Apidologie 29 (1998) 265–281
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Original article

Fossil honey bees and evolution in the genus *Apis* (Hymenoptera: Apidae)

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(Received 22 August 1997; accepted 12 December 1997)

Abstract – A partial revision is provided for some of the more well-known fossil honey bee species. *Apis henshawi* is diagnosed, the holotype described, and a complete taxonomic history presented. The following names are newly synonymized under *A. henshawi*: *A. henshawi dormiens* and *A. aquisextana*. A new species, *A. vetustus* sp. n., is recognized from Oligocene strata. *Synapis petrefacta* is officially transferred into the genus *Apis* (new combination) and *A. fota* and *A. shandongica* are placed into synonymy with *A. miocenica* (new synonymies). The authorship of *A. melisuga* is discussed and the name considered to be a *nomen dubium*. A phylogeny is proposed for *Apis* which incorporates the known fossil species and evolution in the genus discussed. No honey bees are known from before the Oligocene. © Inra/DIB/AGIB/Elsevier, Paris

***Apis* / Apoidea / Cenozoic / paleontology / phylogeny / taxonomy**

1. INTRODUCTION

The honey bees (genus *Apis* L.) are the most well recognized of all insects. Owing to the important role honey bees play in agriculture, it is not surprising that they should factor so heavily in our mythology, art and religion. It *is* surprising, however, that the systematics of such a small and important group should be so confused. Four to twenty-four species have been recognized at one time or another, and the genus has been diced into as many as three genera [3, 20]. As the group is currently classified there are six species, with some authors according distinctive populations of the giant honey bee (*Apis dorsata* F.) or the Asian honey bee (*A. cerana* F.) specific status [21, 38]. Although the taxonomy of these species is in need of monographic study and the taxonomic histories of all species have been compiled by the

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Present address: 1503 Rosewood Terrace Drive, Ballwin, MO 63021, USA author, the focus of the present work is simply to clarify the taxonomy of some of the known fossil honey bees.

The first fossil species of the genus was described as *A. henshawi* by Cockerell [6]. Although previous fossils had been proposed as species of *Apis*, Cockerell's was the first correctly assigned to the genus. By the time of Zeuner and Manning's [42] monograph on the fossil bees of the world, 17 fossil honey bee species or subspecies had been proposed (not including those later removed to other genera). Four species have been added since 1976 by other workers [2, 15, 43, 44]. *Table I* summarizes the currently recognized species of *Apis* along with their geographical and geological distribution. Of the living species, only *A. mellifera* L., has been found in the fossil record from Pleistocene copal [42]. Stauffer [35] reports a fossilized honey comb from the Malay Peninsula of early Quaternary age which is probably the product of, or a close precursor of, *A. cerana* (Stauffer assigns the comb to *A. javana* Enderlein, a junior synonym of *A. cerana*).

The holotype of the most famous of the fossil honey bees, *A. henshawi* (*figure 1*), is located in the Museum of Comparative Zoölogy, Harvard University. This specimen, along with the others in that collection, are among the finest. Many of the finer details of the bees are flawlessly preserved in the specimens (e.g. *figure 8* depicts the pollen press of *A. henshawi*). Due to the inadequacy of the descriptions provided by Zeuner and Manning [42] in their revision, and to the usual splitting of species based on minor size differences in the absence of diagnosable characters by these authors, a more detailed treatment of the fossil bees is required. New des-

Table I. A listing of the honey bee species recognized by the present author (six extant and nine extinct). Fossil taxa are in boldface. The references given are for descriptions, species recognition, or geologic distributions. The distributions of the living species have been beautifully detailed elsewhere [26, 29, 30] and are therefore omitted here.

Taxon	Epoch	Distribution	References
andreniformis	Holocene	Asia	Smith [33]; Wu and Kuang [39, 40]
armbrusteri	Miocene	Germany	Zeuner [41]; Zeuner and Manning [42]
catanensis**	Miocene	Italy	Roussy [28]
cerana	Holocene	Asia	Fabricius [12]
cuenoti	Oligocene	France	Théobald [36]
dorsata	Holocene	Asia	Fabricius [12]
florea	Holocene	Asia, Arabia, Africa	Fabricius [11]
henshawi	Oligocene	Europe	Cockerell [7]; herein
koschevnikovi	Holocene	Asia	von Buttel-Reepen [4]; Tingek et al. [37]
longtibia	Miocene	China	Zhang [44]
melisuga n. dub.*	Miocene	Italy	Handlirsch [13]; Zeuner and Manning [42]
mellifera	Pleisto-Holocene	Cosmopolitan	Linnaeus [19]; Zeuner and Manning [42]
miocenica	Miocene	China	Hong [15]; Zhang [43, 44]; herein
petrefacta	Miocene	Bohemia	Ríha [27]; herein
vetustus	Oligocene	Germany	herein

* See text for discussion of this dubious species.
** This may not be a valid species.

criptions for the fossil honey bees in the Museum of Comparative Zoölogy are provided below along with an attempt to clean up some of the taxonomic difficulties that have crept into the genus.

2. MATERIALS AND METHODS

All measurements were made using an ocular micrometer on a WILD-M5a microscope and should be considered approximate. The following abbreviations are used in the remainder of the text: F, flagellomere; MCZ, Museum of Comparative Zoölogy; S, sternum; T, tergum.

3. SYSTEMATICS

3.1 *Apis henshawi* Cockerell

(*Figures 1–3, 5–6, 8* and *11*)

Apis (*Synapis*) *henshawi* Cockerell, 1907, Entomologist, London, 40, 229.

Apis dormitans Cockerell, 1907 (*non* Heyden, 1862), Entomologist, London, 40, 228.

Apis oligocenica Meunier, 1915, Zt. Deut. Geol. Ges., Berlin, 67, 210.

Synapis kaschkei Statz, 1931, Wiss. Mitt. Ver. Nat-Heimatik, Köln, 1, 50.

Apis henshawi dormiens Zeuner and Manning, 1976, Bull. Brit. Mus. Nat. Hist. (Geol), 27, 241. *Nomen novum pro Apis dormitans* Cockerell, 1907. **New synonymy.**

Apis aquisextana Nel, Martínez-Delclòs, Arillo, and Peñalver, 1996, in Arillo et al., 1996, Bull. Soc. Entomol. France, 101, 60. **New synonymy.**

3.1.1. Diagnosis

Basal vein gently curved and slightly distad cu-a by 1.5 times vein width. Inner angle of third submarginal cell between 2r-m and M nearly orthogonal, much greater than 45°; cell slightly broader on anterior border than posterior border. Distal abscissa of vein M in hind wing present.

