species, *Proplebeia dominicana* (Wille and Chandler), is included in such a survey. Even if *P. dominicana* is excluded, however, the corbiculate apines presently outnumber other bee tribes in the fossil record. This preponderance is perhaps partly owing to the eusocial behavior of these species, with typically large colony sizes. Accordingly, the fossil record of these lineages is better understood than most other bee taxa. Despite this relative clarity, the geological history of Apini is obscured owing to the paucity of critical material from the Oligocene and Miocene of Asia, the region and period of time from which honey bees presumably originated and initially radiated, as well as the complete absence of data from the Pliocene.

Herein I present the description of a new

Miocene species of honey bee from eastern Asia. The specimen described below originates from the middle Miocene Chôjabaru Formation of Iki Island, Japan. The fossil is not only significant because of its geographical location and age but also in that it is a representative of the giant honey bees and is quite similar to modern *Apis dorsata* Fabricius. Indeed, this is the first fossil record for crown-group *Apis* outside of relatively modern records of *A. mellifera* Linnaeus in Pleistocene copal (Foord, 1890; Cockerell, 1909; Engel, personal obs.) and Quaternary remains of honey bee combs (Stauffer, 1979). Morphological terminology for the description follows that of Engel (2001b).

Owing to the low specific diversity of the genus and the relative homogeneity among honey bee species, the recognition of subgenera in *Apis* should perhaps be abandoned, including the Recent subgenera, as has been advocated by some authors (e.g., Michener, 2000). I have, therefore, not formally placed the fossil as to subgenus, but for convenience have indicated in the diagnosis to which group it would belong in such a system (table 1). It should be noted that in the diagnoses presented for the subgenera of *Apis* (Engel, 1999) the shape of the third submarginal cell was mistakenly presented as “angle of posteroapical margin of *first* submarginal cell less than 45°”. In each diagnosis these should have read “angle of posteroapical margin of *third* submarginal cell less than 45°” (the standard wing metrics for *Apis* have been thoroughly explained by Ruttner [1988], Alexander [1991], and other authors). This correction should be kept in mind when attempting to identify honey bee subgenera and supraspecific clades (*vide etiam* Engel, 2001c).

TABLE 1  
Classification of Tribe Apini<sup>a</sup>

Genus <i>APIS</i> Linnaeus
† <i>henshawi</i> species group (=† <i>Synapis</i> Cockerell, † <i>Priorapis</i> Engel)
† <i>A. henshawi</i> Cockerell
† <i>A. "longtibia"</i> Zhang
† <i>A. miocenica</i> Hong
† <i>A. petrefacta</i> (Řřha)
† <i>A. "Miocene 1"</i>
† <i>A. vetusta</i> Engel
† <i>armbrusteri</i> species group (=† <i>Cascapis</i> Engel)
† <i>A. armbrusteri</i> Zeuner
<i>florea</i> species group (= <i>Micrapis</i> Ashmead)
<i>A. andreniformis</i> Smith
<i>A. florea</i> Fabricius
<i>dorsata</i> species group (= <i>Megapis</i> Ashmead)
<i>A. dorsata</i> Fabricius
† <i>A. lithohermaea</i> Engel, n.sp.
<i>mellifera</i> species group (= <i>Apis</i> Linnaeus s.str.)
<i>mellifera</i> subgroup
<i>A. mellifera</i> Linnaeus
<i>cerana</i> subgroup (= <i>Sigmatapis</i> Maa)
<i>A. cerana</i> Fabricius
<i>A. koschevnikovi</i> Enderlein
<i>A. nigrocincta</i> Smith

<sup>a</sup> Because of the dubious status of *A. melisuga* Zeuner and Manning and *A. aquitaniensis* de Rilly, these species are not included (vide Engel, 1999, and appendix 1).

## SYSTEMATIC PALEONTOLOGY

### *Apis lithohermaea*, new species Figures 1–3

**DIAGNOSIS:** This species is a member of the *dorsata* species group (= subgenus *Megapis*: table 1) as evidenced by its large size. The fossil can be immediately separated from the other fossil groups by the more distal position of the basal vein from cu-a (confluent or nearly so in the *henshawi* group) and by the posteroapical angle of the third submarginal cell being slightly less than 45° (greater than 45° in the *henshawi* and *armbrusteri* groups). Thus, this fossil is the first to be discovered that belongs to a clade consisting of the modern honey bee species (Engel, 1998, 1999). Among species of this

clade only *A. dorsata* is characterized by the apomorphic development of an enlarged body size, elongate metabasitarsus, and infuscated wing membranes. From *A. dorsata* the new species can be differentiated by the slightly smaller size, absence of a veinal stub at the apex of the marginal cell, broader anterior border of the second submarginal cell, narrower border between the second submarginal cell and the first medial cell, more elongate second medial cell, narrower anterior border of the third submarginal cell, broader metabasitarsus, and smaller number of postauricular pectens on the inner surface of the metabasitarsus.

