

## 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)

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**Abstract.** New fossil Aculeata are described from the Lower Oligocene of Bechlejovice, the Upper Oligocene of Veselíčko, and the Lower Miocene of the Bílina mine in northern Czech Republic. All specimens are classified into the families Vespidae and Apidae: Apinae (*Apis* sp. and *Bombus* sp.). The comparison with related fossil and extant analogues is provided. The potential presence of pollen grains on metathoracic legs of specimens of *Apis* sp. was tested using scanning electron microscopy and palynological methods.

■ Hymenoptera, Apocrita, Aculeata, Apidae, Vespidae, taxonomy, plant-insect interactions, Tertiary, Oligocene, Miocene, Central Europe

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### Introduction

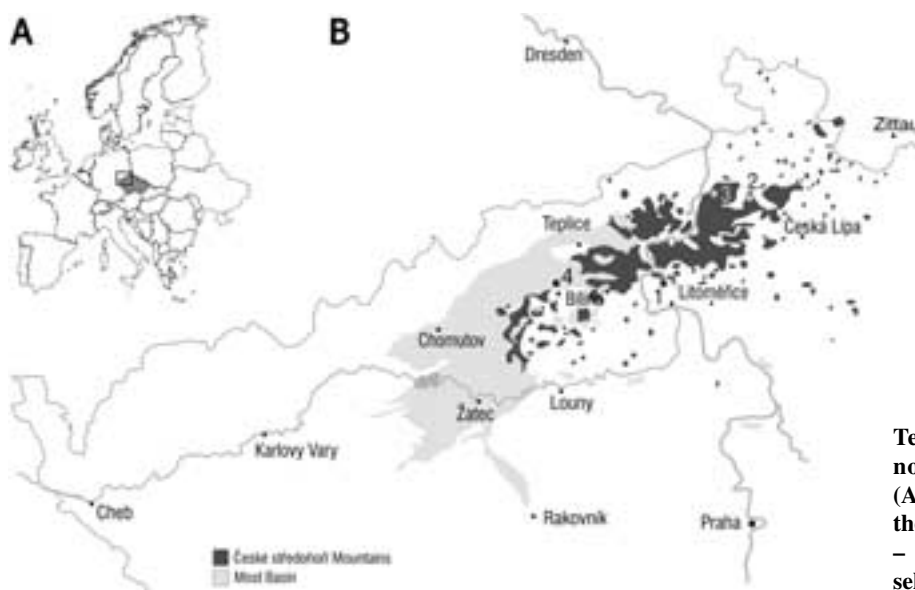
Fossil Aculeata are frequently preserved in worldwide Cenozoic lake deposits, especially by abundant specimens of Formicidae. This family is the most abundant, diverse and ecologically dominant group in extant fauna, with up to 10–15 % of the entire animal biomass in many habitats (Beattie and Hughes 2002). Rasnitsyn (2002: 254) supposed that the rapid evolution and increasing population density of the ants occurred during the Middle and Late Eocene, but ants were already very diverse and frequent in the lowermost Eocene amber of France (Nel et al. 1999b). Further significant Cenozoic group of hymenopterans was Apidae. The number of systematic and palaeoecological studies dealing with fossil bees has increased during past few years (see reviews of Zeuner and Maning 1976, Nel et al. 1999a, Engel 2001). The major interest of this study is to explore the co-evolutional trends between the rapidly developing bees and flowering plants through their fossil history. Other aspect of the present study concerns the possible presence of pollen grains on metathoracic legs of fossil bees, which is a significant evidence of plant-insect interaction (Lutz 1993, Rasnitsyn and Krassilov 1996).

Although, the indirect evidence of fossil bee nests from the Late Cretaceous of Uruguay was indicated by Genise (1999), the oldest surely described adult bees come from the Paleocene of Menat (France) (Piton 1940, Nel and Petrulevicius 2003), the early Eocene of British Columbia (Engel

2003), and the Eocene of Baltic amber (Engel 2001). The Mesozoic age of the Meliliponi-bee *Cretotrigona prisca* (MICHENER et GRIMALDI, 1988), dated from the Late Cretaceous (Maastrichtian) amber of Kinkora in New Jersey, revised by Engel (2000), is controversial and not widely accepted (Rasnitsyn 2002: 251).