3.1.2. Description

Holotype (obverse and reverse impressions): total body length 15.4 mm; total forewing length 7.7 mm. Head length 3.28 mm. Mandibles broader at apex than base (apical width 0.56 mm; basal width 0.36 mm; length 1.26 mm), without teeth; distinct dorso-longitudinal carina on inner surface. Mouthparts long. Combined length of scape and pedicel 1.28 mm; length of flagellum 2.84 mm; F1–9 each about as long as wide, individual lengths 0.28 mm; F10 longer than wide, length 0.32 mm. Vertex with long, simple hairs. Hairs of compound eye long. Diameter of median ocellus 0.24 mm. Mesoscutum apparently without pubescence; scutellum with long hairs. Claws bifid. Basal vein gently curved, distad cu-a by 1.5 times vein width (*figures 5* and *11*); stigma length 0.38 mm, width 0.14 mm; anterior border of first submarginal cell along Rs 0.3 mm in length; length of anterior border of second submarginal cell 0.24 mm, posterior border 1.38 mm; length of anterior border of third submarginal cell 0.92 mm, posterior border 0.9 mm, inner posterior angle between 2r-m and M nearly orthogonal; marginal cell long and bluntly rounded at apex, length 3.12 mm, width 0.4 mm. Hind wing with distal abscissa of vein M present, M gently curved. Scattered hairs on T5–6; pubescence not apparent on preceding terga or sterna; sting length 1.8 mm, length of ramus 0.54 mm.

Legs of reverse counterpart more finely preserved than obverse. Fore femur length 1.76 mm; tibia length 1.24 mm; basitarsus length 1.2 mm. Hind tibia length 2.76 mm, width at apex 0.92 mm; corbicula evident, without hairs except along outer margins (base of setae faintly evident); basitarsus length 1.8 mm, width 1 mm; pollen press barely visible, setal rows on basitarsus not apparent.

Clypeus pale brown, remainder of head dark brown. Scape and pedicel dark brown, flagellum dark brown. Mesosoma dark brown. Legs dark brown except tarsomeres 2–5 pale brown; claws pale brown except apical halves dark brown. T1–2 dark brown; remaining terga progressively paler; sterna pale brown.

Specimen Nr 7513: Total body length 15.1 mm. Head width 3.52 mm. Combined length of scape and pedicel 1.24 mm; F1–9 each about as long as wide; F10 longer than wide; flagellum length 2.24 mm. Long eye hairs apparent on left compound eye. Mesosoma with hairs evident on left side. Tegula oval. Fore tibia length 1.62 mm; basitarsus length 1.18 mm. Hind tibia length 3.24 mm, width at apex 0.76 mm; corbicula without hairs except on borders; hind basitarsus length 1.92 mm, width 0.8 mm, with at least 8 setal comb rows evident; pollen press apparent and well developed (*figure 8*). Basal vein distad cu-a by 1.5 times vein width; stigma length 0.42 mm, width 0.12 mm; marginal cell of indeterminate length (distal portion missing), 0.36 mm wide. Hind wing with distal abscissa of vein M present, M gently curved. Scattered hairs evident on T6 and lateral margins of T5. Sting length 1.76 mm, ramus length 0.72 mm.

Head and mesosoma dark brown to black. Antennae brown. Legs light brown. T1 and T6 dark brown; T2 brown on basal half, apical half pale; T3 brown with apical margin pale; T4 with apical third pale; T5 brown with pale median patch.

3.1.3. Material

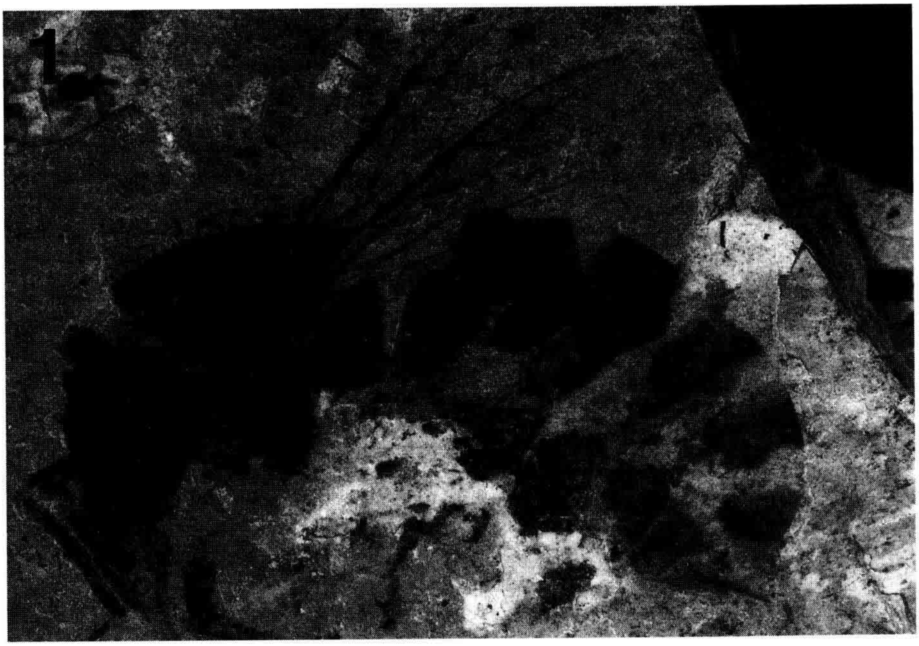
Holotype: worker female, MCZ Nr 6316 (*figure 1*) and reverse of holotype (*figure 2*). Oligocene, Rott, Germany. Additional specimens: worker female, MCZ Nr 7513 (*figure 3*), Oligocene, Rott, Germany; holotype for subspecies *A. henshawi dormiens*, here considered a junior synonym of *A. henshawi henshawi*.