**DESCRIPTION: Female** (worker caste): Total body length 18 mm; forewing length 11.3 mm (preserved portion; perhaps 12 mm in life). Integument of head, mesosoma, and legs dark reddish brown; metasoma reddish brown, slightly lighter in color on first and second metasomal segments. Forewing membrane infuscated; veins light brown except C, Sc + R, and pterostigma dark reddish brown; minute, stub of an appendiculate vein at marginal cell apex absent (typically present in *A. dorsata*); anterior border of second submarginal cell longer than r-rs, nearly as long as anterior border of third submarginal cell (the anterior border of the second submarginal cell in *A. dorsata* is greatly shortened, about as long as r-rs and approximately one-quarter the length of the anterior border of the third submarginal cell); second abscissa Rs originating beyond midpoint of anterior border of first medial cell, i.e., border between second submarginal cell and first medial cell short (in *A. dorsata* the second abscissa originates near the midpoint such that the border between the second submarginal cell and first medial cell is longer); anterior border of the third submarginal cell about as long as its posterior border (in *A. dorsata* the anterior border is slightly longer than the posterior border); venation depicted in figure 3. Mesosoma slightly narrower than metasoma. Mesotibia with lateral fringe of dark setae. Metabasitarsus about as long as metatibia, about as broad as apical width of metatibia, metabasitarsus not tapering in width at apex (i.e., lateral margins not converging toward apex as is typical in *A. dorsata*), with eight or nine postauricular pectens (a.k.a., scopal



Figs. 1–2. Photomicrographs of *Apis lithohermaea* n.sp., holotype. **1.** Part. **2.** Counterpart.

rows, bristle rows, or pollen brush rows) (*A. dorsata*, with its longer metabasitarsus, has 12–14 postauricular pectens; this species is intriguing in that it combines a relatively elongate metabasitarsus with the plesiomorphic condition of fewer pectens; 8–9 pectens is the usual condition for species of the *mellifera* and *florea* groups). Metasomal segments typical for bees of the *dorsata* group in observable characters (e.g., proportions of segments).

**HOLOTYPE:** Part (fig. 1) and counterpart (fig. 2) deposited in the National Science Museum, Tokyo (NSM-P1-7418). Labeled “Holotype, *Apis lithohermaea* Engel”. This material was briefly mentioned by Fujiyama (1970: 69).

**OCCURRENCE:** Chôjaboru Formation (middle Miocene: Langhian?), Iki Island, Nagasaki Prefecture, Kyushu Region, Japan. Insects occur in soft diatomite between amygdular basalts and volcanic conglomerates that constitute the Chôjaboru Formation. The For-

mation is overlain by Pliocene to Pleistocene alkali olivine basalts.

**PRESERVATION:** Overall the preservation is less than spectacular and many interesting characters cannot be observed. However, enough fragmentary detail can be extracted to provide a relatively robust idea as to the identity and relationships of the species. The bee is dorsoventrally compressed with the head thrust to the side with the mandibles open and the antennae missing. The mandible can be easily distinguished projecting from the apex of the head. Only one set of wings can be distinguished, the forewing extending from the body at an acute angle and alongside the metasoma. The hind wing is faintly visible and impressed beneath the forewing. On the same side of the body a foreleg is preserved extending at an orthogonal angle from the body. Fragments of a hind leg (posterior surface exposed) are preserved along the opposing side of the metasoma and posterior portion of the pterothor-

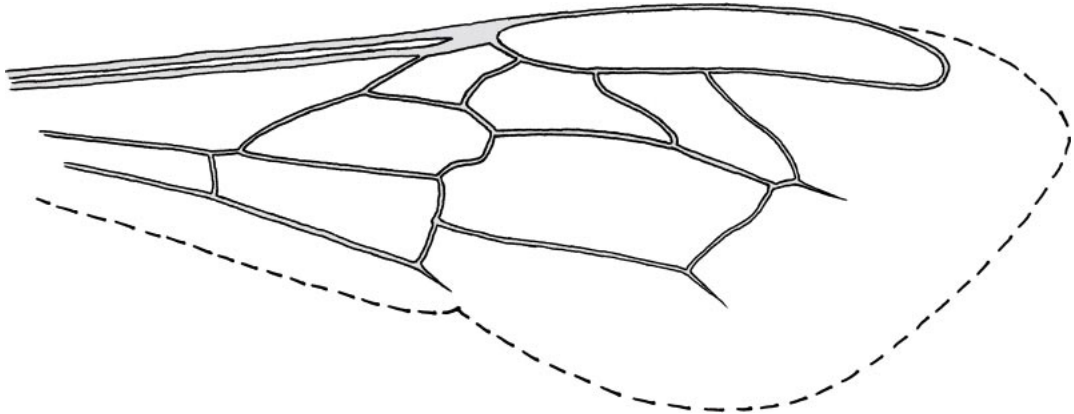


Fig. 3. Forewing venation of *Apis lithohermaea* n.sp. Pattern of membrane infuscation not depicted.

ax. Along with these leg podites are various plant fragments. The sting, mostly retracted, can be discerned at the apex of the metasoma.

**ETYMOLOGY:** The specific epithet is a combination of the Greek words *lithos* (meaning “stone”) and *Hermes* (mythical messenger of the gods) and means “stone messenger”.

**COMMENTS:** The occurrence of an open-nesting honey bee in the middle Miocene of Iki Island is in accord with reconstruction of a warm climate (perhaps warm temperate or even subtropical) for the region at that time.