Despite of the fact that the Tertiary entomofaunas of North Bohemian rift have been studied since 19<sup>th</sup> century, only few papers dealt with fossil hymenopterans. Říha (1979) summarized the Tertiary fossil insect record from the Czech Republic, and mentioned the three hymenopteran families Formicidae, Bombidae, and Apidae, dated from the Upper Eocene to the Lower Miocene of north-western Bohemia. Specimens were described by Heer (1849), Novák (1877), Deichmüller (1881), Samšiňák (1967) and finally by Říha (1973) (fossil bee *Synapis petrefacta* ŘÍHA, 1973 from the Lower Oligocene locality Kundratice near Lito-měřice, in České Středohoří Mountains (Text-fig. 1[1]). The site Veselíčko (Text-fig. 1[2]) is the second Oligocene locality located in the České Středohoří Mountains that was listed by Frič (1869). The third Lower Oligocene locality Bechlejovice (Text-fig. 1[3]) is particularly known for the amphibian fossils (Špínar 1972). All the above mentioned sites represent characteristic Oligocene record in northern Bohemia, which is commonly represented by the paleolake sedimentation of diatomaceous layers (see Prokop 2003).

The Lower Miocene (Eggenburgian/Ottangian) insect fauna of the Most Formation was found in the Bílina mine



**Text-fig. 1. Geographical position of northwestern Bohemia within Europe (A), detailed map of the Most Basin and the České středohoří volcanic areas (B), 1 – Kundratice near Litoměřice, 2 – Veselíčko, 3 – Bechleovice, 4 – Bílina mine.**

situated near Bílina town (Text-fig. 1[4]). The insects are preserved in three fossiliferous fluvio-lacustrine horizons (Lake Clayey Horizon [LCH], Delta Sandy Horizon [DSH], Clayey Superseam Horizon [CSH]) above coam seam (Prokop 2003). The Hymenoptera (mainly ants) are dominantly represented in the fossiliferous horizons LCH and CSH. The examined material of Apidae and Vespidae from the Bílina mine comes mainly from CSH, which is interpreted as a deep peat swamp with occasional flooding. Several other findings were collected in LCH that is a typical shallow lake palaeoenvironment (see Prokop 2003). This site is especially known because of its rich macro-palaeobotanical record and the detailed sedimentology (Kvaček 1998, Rajchl and Uličný 1999, Sakala 2000).

We follow an amended venation nomenclature used by Nel et al. (1999). The first article of hind tarsus is specified here as the basitarsus (*sensu* Snodgrass 1956).

## Systematic palaeontology

Family **Apidae** LATREILLE, 1802  
Subfamily **Apinae** LINNAEUS, 1758

Genus ***Apis*** LINNAEUS, 1758

***Apis* sp. indet.**

Pl. 1, figs 1–6,10; text-figs 2–4

**Material.** ZD0001 (coll. Bílina mine), nearly a complete insect (part and counterpart) in dorsal view; forewings preserved; body partly deformed; no coloration preserved; metathoracic legs quite well preserved.

ZD0002 (coll. Bílina mine), nearly a complete body (part and counterpart) in lateral view; forewings poorly preserved in proximal part; metathoracic leg well preserved.

ZD0112 (coll. Bílina mine), deformed body in dorsal view; forewing preserved in distal part, coloration not preserved.

ZD0186 (coll. Bílina mine), nearly a complete metathoracic leg (imprint) in lateral view, distal part of tarsus and proximal part of basitarsus is missing, pilosity is preserved.

ZD0203 (coll. Bílina mine), a complete forewing with well preserved wing venation (imprint).

ZD0232 (coll. Bílina mine), medial part of forewing with well preserved wing venation (imprint).

**Age and Horizon.** Lower Miocene (Eggenburgian/Ottnagian), Bílina mine, Czech Republic.

ZD0001, ZD0002, ZD0112, ZD0203 Clayey Superseam Horizon (CSH), ZD0232 Lake Clayey Horizon (LCH).