3.1.4. Preservation

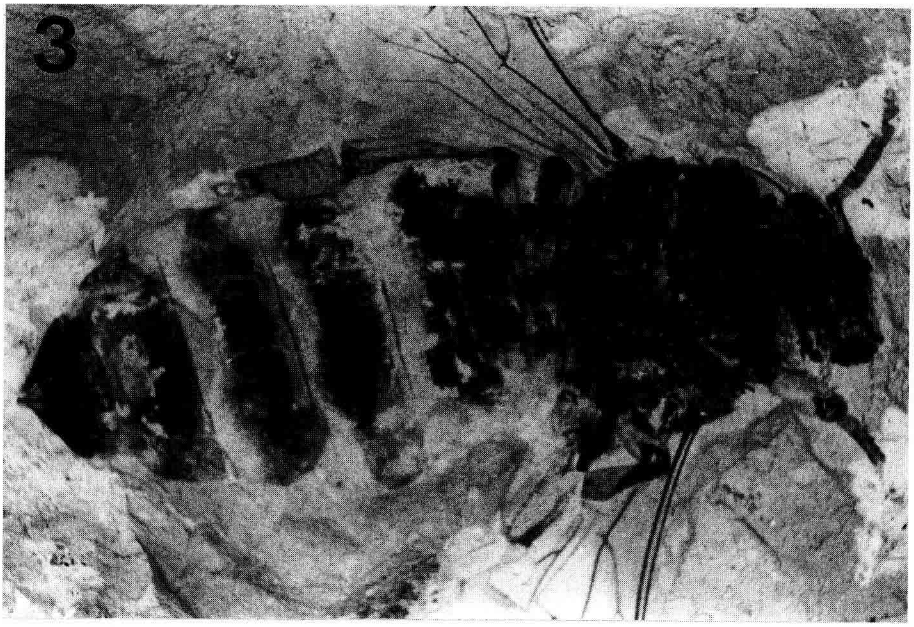
The holotype and its counterpart are preserved in profile (*figures 1* and *2*). The mouthparts are faintly evident and extended below the head. The mandibles are spread with the antennae extended parallel to the face just in front of them. The head is slightly turned so that the front of the face is seen obliquely. The holotype has the wings extended away form the body at an acute angle. The distal veins are only faintly preserved, except the connections of 1m-cu and 2m-cu with the submarginal cells are not visible. The forewings and hind wings are overlaid and venation of the hind wing can be pieced together through the forewings. The basal portions of the legs are not preserved; however the tarsi and fragments of the legs are evident below the body. Specimen Nr 7513 is preserved with the dorsum exposed (*figure 3*). The head is compressed dorso-ventrally with the left antenna extended just in front of and away from the head. The wings are extended away from the body to the sides with the venation incompletely preserved, although the venation is stronger in this specimen than in any of the others (*figure 6*). The left hind leg sits along the side of the abdomen and is turned so that the tibia-basitarsus junction is clear (*figure 8*).

3.1.5. Remarks

Zeuner and Manning [42] state that the basal vein of *A. henshawi* is confluent with cu-a, a comment which is clearly erroneous when the holotype is examined (*figures 5* and *11*). This character was used to distinguish between *A. henshawi henshawi* and their own *A. henshawi dormiens* which they described as having the basal vein slightly distad of cu-a. Likewise, the absence of eye hairs was used as a diagnostic feature of *A. henshawi dormiens* (the presence of such hairs is a synapomorphy of *Apis*), while in fact their spe-



Figures 1 and 2. *Apis henshawi* Cockerell. **1.** Holotype, MCZ Nr 6316. **2.** Reverse counterpart of holotype.



Figures 3 and 4. *Apis* species. **3.** *Apis henshawi* Cockerell, MCZ Nr 7513. **4.** *A. vetustus* new species, holotype, MCZ Nr 7514.

cimen shows long eye hairs preserved on at least the left compound eye. In whole, both specimens have identical venation (*figures 5* and *6*) and structural characters, therefore the recognition of two subspecific forms is superfluous.

More recently, the errors discussed above led Arillo et al. [2] to distinguish a new species of fossil *Apis* on the basis of this character. These authors distinguished their species, *A. aquisextana*, by the slightly distal position of the basal vein. Their species is, in fact, no different from *A. henshawi* and it is unfortunate that the confusion begun by Zeuner and Manning [42] should mislead later workers. In defense of Zeuner and Manning's work, however, it must be noted that both of these authors had passed away many years before the final publication of their work (Professor Zeuner in 1963 and Dr Manning in 1966). Thus several errors, of which only time and their unfortunate deaths are to blame, may have accrued during the intervening period.

Additional confusion stems from the fact that Arillo et al. [2] have failed to use valid family-group names for bees. For example, these authors use the names Rophitidae and Sphecodinae in place of Halictidae and Halictinae, and cite Michener [23] for the usage. In actuality, Michener [23] states clearly, even in his short abstract, that the previous two names are not to be used. Michener [24] later petitioned the International Commission on Zoological Nomenclature for the correct usage of these names and the Commission passed an opinion in agreement [18]. Thus, the family-group names used by Arillo et al. [2] are invalid and should not be followed.

Lastly, Théobald's [36] species *A. cuenoti* may also be a junior synonym of *A. henshawi*. However, far too little information is available on this species to place it here with confidence.

3.2. *Apis vetustus* Engel, new species

(*Figures 4, 7* and *12*)

3.2.1. Diagnosis

Basal vein linear, confluent with cu-a. Inner angle of third submarginal cell between 2r-m and M nearly orthogonal, much greater than 45°; cell broader along posterior border than anterior border. Vein M of hind wing gently curved.

3.2.2. Description

Total body length 15.9 mm; forewing length 7.28 mm. Head length 2.72 mm, width 3.56 mm. Hypostoma length 1.72 mm, width 0.88 mm. Pubescence of head and mesosoma not apparent. Mesosoma width 4.84 mm. Fore coxa wider than long; trochanter slightly longer than wide; remainder of fore leg missing. Mid-coxa twice as long as wide; trochanter and femur not preserved; tibia length 1.76 mm; basitarsus length 1.6 mm. Hind legs not preserved. Basal vein straight, confluent with cu-a (*figures 7* and *12*); stigma length 0.36 mm, width 0.14 mm; anterior border of first submarginal cell along Rs 0.34 mm long; length of anterior border of second submarginal cell 0.28 mm, posterior border 1.28 mm; length of anterior border of third submarginal cell 0.9 mm, posterior border 0.98 mm, inner angle between 2r-m and M nearly orthogonal; marginal cell long and rounded at apex, length 1.56 mm, width 0.2 mm. Vein M of hind wing gently curved, distal portion not preserved. Hairs not visible on apical sterna and lateral margins of T5.

Head and mesosoma dark brown. Legs dark brown except tarsomeres 2–5 light brown; claw dark brown. Sterna pale brown except apical sternum dark brown; lateral margins of terga dark brown.