## DISCUSSION

Honey bees are ubiquitous animals today, being important in both agricultural and natural ecosystems. The tribe consists of distinctive bees that perhaps arose and first diversified in the Early Oligocene, after the Eocene–Oligocene climatic transitions (fig. 4). Certainly the lineage that gave rise to *Apis* had been around for millennia prior to this, as evidenced by the presence of numerous corbiculate bees allied to Apini in the Eocene (Meliponini alone is known from as far back as the Maastrichtian; Michener and Grimaldi, 1988; Engel, 2000, 2001b). However, stem-group Apini have not yet been discovered and bees with the synapomorphies we use to circumscribe the group first appear in the Late Oligocene. Interestingly, the middle Eocene Baltic amber fauna contains a group of

taxa, placed in the extinct tribe Electrapini, which may represent a stem-group lineage relative to the living tribes Apini and Meliponini (Engel, 2001b). This group contains a mix of *Bombus*- or *Apis*-like bees (the genus *Thaumastobombus* in particular resembles primitive *Apis* species). The Baltic amber fossil figured by Poinar (2003) and attributed to *Apis* is a misidentification (the figure very clearly shows a nice specimen of an electrapine). It is perhaps from among taxa similar to the electrapines, which are unknown after the Eocene, that the honey bees as we understand them arose.

As previously discussed, definitive *Apis* likely originated in the Early Oligocene and radiated throughout Eurasia at that time. The distribution of the group at this time was perhaps limited by temperature extremes since species were presumably all open-nesting (i.e., building exposed combs; cavity-enclosed combs are an apomorphic feature of the *mellifera* group; Engel and Schultz, 1997; Engel, 1998). The clade of living species perhaps originated in the uppermost Oligocene or lowermost Miocene (revised from the Late Miocene hypothesis of Engel, 1998, 1999, based on the current fossil) (fig. 4). The development of cavity-nesting behavior in the latest Miocene or earliest Pliocene enabled this lineage to invade more cool temperate areas (e.g., Europe and northern Asia). Competition among species perhaps led to relatively monospecific honey bee cultures in

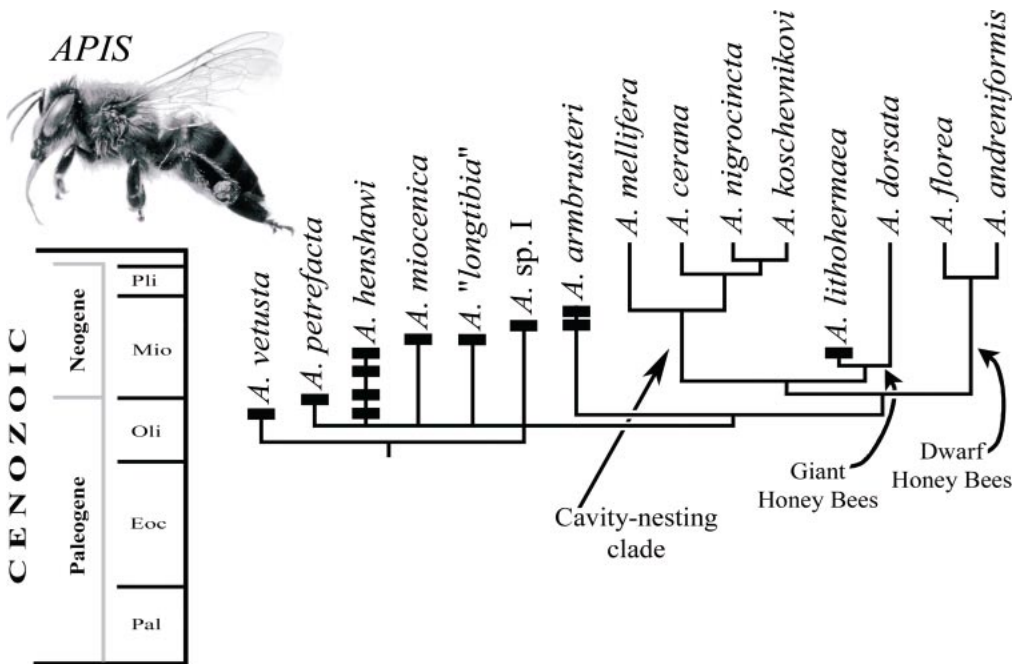


Fig. 4. Phylogeny of the genus *Apis* (vide Engel and Schultz, 1997; Engel, 1998, 1999) with the position of *Apis lithohermaea* n.sp., and other major fossils (black bars) indicated. The genus is represented by a habitus of *A. mellifera* L. *Apis longtibia* Zhang is very likely a synonym of *A. miocenica* Hong (and hence the name is used in quotation marks); *A. petrefacta* (Říha) may similarly be a synonym of *A. henshawi* but such a placement is less evident and therefore the name has not been placed inside quotation marks. For an explanation of “Miocene 1” refer to text footnote 3.

any given area and resulted in a low, modern specific diversity.