**Description.** ZD001: Body 15.0 mm long; head and thorax not well preserved; abdomen 8.7 mm long and 7.9 mm wide; prothoracic and mesothoracic legs absent or not well preserved; a well preserved metathoracic legs; metathoracic tibia widened, 3.9 mm long and 0.9 mm wide; metathoracic basitarsus distally widened, 3.4 mm long and 1.4 mm wide; second and third tarsal segments prominently pilose, forewing 14 mm long and 4.7 mm wide; cell [2R] very elongate, 5.9 mm long and 0.8 mm wide, distally closed and clearly narrowed at distal end; cell [R] 5.6 mm long; cell [1R] 2.1 mm long and 0.6 mm wide; cell [1Rs] 2.8 mm long and 0.6 mm wide; cell [2Rs] 2.8 mm long and 0.9 mm wide; XY 1.4 mm, VS 1.4 mm, ratio XY/VS 1.0; cross-vein 1cu-a close to the bifurcation of M and CuA; NO 0.6 mm, OS 2.4 mm (*sensu* Louis 1966); costal margin of cell Rs distinctly shorter than posterior margin; WX 0.8 mm, NS 3.0 mm; angle YVS = 30° (defined by the three remarkable points Y, V and S of *Apis* wing venation, see definitions in Nel et al. 1999a: text-fig. 2A).

ZD0186: A metathoracic leg well preserved; coxa robust basally, 2.1 mm long and 2.5 mm wide; metathoracic femora 5.8 mm long and 1.7 mm wide, shortly pilose in the middle; metathoracic tibia widened distally, 5.7 mm long and 1.5 mm wide with prominent long pilosity at its distal edge; metathoracic basitarsus distally pilose, 3.1 mm long and 1.5 mm wide.

ZD0203: Forewing 9.9 mm long and 3.3 mm wide; cell [2R] very elongate (3.6 mm long and 0.5 mm wide), distally closed and clearly narrowed at distal end; cell [R] 4.3 mm long; cell [1R] 1.5 mm long and 0.5 mm wide; cell [1Rs] 1.3 mm long and 0.5 mm wide; cell [2Rs] 1.0 mm long and 0.6 mm wide; XY 0.9 mm, VS 1.0 mm, ratio XY/VS 0.9; cross-vein 1cu-a close to the bifurcation of M and CuA; NO 0.4 mm, OS 1.1 mm; costal margin of cell Rs distinctly shorter than posterior margin; WX 0.3 mm, NS 1.6 mm; angle YVS = 32°.

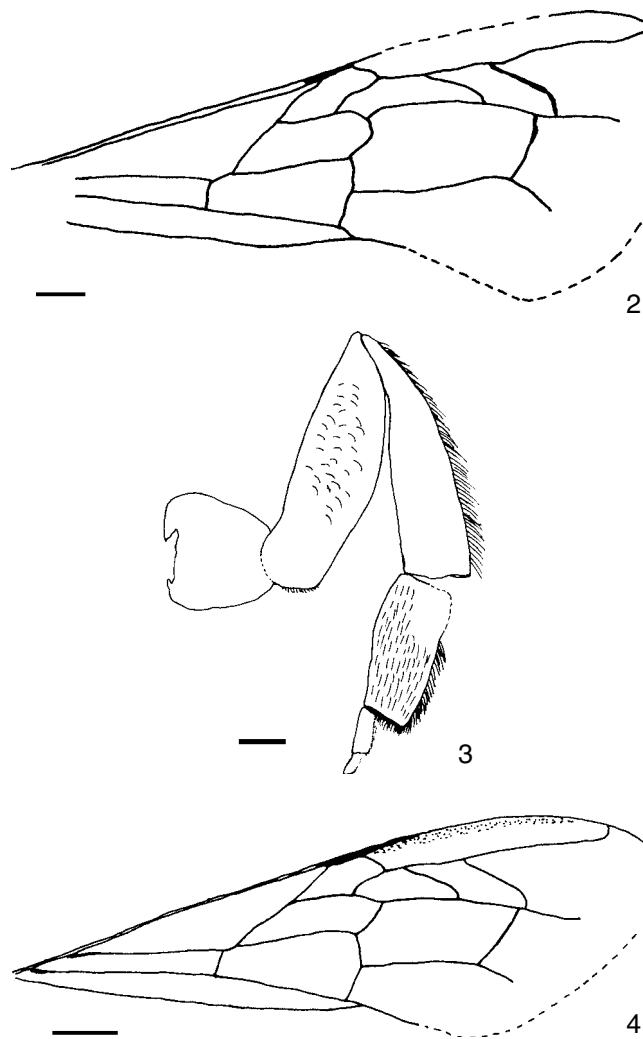
ZD0232: Medial part of forewing approximately 9 mm long and 3 mm wide; cell [2R] very elongate, about 2.8 mm long and 0.7 mm wide, clearly narrower at distal end; cell [R] about 4.1 mm long; cell [1R] 1.7 mm long and 0.5 mm wide; cell [2Rs] 0.8 mm long, XY 0.9 mm; cross-vein 1cu-a close to the bifurcation of M and CuA; NO 0.6 mm, OS 1.4 mm; costal margin of Rs distinctly shorter than posterior margin; WX 0.5 mm NS 1.8 mm.