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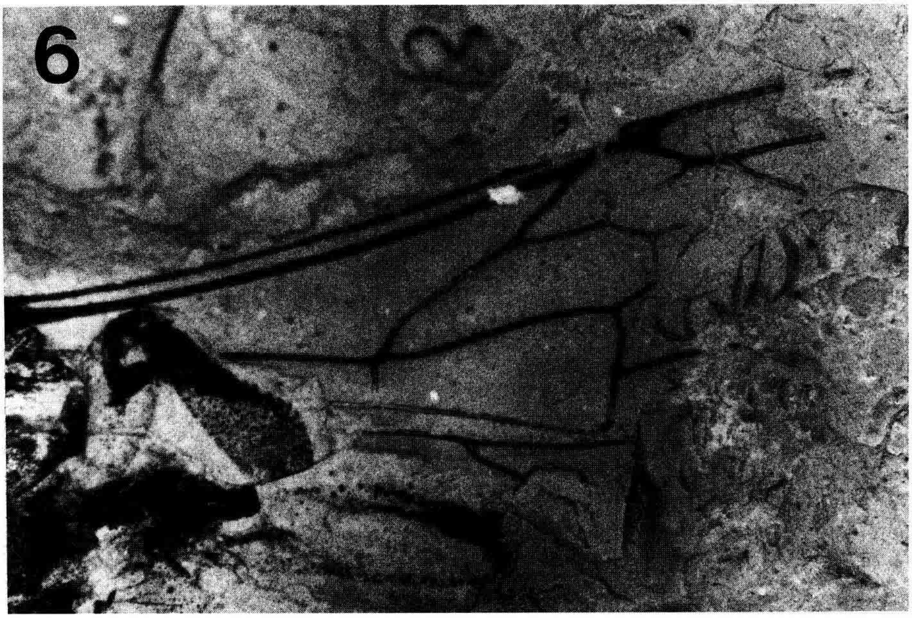

Figures 5 and 6. Forewing details of *Apis henshawi* Cockerell. **5.** Holotype, MCZ Nr 6316. **6.** Right wing of MCZ Nr 7513.

3.2.3. Type material

Holotype: worker female, MCZ Nr 7514 (previously a paratype specimen for *A. henshawi dormiens*), Oligocene, Germany.

3.2.4. Preservation

The bee is preserved with the venter exposed (*figure 4*). The head is thrust forward exposing the hypostomal fossa and postgena. The legs are only partially preserved with most of the apical portions lost. The basal portion of the right wing is visible, while the left forewing is extended and the venation faint but visible. Only the basal portion of the left hind wing is faintly preserved below the forewing. There is debris, perhaps plant matter, just in front of the head.

3.2.5. Etymology

The specific epithet is the Latin word *vetustus* meaning 'aged' in reference to the geological age of this species.

3.2.6. Remarks

This specimen was referred to by Cockerell (1907: 228) as possibly being a separate species from the species he later described in the same paper as *A. henshawi*. He based this decision on the straight basal vein. Cockerell also commented that there are "... dark spots at the sides of the abdominal segments...". The dark spots Cockerell refers to are the lateral margins of the darker terga wrapping around the metasoma to cover the lateral margins of the sterna.

3.3. *Apis miocenica* Hong

Apis miocenica Hong, 1983, Bull. Tianjin Inst. Geol. Min. Res., 8, 10.

Apis fota Zhang, 1989, Fossil insects from Shanwang, Shandong, China, 323. **New synonymy**.

Apis shandongica Zhang, 1989, Fossil insects from Shanwang, Shandong, China, 325. **New synonymy**.

3.3.1. Remarks

I have not had the opportunity to see the holotypes of these species which are located at a small provincial museum in China. However, the original descriptions, figures and photographs of the specimens have been at my disposal and it is clear that the species are not distinct. Both *A. fota* and *A. shandongica* are defined solely on the basis of color differences from *A. miocenica*. For example, the differences given by Zhang [43] for defining *A. fota* from *A. miocenica* are the darker coloration of the hind tibia and metasoma, along with a broader width to the color bands on the metasomal terga. A. similar diagnosis is given for *A. shandongica*. Such characters are known to vary within extant species, even within a single colony, and are not useful for distinguishing *Apis* species. Zhang's line drawings depict some minor differences of wing venation; however, the photographs of the specimens show no differences at all. I, therefore, have no trouble in placing these species under *A. miocenica* until the types can be examined by a bee systematist and authentic structural differences discovered, should they exist.

Zhang [43], after redescribing *A. miocenica*, comments that this species is closely related to *A. mellifera* and that the wing venation of the two species is essentially identical. The photograph provided by him of the holotype and the figures presented by Hong [15], as part of the original description, shows the basal vein distad of cu-a by about 2–3 times the width of a vein and a strong distal abscissa of vein M in the hind wing (similar to *figure 10*). *A. mellifera* L. lacks the distal abscissa of vein M and, like the other living species, has the basal vein strongly distad of cu-a (e.g. *figure 9*). *A. miocenica* appears more clo-

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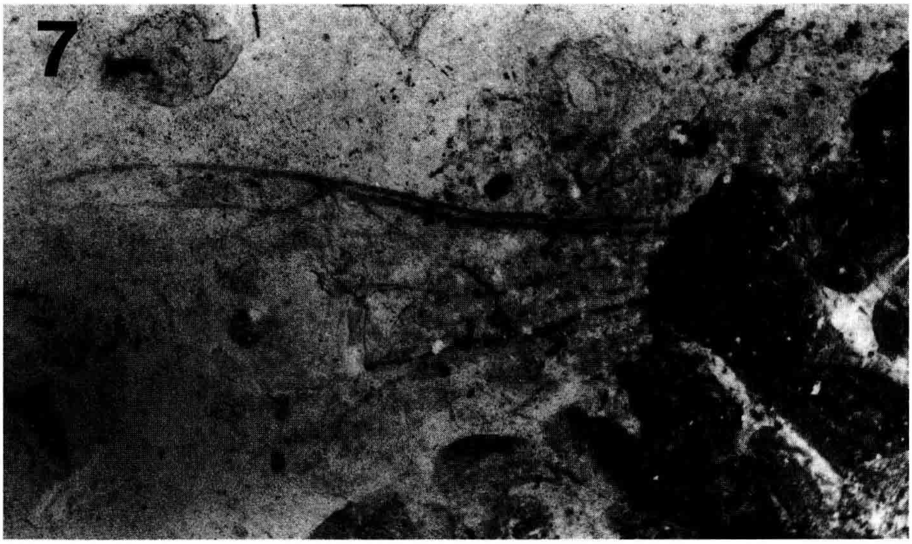

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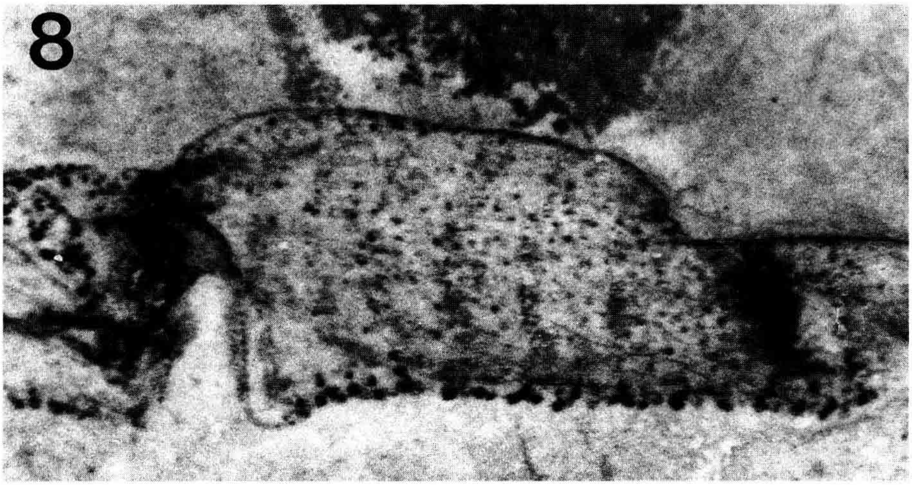


Figures 7 and 8. *Apis* species. **7.** Left forewing of *Apis vetustus* new species, holotype, MCZ Nr 7514. **8.** Left hind basitarsus of *A. henshawi* Cockerell, MCZ Nr 7513, showing details of pollen press and setal comb rows.

sely related to *A. henshawi* than to *A. mellifera* or any of the other extant species.