Contrary to my earlier assertion (Engel, 1998), specific diversity in *Apis* may have indeed slightly declined over geological time as originally suggested by Culliney (1983) (table 1; fig. 4). At present, such a decline is barely evident, but assuming that we have scarcely begun to sample the past diversity of *Apis* from Asia (most fossils come from Europe), then additional fossil taxa will undoubtedly be discovered there. Thus, *Apis* of the past would become more diverse than the genus at present (presently the number of species are nearly equal). If such a pattern of declining diversity can eventually be further supported by new paleontological discoveries, then such a decline is similar to that which has been noted generally among the highly eusocial corbiculate bee tribes (Engel, 2001a, 2001b). Aggressive competition in honey bees may have contributed to a decline

in specific diversity over geological time. Certainly advanced eusocial species such as *A. mellifera* are known to influence the foraging patterns, abundance, and fecundity of other species (e.g., birds and other bees, particularly other eusocial bees) through competition for resources (Eickwort and Ginsberg, 1980; Paton, 1993; Buchmann, 1996; Sugden et al., 1996; Paini and Roberts, 2005). Indeed, *A. mellifera* workers are aggressive enough to steal pollen directly from foragers of native bee species—so-called cleptoclecty (Thorp and Briggs, 1980; Jean, 2005). In fact, introduced populations of *A. mellifera* have been observed to aggressively displace native populations of *A. cerana* (e.g., Sakagami, 1959). Intensely competitive interactions among honey bee species over expanses of geological time is possibly one factor that, in combination with factors such as global climate change, may have altered *Apis* diversity.

Nel et al. (1999)<sup>2</sup> have presented excellent documentation of wing variation in what appears to be the common Oligocene–Miocene European species *A. henshawi* Cockerell (*A. aquisextana* Nel et al. and *A. aquisextusensis* Nel et al. are both synonyms of *A. henshawi*; Engel, 1999; vide appendix 1) and the Miocene species *A. armbrusteri* Zeuner. From their article one would be impressed by a drastic decline in honey bee species since the Oligocene–Miocene. These authors have, however, followed the morphometric system

<sup>2</sup> In 1999 (Engel, 1999) I had noted that Nel et al.'s (1999) assertion that no phylogenetic hypotheses had been produced incorporating fossils was erroneous. Indeed, Buttel-Reepen (1906) and Statz (1931) had produced early phylogenetic analyses of *Apis* incorporating fossils, and even Pongrácz's (1931) rather anagenetic assertion as to the evolutionary development of *A. mellifera* from *A. oligocenica* Meunier is a hypothesis of descent (i.e., a phylogeny of that lineage). Prokop and Nel (2003) enigmatically rejected my claim on the grounds that those hypotheses of relationship were prior to the advent of cladistics (a.k.a., phylogenetic systematics) and were, therefore, not phylogenetic. This is, of course, an absurd notion. Cladistics or phylogenetic systematics is a method of analysis to arrive at a hypothesis of relationships but has no claim to being the sole means of producing phylogenetic hypotheses (although it is assuredly the most rigorous and robust). Phylogenetic hypotheses can be arrived at using sundry methods and *any* statement purporting to unite two or more taxa can be considered a phylogenetic hypothesis, and any discussion of traits distributed across that topology or used to argue for a topology (whether "evolutionary", "phenetic", or "cladistic") may be considered an "analysis". Indeed, hundreds of workers prior to the advent of cladistic methodology produced phylogenies for all manner of organisms based on various criteria and methodologies; some were more or less defensible, but they were phylogenetic analyses and hypotheses nonetheless (e.g., Haeckel, 1866; Handlirsch, 1908; Crampton, 1924, 1928, 1938; Lorenz, 1941; Michener, 1944). Indeed, although some of these authors merely proposed phylogenetic hypotheses in words, many (if not most) explicitly depicted their hypotheses of relationship as trees and, quite correctly, termed them "phylogenies", "Stammbäume", or the equivalent. Similarly, polytomies are as much a part of phylogenetic analysis as anything else and may represent actual, historical events (e.g., the end product of centrifugal speciation or peripheral isolation models predict a polytomy). Simply because a hypothesis was produced prior to the codification of cladistics (phylogenetic systematics) does not nullify it as a hypothesis nor as a "phylogeny". Similarly, polytomies as part of a hypothesis, whether complete or partial, do not disqualify the analysis from being phylogenetic. Thus, my original statement from 1999 was correct, contrary to the erroneous opinion of Prokop and Nel (op. cit.).

of Ruttner (1988) and thereby arrived at several "species" denoted with letters as "A–J".<sup>3</sup> As has been thoroughly demonstrated by the work of Hepburn and Radloff (1998) and Hepburn et al. (1998) for honey bees in Africa, such morphometric measures of wing venation do not characterize natural entities, and clustering systems based on other characters produce entirely incongruent groups of subspecies or species. Thus, morphometric clusters in *Apis* generally do not correlate with other morphological attributes, mitochondrial DNA haplotypes (Moritz et al., 1994, 1998), or general biological attributes such as presence versus absence of thelytokous parthenogenesis or ovariole number (Hepburn and Crewe, 1991). The recognition of taxa, specific or subspecific, in *Apis* based solely upon morphometric clusters of wing venation is highly suspect (summarized in Hepburn and Radloff, 1998; Hepburn et al., 1998; Hepburn, 2000). Indeed, the use of highly variable characters (e.g., drone flight times, metasomal banding coloration) for recognition of honey bee species in the absence of fixed, diagnostic apomorphic traits (or diagnostic combination of apomorphies) is not recommended. Remarkably, only a few traits of wing venation appear to be truly diagnostic for species-group taxa in *Apis*.