A. longtibia Zhang [44], although also defined primarily on the basis of minor color differences from *A. miocenica*, possibly has at least one apomorphy of the wing venation that for the time being allows it to retain its specific status. This species has the basal half of vein M in the hind wing strongly angulate, forming a distinctive point just after it branches from M+Cu. This vein is gently curved in all other *Apis* species.

3.4. *Apis petrefacta* (Ríha), new combination

Synapis petrefacta Ríha, 1973, Vestn. Ústred ústavu geol., 48, 217.

3.4.1. Remarks

This species is from Oligocene deposits in the Ceské Stredhorí Mountains, Czech Republic. Based on both the description of the species and the figures presented by Ríha [27] this is a honey bee species. *Synapis* Cockerell is a junior synonym of *Apis* and therefore this species is officially placed within the genus. The status of this species will have to await future study.

3.5. *Apis (?) melisuga* Zeuner and Manning, nomen dubium

'Apidae' *melisuga* Handlirsch, 1907, Die fossilen Insekten und die Phylogenie der rezenten Formen, 893. Unavailable following International Code of Zoological Nomenclature, 1985, 3rd ed., Art. 11h (iii).

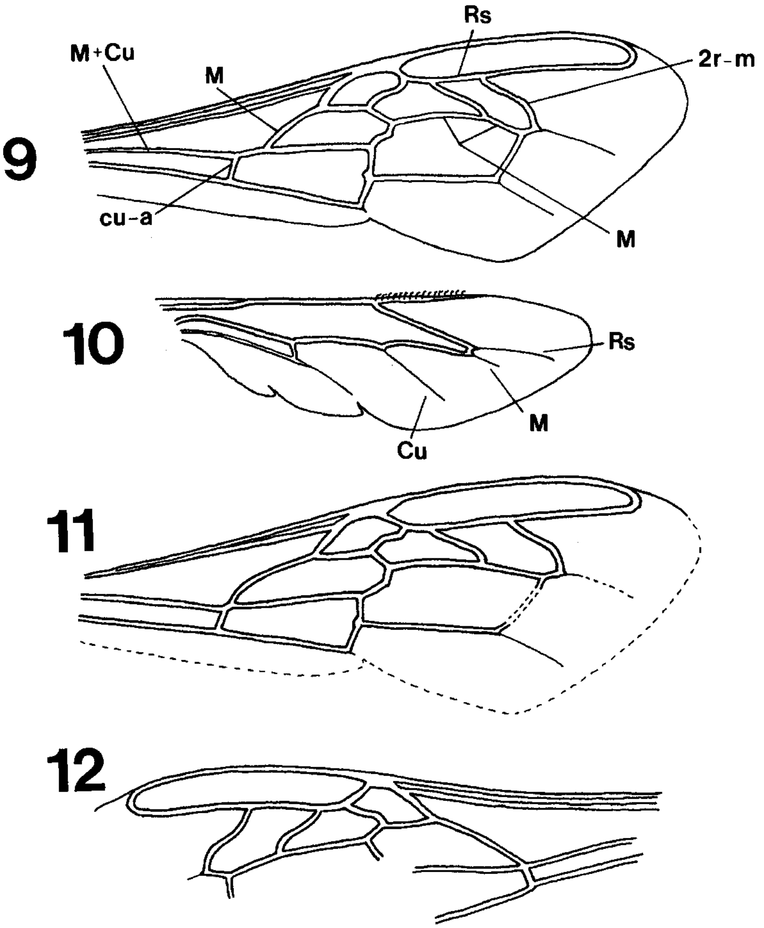
Apis melisuga Zeuner and Manning, 1976 (*non* Handlirsch, 1907), Bull. Brit. Mus. Nat. Hist. (Geol.), 27, 248.

3.5.1. Remarks

This fossil was mentioned by Handlirsch [13] simply as "'Apidae' *melisuga*" in his seminal work on fossil insects. The comments given by Handlirsch, which were to constitute his description of the species, was that the specimen resembled *A. mellifera*. Since the name was not published in combination with any generic assignment nor a differential diagnosis it cannot be considered valid. Zeuner and Manning [42], however, assigned *melisuga* to *Apis* based on Handlirsch's remark. Their publication of the epithet is the first valid usage in combination with a generic name and it must therefore be referred to as *A. melisuga* Zeuner and Manning (*non* Handlirsch). However, Zeuner and Manning's description of the species was a simple regurgitation of Handlirsch's comments, with the addition that the legs are suggestive of *Apis*. The wings of the specimen were apparently not preserved. There is no reason to believe, in the absence of the type (the whereabouts of which is unknown, and was so even to Zeuner and Manning), that Handlirsch's specimen was indeed a honey bee. The name *A. melisuga* should therefore be considered a *nomen dubium*, and, given the nature of the 'description', perhaps even a *nomen nudum*.

4. DISCUSSION

The first person to place the fossil honey bees into an explicit phylogenetic framework with the living species was von Buttel-Reepen [4]; however the fossil species he used in his study have all been removed from *Apis*. His species *A. meliponoides* (= *Electrapis meliponoides*) was placed as the most primitive ancestor of the lineage producing *A. mellifera*, while the other honey bee species were believed to have diverged prior to this in the middle Eocene. *A. meliponoides* eventually gave way to *A. adamitica* Heer (= *Lithurgus adamiticus*, a megachilid genus not even remotely related to the apines) and ultimately *A. mellifera*. Statz [34] updated von Buttel-Reepen's phylogeny correctly placing *A. meliponoides* in the 45 million year old Baltic amber genus *Electrapis* (after Cockerell [7]) and removing *L. adamiticus* altogether. Statz kept the relationships among the *Apis* species as was proposed by von Buttel-Reepen and retained *E. meliponoides* as ancestral to the lineage producing *A. mellifera*. Statz's scheme, however, replaced *A. dormitans* as the immediate ancestor of *A. mellifera*, with his own new species *A. kaschkei*. He



Figures 9–12. Wing venation of *Apis* species. **9.** Forewing of *Apis cerana* Fabricius. The free portion of M just beyond cu-a is commonly referred to as the 'basal vein'. **10.** Hind wing of *A. cerana* Fabricius. **11.** Left forewing of *A. henshawi* Cockerell, holotype, MCZ Nr 6316. The apparent fusion of C and Sc+R at the wing base is an artifact of preservation. The wing is slightly crumpled at its base resulting in C being folded under Sc+R proximally. Dotted lines indicated areas which are reconstructed. **12.** Left forewing of *A. vetustus* new species, holotype, MCZ Nr 7514.

considered *A. dormitans* and *A. henshawi* to have branched from this lineage between *E. meliponoides* and *A. kaschkei* in the late Oligocene. Just over a half a century later, Ruttner et al. [31] and Ruttner [29] examined morphometric values of wing venation for living and fossil honey bees along with their close relatives. These studies produced compound clusters of *Bombus* spp., *A. cerana* + *A. mellifera*, *A. florea*, and *A. henshawi* + *A. armbrusteri* + *A. dorsata*. *A. florea* had an isolated position near the *A. henshawi* + *A. armbrusteri* + *A. dorsata* cluster, with the next nearest group being that of *A. cerana* + *A. mellifera*. This pattern is generally in accord with recent examinations of *Apis* phylogeny [1, 10] as well as the results

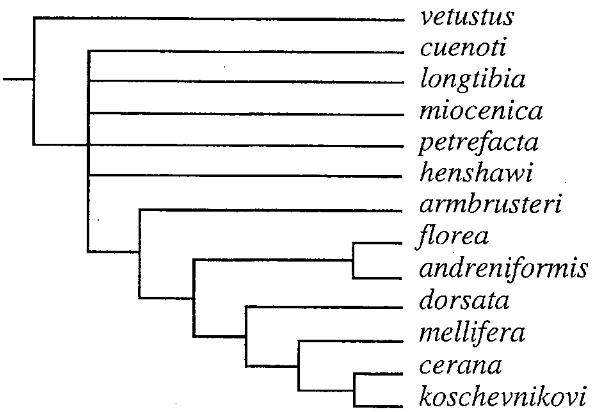


Figure 13. A hypothesis of phylogenetic relationships among the honey bees (Apini: *Apis*).

discussed below. Interestingly, the single species of *Electrapis* examined (presumably *E. minuta*) took a position nearest to *Bombus*. The overall conclusions of these studies were of an elongation of venation towards the apex and the proximal migration of 2r-m along Rs (see *figure 9*), but that in general *Apis* wing venation had not changed drastically since the Miocene. Most recently Hong and Miao [17] attempted to explain honey bee evolution in the light of the Jurassic fossil, *Palaeapis beiboziensis* [16]. *Palaeapis*, however, is not a primitive honey bee nor even a bee at all, but instead an aculeate wasp (see also Michener [25]) and can shed no light onto early bee history.

It is difficult to place any of the fossil species into *Apis* phylogeny due to the lack of information for most characters needed to perform a comprehensive cladistic analysis. Honey bees are fairly homogeneous and in the absence of information on the males, nesting biology, etc., it is not possible to include the fossils in a meaningful cladistic study with the extant species. Despite this trouble, some information can be gleaned from the little data available. A hypothesis of relationships among the honey bees is presented in *figure 13*. The polarity of characters for the following outline of relationships was determined by comparing those states present in the living and fossil honey bees to the only other representative of the tribe Apini, namely the genus *Electrapis*, and to the Meliponini, sister tribe to the Apini [5, 32]. The extant species of honey bees (see *table I*) are here considered to constitute a monophyletic group, with relationships among them derived from a recent 'total evidence' analysis of *Apis* phylogeny [10] corroborating those relationships presented by Alexander [1]. This monophyly is based upon the sharing of a less than 45° angle between veins 2r-m and M in the forewing (*figure 9*) as described by Alexander (1991: his angle BDE). The closest apparent relative of the modern species is *A. armbrusteri* Zeuner which shares the strongly distad basal vein relative to cu-a (similar to that seen in *figure 9*). It is set outside of the clade of living species by the greater than 45° angle between 2r-m and M. *A. vetustus* is apparently the most plesiomorphic of the known fossils owing to the confluence of cu-a with the basal vein and the linear basal vein (*figure 12*: similar to that state found in *Electrapis*). The remaining species fall intermediate between *A. vetustus* and *A. armbrusteri*. The basal vein in all of these species is gently curved and offset from cu-a by 1.5–2 times the vein's width (similar to *figure 11*). Based on the current information, it is not possible to resolve relationships among these five species. All of the fossil species, for which data exist, have the distal abscissa of vein M in the hind wing, a feature correctly determined by Alexander [1] to be primitive within *Apis*. I have not been able to place *A. catanensis* Roussy [28] in the scheme described above or to determine the validity of this fossil as a species of *Apis*. This specimen will have to await future study.

All of the fossil species of the genus were likely to have been highly eusocial. A cladistic reconstruction of this behavior on apine phylogeny supports a single origin of advanced eusociality in the ancestor of Apini and Meliponini [5, 32]. Thus eusociality is a primitive character of the honey bees and their ancestor would have already been living in such societies. Additionally, the known fossil specimens are all morphologically suggestive of workers, supporting the notion that these species were eusocial (a characteristic also seen in fossils of the sister genus *Electrapis*: [9]). It is not possible to determine whether any of the fossil species would have had the familiar 'waggle dance' language that is present among the species of today. This character may have arisen in the common ancestor of the living species only, or have been present in a few or all of the fossil species as well. The primitive nesting biology of the living species was to construct a comb in the open. It is therefore logical to conclude that the fossil species known today were open-nesting as well; however, this may never be known with certainty.

It is likely that *Apis* arose sometime in the early Oligocene. Extending one of the conclusions of Ruttner et al. [31] and Ruttner [29] back an epoch, it appears as though *Apis* wing venation has changed relatively little since the middle Oligocene. The general vein patterns are remarkably similar from species occurring in Oligocene strata to those of today (e.g. compare *figures 9, 11* and *12*). *Apis* diversity appears not to have changed much through time as was suggested by Culliney [8] who regarded the genus as having lost diversity since the Oligocene. If anything, the crude evidence available suggests that *Apis* diversity has slightly increased as only three species are currently known from the Oligocene, followed by another five species from the Miocene (not including *A. melisuga*), eventually leading up to the six species recognized today.