The recognition of species in living *Apis* is rife with difficulties, making paleontological studies all the more challenging for this group of bees. Honey bees exhibit dramatic ranges of variation over huge geographical distributions, and peripheral isolation may be the primary mechanism of speciation in the genus (thereby leaving large paraphyletic, ancestral populations difficult to characterize

<sup>3</sup> Although "species" A, B, and C are apparently *A. henshawi* and D, E, F, and H are apparently *A. armbrusteri*, G and I likely belong to a distinct species here referred to as "Miocene 1" (fig. 4 and table 1), noteworthy for the peculiar shape of the third submarginal cell and infuscation of the leading margin of the forewing, among other traits (E could also belong here, but the figures look more like preservational artifacts rather than diagnostic characteristics). "Species" J similarly appears to be a distinct taxon, but is more dubious, as it could be *A. armbrusteri* if the distal abscissa of M in the hind wing is erroneously recorded as absent or is merely difficult to see in the available material. The material of G, I, and J should be restudied and some of the anomalous venations in the line drawings examined for deformations by preservation.



relative to peripheral derivatives). A picture of relatively recent honey bee history (e.g., affects of Pleistocene climatic and oceanic changes) is coming into focus simply through the study of present-day populations. A more ancient perspective will certainly reveal a rich and complicated evolutionary history. Further paleomellittological work will be required, particularly in southern Asia, to further resolve the origin, radiation, and possible post-Miocene decline (if any) of the honey bees.

#### ACKNOWLEDGMENTS

I am grateful to T. Kase (National Science Museum, Tokyo) for his patience during the long gestation of this study and for the loan of the material discussed herein. Dr. Vladimir Blagoderov and an anonymous reviewer provided valuable critiques of the manuscript and I am grateful for their suggested improvements. Support for this project was provided by NSF EF-0341724. This is contribution 3429 of the Division of Entomology, Natural History Museum and Biodiversity Research Center, University of Kansas.

#### REFERENCES

- Alexander, B.A. 1991. A cladistic analysis of the genus *Apis*. In D.R. Smith (editor), *Diversity in the genus Apis*: 1–28. Boulder: Westview Press, xiv + 265 pp.
- Amssalu, B., A. Nuru, S.E. Radloff, and H.R. Hepburn. 2004. Multivariate morphometric analysis of honeybees (*Apis mellifera*) in the Ethiopian region. *Apidologie* 35(1): 71–81.
- Arillo, A., A. Nel, and V.M. Ortúño. 1996. Two fossil bees from the Oligocene of Izarra (Alava, Spain) (Hymenoptera, Apoidea). *Bulletin de la Société Entomologique de France* 101(1): 59–64.
- Ashmead, W.H. 1904. Remarks on honey bees. *Proceedings of the Entomological Society of Washington* 6: 120–122.
- Buchmann, S.L. 1996. Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. In A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich, and I. Williams (editors), *The conservation of bees*: 125–142. London: Academic Press, viii + [2] + 254 pp.
- Buttel-Reepen, H., von. 1906. *Apistica*. Beiträge zur Systematik, Biologie, sowie zur geschichtlichen und geographischen Verbreitung der Honigbiene (*Apis mellifica* L.), ihrer Varietäten und der übrigen *Apis*-Arten. *Mitteilungen aus dem Zoologischen Museum in Berlin* 3: 117–201.
- Cockerell, T.D.A. 1907. A fossil honey-bee. *Entomologist* 40: 227–229.
- Cockerell, T.D.A. 1909. Some European fossil bees. *Entomologist* 42: 313–317.
- Crampton, G.C. 1924. The phylogeny and classification of insects. *Journal of Entomology and Zoology, Pomona College* 16: 33–47.
- Crampton, G.C. 1928. The grouping of the insect orders and their lines of descent. *Entomologist* 61: 82–85.
- Crampton, G.C. 1938. The interrelationships and lines of descent of living insects. *Psyche* 45: 165–181.
- Culliney, T.W. 1983. Origin and evolutionary history of the honeybees, *Apis*. *Bee World* 64(1): 29–38.
- Eickwort, G.C., and H.S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. *Annual Review of Entomology* 25: 421–446.
- Engel, M.S. 1998. Fossil honey bees and evolution in the genus *Apis* (Hymenoptera: Apidae). *Apidologie* 29(3): 265–281.
- Engel, M.S. 1999. The taxonomy of Recent and fossil honey bees (Hymenoptera: Apidae; *Apis*). *Journal of Hymenoptera Research* 8(2): 165–196.
- Engel, M.S. 2000. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). *American Museum Novitates* 3296: 1–11.
- Engel, M.S. 2001a. Monophyly and extensive extinction of advanced eusocial bees: insights from an unexpected Eocene diversity. *Proceedings of the National Academy of Sciences of the United States of America* 98(4): 1661–1664.
- Engel, M.S. 2001b. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.
- Engel, M.S. 2001c. The honey bees of Thailand (Hymenoptera: Apidae). *Natural History Bulletin of the Siam Society* 49(1): 113–116.
- Engel, M.S. 2003. A replacement name in *Apis* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 76(1): 71.
- Engel, M.S., and T.R. Schultz. 1997. Phylogeny and behavior in honey bees (Hymenoptera: Apidae). *Annals of the Entomological Society of America* 90(1): 43–53.
- Foord, A.S. 1890. Note on a collection of East Coast amber belonging to Mrs. Burwood of Yarmouth. *Transactions of the Norfolk and Norwich Naturalist's Society* 5: 92–95.
- Fujiyama, I. 1970. Fossil insects from the Chô-