ACKNOWLEDGMENTS

Special thanks are due to G. Chavarría (formerly of the MCZ), S Cover, and P. Perkins (both of the MCZ) for help during my visits to their collection. My advisor, J.K. Liebherr, kindly provided access to a camera-microscope mount for production of the figures presented in this work. The late W.L. Brown Jr (1922–1997) aided in the difficult interpretation of *A. melisuga*'s taxonomic status, he is gratefully acknowledged and dearly missed. I am indebted to M. Wang, Boston University and the MCZ, for graciously translating Chinese papers on fossil insects for me. I am grateful to P. Ríha for sending me original copies of his work on tertiary insects, and to D. Ren and Y.C. Hong for original copies of work on the fossil insect fauna of China. I am also thankful to G.W. Otis for allowing me to examine specimens of *A. nuluensis*, at which time I failed to find characters to support it under a phylogenetic species concept and thus have not included it in my table of *Apis* species. I am further indebted to G. Chavarría and two anonymous reviewers for reading an earlier version of the paper. Their valuable insights helped to improve this study. Support for this research was provided by a National Science Foundation Predoctoral Fellowship. This work is dedicated in loving memory of B.A. Alexander (1952–1996), a dear friend and mentor. Byron's

work on honey bee phylogeny was one of my first introductions to systematics, and his interest in me, even though I was a student of chemistry and cell biology, forever changed my life. He is sorely missed.

Résumé – Les abeilles mellifères fossiles et l'évolution dans le genre *Apis* (Hymenoptera, Apidae). La première abeille mellifère, *Apis henshawi*, est décrite entièrement pour la première fois et les spécimens de l'empreinte et de la contre-empreinte de l'holotype et du paratype sont illustrés. En outre une nouvelle espèce d'abeille mellifère, *A. vetustus* n. sp., provenant de l'Oligocène d'Allemagne est décrite et illustrée. *A. henshawi dormiens* et *A. aquisextana* sont considérés comme de nouveaux synonymes de *A. henshawi*, tandis que *A. fota* et *A. shandongica* sont considérés comme synonymes de *A. miocenica*. *Synapis petrefacta* est officiellement transferré dans le genre *Apis*. Zeuner et Manning (et non Handlirsch) sont reconnus comme les auteurs de *A. melisuga*, le nom étant considéré comme un *nomen dubium*. L'analyse comparative de la vénation alaire est utilisée pour inclure les abeilles mellifères fossiles dans un cadre phylogénétique qui comprend les espèces vivantes. On considère ici que les espèces vivantes forment un groupe monophylétique. D'après ces résultats les taxons éteints forment un groupe paraphylétique qui conduit à un clade des espèces existantes avec *A. armbrusteri,* qui représente le fossile le plus apparenté à la faune moderne. Le genre semble avoir acquis une diversité depuis son origine dans l'Oligocène inférieur. On résume brièvement la diversité du genre *Apis* qui comprend 14 espèces vivantes et éteintes, considérées sous toutes réserves comme valides. © Inra/DIB/AGIB/Elsevier, Paris

***Apis* / Apoidea / Cénozoïque / paléontologie / fossile / systématique / phylogenèse**

Zusammenfassung – Fossile Honigbienen und Evolution in der Gattung *Apis* (Hymenoptera: Apidae). Die erste fossile Honigbiene, *Apis henshawi*, wird erstmalig genau beschrieben und Exemplare des Holotypus und Paratypus werden vorder - und rückseitig abgebildet. Weiterhin wird eine neue fossile Honigbiene aus dem Oligozän in Deutschland als *A. vetustus* (neue Art) beschrieben und abgebildet. *A. henshawi dormiens* und *A. aquisextana* werden neuerdings als jüngstgenannte Synonyme von *A. henshawi* angesehen, während *A. fota* und *A. shandongica* als jüngstgenannte Synonyme von *A. miocenia* eingestuft werden. *Synapis petrefacta* wird offiziell in die Gattung *Apis* übernommen. Die Autorenschaft von *A. melisuga* wird richtig als Zeuner und Manning festgesetzt (nicht Handlirsch), der Name wird als ein *nomen dubium* angesehen. Unter Verwendung von Vergleichsdaten der Flügeladerung werden die fossilen Honigbienen in einen phylogenetischen Rahmen eingeordnet, der auch die lebenden Arten enthält. Hierbei wird angenommen, dass die rezenten Arten eine monophyletische Gruppe bilden. Die ausgestorbenen Taxa sind nach diesen Befunden ein paraphyletischer Zusammenschluss , die zu den *cladus* der bestehenden Arten hinführt. Hierbei stellt *A. armbrusteri* das zu der modernen Bienenfauna nächstverwandte Fossil dar. Die Vielfalt der Gattung scheint seit ihrem Ursprung im frühen Oligozän zugenommen zu haben. Es wird eine kurze Zusammenfassung der Vielfalt von *Apis* mit den 14 vorläufig als gültig angesehenen lebenden und ausgestorbenen Arten gegeben. © Inra/DIB/AGIB/Elsevier, Paris

***Apis* / Apoidea / Zenozoisch / Paläontologie / Taxonomie / Phylogenese**

REFERENCES

[1] Alexander B.A., A cladistic analysis of the genus *Apis*, in: Smith D.R. (Ed.), Diversity in the Genus *Apis*, Westview Press, Boulder, CO, 1991, pp. 1–28.

[2] Arillo A., Nel A., Ortuño V.M., Two fossil bees from the Oligocene of Izarra (Alava, Spain) (Hymenoptera, Apoidea), Bull. Soc. Entomol. France 101 (1996) 59–64.

[3] Ashmead W.H., Remarks on honey bees, Proc. Entomol. Soc. Wash. 6 (1904) 120–122

[4] Buttel-Reepen H. von, Apistica, Beiträge zur Systematik, Biologie, sowie zur geschichtlichen und geographischen Verbreitung der Honigbiene (*Apis mellifica* L.), ihrer Varietäten und der übrigen *Apis*-Arten, Mitt. Zool. Mus. Berlin 3 (1906) 117–201.

[5] Chavarría G., Carpenter J.M., 'Total evidence' and the evolution of highly social bees, Cladistics 10 (1994) 229–258.

[6] Cockerell T.D.A., A fossil honey-bee, Entomologist, London 40 (1907) 227–229.

[7] Cockerell T.D.A., Descriptions of Hymenoptera from Baltic amber, Schr. Phys-ökon. Ges. 50 (1909) 1–20.

[8] Culliney T.W., Origin and evolutionary history of the honeybees, *Apis*. Bee World 64 (1983) 29-38.

[9] Engel M.S., A new species of the Baltic amber bee genus *Electrapis* (Hymenoptera: Apidae), J. Hym. Res. 7, in press, 1998.