- jabaru Formation, Iki Island, Japan. *Memoirs of the National Science Museum (Tokyo)* 3: 65–74.
- Goetze, G.K.L. 1964. Die Honigbiene in natürlicher und künstlicher Zuchtauslese, Teil 1: Systematik, Zeugung und Vererbung. *Monographien zur Angewandte Entomologie* 19: 1–120.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen: Allgemeine Grundzüge der Organischen Formen-Wissenschaft, mechanische begründet durch die von Charles Darwin reformirte Descendenz-Theorie: Zweiter Band: Allgemeine Entwicklungsgeschichte der Organismen*. Berlin: Reimer, clx + 462 pp.
- Handlirsch, A. 1908. *Die Fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen*. Leipzig: Engelmann, 1121–1430 pp.
- Hepburn, H.R. 2000. Honeybee (*Apis mellifera*) classification and the confounding effects of trinomial nomenclature. In M.M.G. Bitondi and K. Hartfelder (editors), *Anais do IV Encontro Sobre Abelhas: 188–196*. Ribeirão Preto: Universidade de São Paulo, xxix + [1] + 363 pp.
- Hepburn, H.R., and R.M. Crewe. 1991. Portrait of the Cape honeybee, *Apis mellifera capensis*. *Apidologie* 22(6): 567–580.
- Hepburn, H.R., and S.E. Radloff. 1998. Honeybees of Africa. Berlin: Springer Verlag, xv + 370 pp.
- Hepburn, H.R., S.E. Radloff, and S. Fuchs. 1998. Population structure and the interface between *Apis mellifera capensis* and *Apis mellifera scutellata*. *Apidologie* 29(4): 333–346.
- Hepburn, H.R., D.R. Smith, S.E. Radloff, and G.W. Otis. 2001. Intraspecific categories of *Apis cerana*: morphometric, allozymal and mtDNA diversity. *Apidologie* 32(1): 3–23.
- Heyden, C., von. 1862. Gliederthiere aus der Braunkohle des Niederrhein's, der Wetterau und der Röhn. *Palaeontographica* 10: 62–82.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature [4th ed.]* London: International Trust for Zoological Nomenclature, xxix + 306 pp.
- Jean, R.P. 2005. Quantifying a rare event: pollen theft by honey bees from bumble bees and other bees (Apoidea: Apidae, Megachilidae) foraging at flowers. *Journal of the Kansas Entomological Society* 78(2): 172–175.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*, ed. 10, vol. 1, Reformata. Holmiae [Stockholm]: Salviae, 824 pp.
- Lorenz, K. 1941. Vergleichende Bewegungsstudien an Anatinen. *Journal für Ornithologie* 89: 194–294.
- Maa, T.C. 1944. On the classification and phylogeny of the honeybees. *Entomology Shaowuana* 1: 4–5. [In Chinese. This journal and paper could not be traced and I have, therefore, followed Maa's (1953) restatement of its contents.]
- Maa, T.C. 1953. An inquiry into the systematics of the tribus Apidini or honeybees (Hym). *Treubia* 21(3): 525–640.
- Meunier, F. 1915. Über einige fossil Insekten aus der Braunkohlenschichten (Aquitaniens) von Rott (Siebengebirge). *Zeitschrift der Deutschen Geologischen Gesellschaft* 67: 205–217, 219–230.
- Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History* 82(6): 151–326.
- Michener, C.D. 2000. *The bees of the world*. Baltimore: Johns Hopkins University Press, xiv + [1] + 913 pp.
- Michener, C.D., and D.A. Grimaldi. 1988. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). *American Museum Novitates* 2917: 1–10.
- Moritz, R.F.A., M. Beye, and H.R. Hepburn. 1998. Estimating the contribution of laying workers to population fitness in African honeybees (*Apis mellifera*) with molecular markers. *Insectes Sociaux* 45(3): 277–287.
- Moritz, R.F.A., J.M. Cornuet, P. Kryger, L. Garnery, and H.R. Hepburn. 1994. Mitochondrial DNA variability in South African honeybees (*Apis mellifera* L.). *Apidologie* 25(2): 169–178.
- Nel, A., X. Martínez-Delclòs, A. Arillo, and E. Peñalver. 1999. A review of the Eurasian fossil species of the bee *Apis*. *Palaeontology* 42(2): 243–285.
- Paini, D.R., and J.D. Roberts. 2005. Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaeus alcyoneus*). *Biological Conservation* 123(1): 103–112.
- Paton, D.C. 1993. Honeybees in the Australian environment. *Bioscience* 43(2): 95–103.
- Peng, Y.S., M.E. Nasr, and S.J. Locke. 1989. Geographical races of *Apis cerana* Fabricius in China and their distribution: review of recent Chinese publications and a preliminary statistical analysis. *Apidologie* 20(1): 9–20.
- Poinar, G., Jr. 2003. Amber. In V.H. Resh and R.T. Cardé (editors), *Encyclopedia of insects*: 9–12. New York: Academic Press, xxviii + [1] + 1266 pp.
- Pongrácz, A. 1931. Bemerkungen über die Insektenfauna von Oeningen nebst Revision der

- Heer'schen Typen. Verhandlungen des Naturhistorisch-Medizinischen Vereins zu Heidelberg 17: 104–125.
- Prokop, J., and A. Nel. 2003. New fossil Aculeata from the Oligocene of the České Středohoří Mts. and the Lower Miocene of the Most Basin in northern Czech Republic (Hymenoptera: Apidae, Vespidae). *Acta Musei Nationalis Pragae, Series B Historia Naturalis* 59(3–4): 163–171.
- Rilly, F., de. 1924. Une ancêtre: L'abeille aquitaine. *L'Apiculteur* 68(10): 308–310.
- Rilly, F., de. 1949. Une abeille fossile Française: *L'Apis aquitaniensis*. *La Nature* 3168: 125.
- Roussy, L. 1937. Contributions a l'étude de l'abeille tertiaire, de ses parasites et de ses ennemis. *La Gazette Apicole, Montfavet* 388: 49–72.
- Ruttner, F. 1988. Biogeography and taxonomy of honeybees. Berlin: Springer Verlag, xxii + 284 pp.
- Ruttner, F. 1992. Naturgeschichte der Honigbienen. Munich: Ehrenwirth, 357 pp.
- Sakagami, S.F. 1959. Some interspecific relations between Japanese and European honeybees. *Journal of Animal Ecology* 28: 51–68.
- Smith, D.R. 1991. Mitochondrial DNA and honey bee biogeography. In D.R. Smith (editor), *Diversity in the genus Apis*: 131–176. Boulder: Westview Press, xiv + 265 pp.
- Statz, G. 1931. Eine neue Bienenart aus Rott am Siebengebirge. Ein Beitrag zur Kenntnis der fossilen Honigbienen. *Wissenschaftlichen Mitteilungen des Vereins für Natur- und Heimatkunde, Köln* 1: 39–60.
- Stauffer, P.H. 1979. A fossilized honeybee comb from Late Cenozoic cave deposits at Batu Caves, Malay Peninsula. *Journal of Paleontology* 53(6): 1416–1421.
- Sugden, E.A., R.W. Thorp, and S.L. Buchmann. 1996. Honey bee-native bee competition in Australia: focal point for environmental change and apicultural response. *Bee World* 77: 26–44.
- Théobald, N. 1937. Les insectes fossiles des terrains Oligocènes de France. Nancy: George Thomas, 473 + [1] pp., 29 pls.
- Thorp, R.W., and D.L. Briggs. 1980. Bees collecting pollen from other bees (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 53(1): 166–170.
- Wu, Y., and B. Kuang. 1986. A study of the genus *Micrapis* (Apidae). *Zoological Research* 7(2): 99–102. [In Chinese]
- Wu, Y., and B. Kuang. 1987. Two species of small honeybee—a study of the genus *Micrapis*. *Bee World* 68(3): 153–155.
- Zeuner, F.E., and F.J. Manning. 1976. A monograph on fossil bees (Hymenoptera: Apoidea). *Bulletin of the British Museum (Natural History), Geology* 27(3): 149–268.

## APPENDIX 1

NOMENCLATORIAL NOTES IN *APIS*

The following account provides nomenclatorial updates to my earlier catalog of *Apis* taxonomy (Engel, 1999, 2003). Particularly pertinent is the revised nomenclature for *A. henshawi*, but I have also appended the status of *A. aquitaniensis* as well as one subspecific epithet in *A. mellifera* and three names for subspecies in *A. cerana* that have recently appeared in the literature and that require comment. It may soon be prudent to provide an actual monograph of *Apis*, the notes for which I have already compiled.

†*Apis henshawi* Cockerell

- Apis* (*Synapis*) *henshawi* Cockerell, 1907: 229.  
*Apis dormitans* Cockerell, 1907: 228. *Nomen praeoccupatum* (nec Heyden, 1862).  
*Apis oligocenica* Meunier, 1915: 210.  
*Synapis dormitans* (Cockerell); Statz, 1931: 45.  
*Synapis henshawi* (Cockerell); Statz, 1931: 45.  
*Synapis kaschkei* Statz, 1931: 50.  
*Apis cuenoti* Théobald, 1937: 401.  
*Apis oligocaenica* Goetze, 1964: 9. *Lapsus calami*.

- Apis henshawi* Goetze, 1964: 9. *Lapsus calami*.  
*Apis kaschkei* Goetze, 1964: 9. *Lapsus calami*.  
*Apis henshawi dormiens* Zeuner and Manning, 1976: 241. *Nomen novum pro Apis dormitans* Cockerell, 1907.  
*Apis henshawi kaschkei* (Statz); Zeuner and Manning, 1976: 243.  
*Apis aquisextana* Nel, Martínez-Delclòs, Arillo, and Peñalver In Arillo et al., 1996: 60.  
*Apis aquisextusensis* Nel, Martínez-Delclòs, Arillo, and Peñalver, 1999: 253. **New synonymy.**

COMMENTS: The name *aquisextusensis* was unnecessarily proposed in 1999 (Nel et al., 1999) for a species proposed three years earlier by the same authors and based on the same material (Arillo et al., 1996). The specimens upon which the species *A. aquisextusensis* was based were first mentioned by Arillo et al. (1996), and at that time referred to as *A. aquisextana*. Since Arillo et al. (1996) provided a type designation and diagnosis for *A. aquisextana* the name became validated in that article (ICZN, 1999). Later, in a treatment of fossil honey bees, this species was recognized as a junior synonym of the more widely distributed Oli-

go–Miocene species *A. henshawi* (Engel, 1998). Confusingly, while reviewing fossil honey bees from Europe, the same authors who proposed *A. aquisextana* proposed a second name for specimens of the same type series (Nel et al., 1999). In their second contribution, however, these authors designated a different specimen as the holotype and employed the name *A. aquisextusensis* (Nel et al., 1999). Since a name had already been proposed based on the same material, *A. aquisextusensis* immediately became a junior synonym of *A. aquisextana* (and thereby indirectly of *A. henshawi*). Owing to this confusion, I herein provide a revised taxonomic summary for *A. henshawi* and officially propose the required synonymy of *A. aquisextusensis*.