[10] Engel M.S., Schultz T.R., Phylogeny and behavior in honey bees (Hymenoptera: Apidae), Ann. Entomol. Soc. Am. 90 (1997) 43–53.

[11] Fabricius J.C., Mantissa insectorum sistems eorum species nuper detectas adiectis characteribus genericus, differentiis specificis, emendantionibus, observationibus, vol. 1, Proft., Hafniae, Denmark, 1787.

[12] Fabricius J.C., Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus, vol. 2, Proft., Hafniae, Denmark, 1793.

[13] Handlirsch A., Die fossilen Insekten und die Phylogenie der rezenten Formen, Engelmann, Leipzig, Germany, 1907.

[14] Heyden C. von, Gliedertiere aus der Braunkohle des Niederrheins, der Wetterau und der Rhön, Palaeontographica 10 (1862) 62–82.

[15] Hong Y.C., Fossil insects in the diatoms of Shanwang, Bull. Tianjin Inst. Geol. Min. Res. 8 (1983) 1–11 [In Chinese, with English summary].

[16] Hong Y.C., New fossil insects of the Laiyang Group from the Laiyang Basin, Shandong Prov, Prof. Pap. Stratig. Palaeontol. 11 (1984) 31–41 [in Chinese, with English summary].

[17] Hong Y.C., Miao S.J., Fossil bee and its origin with discussion on the origin of the angiosperms, Mem. Beijing Nat. Hist. Mus. 51 (1992) 1–19 [In Chinese, with English summary].

[18] ICZN, Opinion 1713. Some bee family-group names (Insecta, Hymenoptera): names based on *Colletes* Latreille, 1802, on *Paracolletes* Smith, 1853, on *Halictus* Latreille, 1804, on *Anthidium* Fabricius, 1804 and on *Anthophora* Latreille, 1803 given precedence over some senior names, Bull. Zool. Nomenclature 50 (1993) 85–89.

[19] Linnaeus C., Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, vol. 1, ed 10, Salvii, Stockholm, Sweden, 1758.

[20] Maa T., An inquiry into the systematics of the tribus Apidini or honeybees (Hym), Treubia 21 (1953) 525–640.

[21] McEvoy M.V., Underwood B.A., The drone and species status of the himalayan honey bee, *Apis laboriosa* (Hymenoptera: Apidae), J. Kans. Entomol. Soc. 61 (1988) 246–249.

[22] Meunier F., Über einige fossile Insekten aus dem Braunkohlenschichten (Aquitanien) von Rott (Siebengebirge), Z. Dtsch. Geol. Ges. Berlin 67 (1915) 205–217, 219–230.

[23] Michener C.D., Family-group names among bees, J. Kans. Entomol. Soc. 59 (1986) 219–234.

[24] Michener C.D., Case 2535. Proposed precedence of some bee family-group names (Insecta, Hymenoptera): names based on *Colletes* Latreille, 1802, on *Paracolletes* Smith, 1853, on *Halictus* Latreille, 1804, on *Anthidium* Fabricius, 1804 and on *Anthophora* Latreille, 1803 to have precedence over some senior names, Bull. Zool. Nomenclature 48 (1991) 227–235.

[25] Michener C.D., Genus-group names of bees and supplemental family-group names, Sci. Pap., Nat. Hist. Mus., Univ. Kans. 1 (1997) 1–81.

[26] Otis G.W., Distributions of recently recognized species of honey bees (Hymenoptera: Apidae; *Apis*) in Asia, J. Kans. Entomol. Soc. suppl. 69 (1996) 311–333.

[27] Ríha P., *Synapis petrefacta* sp n, eine neue Bienenart aus dem Tertiar des Bohmischen Mittelgebirges, Vestn Ústred ústavu geol. 48 (1973) 217–220.

[28] Roussy L., Insectes et abeilles de l'ambre de Sicile, Gazette Apic. 635 (1960) 5–8.

[29] Ruttner F., Biogeography and Taxonomy of Honeybees, Springer-Verlag, Berlin, Germany, 1988.

[30] Ruttner F., Naturgeschichte der Honigbienen. Ehrenwirth, Munich, Germany, 1992.

[31] Ruttner F., Wilson E.C., Snelling R., Vorwohl G., Kauhausen D., Die Evolution des Flügelgeäders der Honigbienen, Apidologie, 17 (1986) 348–350.

[32] Schulz T.R., Engel M.S., Prentice M., Resolving conflict between morphological and molecular evidence for the origin of eusociality in the corbiculate bees (Hymenoptera: Apidae): A hypothesis-testing approach. Sci. Papers, Natural History Museum, Univ. Kansas (in press), 1998.

[33] Smith F., Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by AR Wallace. Proc. Linn. Soc., London Zool. 2 (1858) 42–130.

[34] Statz G., Eine neue Bienenart aus Rott am Siebengebirge. Wiss. Mitt. Ver. Nat-Heimatik Köln 1 (1931) 39–60.

[35] Stauffer P.H., A fossilized honeybee comb from Late Cenozoic cave deposits at Batu Caves, Malay Peninsula, J. Paleontol. 53 (1979) 1416–1421.

[36] Théobald N., Les insectes fossiles des terrains oligocènes de France, George Thomas, Nancy, France, 1937.

[37] Tingek S., Mardan M., Rinderer T.E ., Koeniger N., Koeniger G., Rediscovery of *Apis vechti* (Maa, 1953): the Saban honey bee, Apidologie 19 (1988) 97–102.

[38] Tingek S., Koeniger G., Koeniger N., Description of a new cavity nesting species of *Apis* (*Apis nuluensis* n. sp.) from Sabah, Borneo, with notes on its occurrence and reproductive biology, Senckenbergiana Biol. 76 (1996) 115–119.

[39] Wu Y., Kuang B., A study of the genus *Micrapis* (Apidae), Zool. Res. 7 (1986) 99–102 [In Chinese].

[40] Wu Y., Kuang B., Two species of small honeybee - a study of the genus *Micrapis*, Bee World 68 (1987) 153–155.

[41] Zeuner F.E., Die Insektenfauna des Böttinger Marmors, Fortschr. Geol. Palaeontol., Berlin 9 (1931) 247–406.

[42] Zeuner F.E., Manning F.J., A monograph on fossil bees (Hymenoptera: Apoidea), Bull. Brit. Mus. Nat. Hist. (Geol.) 27 (1976) 151–268.

[43] Zhang J.F., Fossil Insects from Shanwang, Shandong, China. Shandong Science and Technology Publishing House, Jinan, China, 1989 [in Chinese, with English summary].

[44] Zhang J.F., New fossil species of Apoidea (Insecta: Hymenoptera), Acta Zootax Sinica 15 (1990) 83–91 [In Chinese, with English summary].