†*Apis aquitaniensis* de Rilly

“Abeille Aquitanienne” de Rilly, 1924: 309.  
*Apis aquitaniensis* de Rilly, 1949: 125.

COMMENTS: Rilly first mentioned this fossil in a brief article in an apicultural serial (Rilly, 1924) but simply referred to the species with a vernacular. The first proposal of a Latinized epithet for the same fossil appeared a quarter of a century later (Rilly, 1949). Rilly’s figures and “descriptive” comments are poor and do not permit authoritative identification. His material is reported to have been deposited in the Museum de Marseille (Roussy, 1937). Repeated letters to directors and curators of this institution, however, have failed to invoke any response. From the little available evidence it is likely that this is a synonym of *A. henshawi*. Until the holotype can be located and examined, it is retained as a separate species but of uncertain taxonomic status.

*Apis mellifera woyigambella* Amssalu et al.,  
*nomen nudum*

*Apis mellifera woyi-gambella* Amssalu, Nuru, Radloff, and Hepburn, 2004: 79. *Nomen nudum*.

*Apis mellifera woyi-gambell* Amssalu, Nuru, Radloff, and Hepburn, 2004: 71. *Lapsus calami*.

COMMENTS: This subspecific epithet is plagued by any number of troubles. Firstly, the ICZN (1999) explicitly prohibits the use of hyphenation or other marks (e.g., umlauts, diereses, diacritics) and the name must be emended to a single word. More troubling, however, is that the name as proposed is not available in zoological nomenclature. The subspecies was not provided with a description in words purported to differentiate the taxon, and no holotype (or type series of any kind!) was designated, as expressly required by the ICZN

(1999) for the purpose of nomenclatural stability. The name must be considered a *nomen nudum* and may not be used. In general, however, I believe subspecies within *Apis* should all be synonymized under their respective species and I have, therefore, not attempted to validate a name for this form herein. If ever validated, then this name will take its authorship and date from any such later publication in cases of competing priority.

*Apis cerana hainanensis* Hepburn et al.,  
*nomen nudum*

*Apis cerana hainanensis* Hepburn, Smith, Radloff, and Otis, 2001: 6. *Nomen nudum*.

COMMENTS: Hepburn et al. (2001) unnecessarily introduced, into an already voluminous and confusing taxonomic literature, two additional names for forms of the widely distributed Eastern honey bee, *Apis cerana* (*vide etiam* “*abaensis*” under *A. cerana heimifeng*, *infra*). Both names are *nomina nuda* under the current ICZN rules (ICZN, 1999) and therefore are not available for usage as epithets. The name “*abaensis*” was proposed for a form that had already been validated under another name (*heimifeng*). The name *A. cerana hainanensis*, however, was a novel introduction for a variety on Hainan Island that had not previously been given a Latinized name. Thus, in order to retain this form as a valid subspecies it must be proposed anew. In general, however, subspecies within *Apis* should all be synonymized under their respective species and I have, therefore, not attempted to validate a name for this form herein. If ever validated, then this name will take its authorship and date from any later publication in cases of competing priority.

*Apis cerana heimifeng* Engel

*Apis cerana heimifeng* Engel, 1999: 179.

*Apis cerana abaensis* Hepburn, Radloff, Smith, and Otis, 2001: 6. *Nomen nudum*.

COMMENTS: Peng et al. (1989) performed a preliminary morphometric study of variation in the Asian honey bee, *A. cerana*. From these studies they recognized several distinctive morphoclusters that they termed races and to which they gave vernacular names (for purposes of discussion). One race was identified with the vernacular name “*Aba race*” and later validated as *A. cerana heimifeng*. Peng et al. (1989) never employed their name “*Aba*” as a Latinized taxonomic entity. Recently, Hepburn et al. (2001) have unfortunately turned this vernacular name into a Latinized epithet by employing it as a subspecific name for which it was never intended, rather than use an

already valid taxonomic name for this morphotype.

*Apis cerana skorikovi* Engel

*Apis cerana skorikovi* Maa, 1944: 4. *Nomen nudum*.

*Apis cerana*, Himalaya race, Ruttner, 1988: 121, 158.

*Apis cerana*, Xizang race, Peng et al., 1989: 15.

*Apis cerana himalaya* Smith, 1991: 154. *Nomen nudum*.

*Apis cerana himalayana* Ruttner, 1992: 296; Hepburn et al., 2001: 6. *Nomen nudum*.

*Apis cerana skorikovi* Engel, 1999: 180.

COMMENTS: Although the names *himalaya* and *himalayana* (the latter overlooked in my 1999 treatment) as Latinized epithets are *nomina nuda* and therefore unavailable, it has not stopped them from being used frequently in the literature (e.g., Hepburn et al., 2001). A validly proposed name is available for this race, i.e., *A. cerana skorikovi*, and should be used to the exclusion of other sub-specific epithets.

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site <http://library.amnh.org/pubs>. Inquire about ordering printed copies via e-mail from [scipubs@amnh.org](mailto:scipubs@amnh.org) or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.

⊗ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).