**Discussion.** The structure of metathoracic leg and its pilosity prove the specimens ZD0001 and ZD0186 to be workers (Snodgrass 1956). These bees do not fall in the subgenera *Cascapis* ENGEL, 1999 and *Synapis* COCKERELL, 1907 *sensu* ENGEL (1998, 1999) but in subgenera *Apis*, *Megapis* and *Micrapis sensu* ENGEL (1998, 1999) because of the angle YVS (= inner angle of third submarginal cell) distinctly less than 45°. The prefurcal position of the transverse vein 1cu-a also excludes affinities with *Synapis*. The absence of information concerning the distal abscissa of vein M in hindwing renders the discrimination between *Apis*, *Megapis* and *Micrapis* impossible. It is difficult to establish the limits of the intraspecific variation, using a biometrical analysis comparatively with recent taxa (Nel et al. 1999a), so we leave these specimens in open nomenclature. Nevertheless, one wing is distinctly smaller than the others, suggesting the possible presence of two distinct species, as in the Upper Miocene outcrops of Saint-Bauzile and Sainte Reine in France (Nel et al. 1999a). The small forewing fits in the range length of subgenus *Apis* (7–10 mm long) and the large specimens fit in the range length of subgenus *Megapis* (12–15 mm) (Engel 1999). Only the discovery of a great number of specimens will allow testing this hypothesis. Another possible explanation could be due to large intraspecific variability among various forms of modern species.

Three specimens (ZD0002, ZD0186 and ZD0232), thus their attribution to the same taxon is only hypothetical.

The large bee that we describe looks rather similar to the *Apis* 'species' E, G, and I from the Upper Miocene of Western Europe (Austria and South France) (Nel et al. 1999a). All those fossils are similar in wing venation and size range to extant *Apis dorsata* FABRICIUS, 1798 that is now living in India and South-East Asia. But the wing dimensions of *A. dorsata* are more important. These bees support the hypothesis of Nel et al. (1999a) concerning the existence of Western Palearctic species related to *A. dorsata*, during the Miocene. Present discoveries also fill the gap among European localities in fossil record within Miocene.

**Notes:** (1) Jeremies et al. (1998) described a bee



**Text-figs. 2-4.** *Apis* sp. indet., Lower Miocene (CSH), Bílina mine, 2 - detail of wing venation (ZD0001, coll. Bílina mine), 3 - ?*Apis* sp. metathoracic leg (ZD0186, coll. Bílina mine), 4 - wing venation (ZD0203, coll. Bílina mine). Scale 1 mm.

forewing from the Lower Oligocene locality Seiffhennersdorf/Oberlausitz (Germany – edge of České Středohoří Mts, close to Czech Republic) and compared it to recent species *Apis mellifera* LINNAEUS, 1758, but there is no clear evidence because of a lack of several characters. It would need a complete revision before any definite subgeneric attribution.

(2) Engel (1998) indicated that *Apis cuenoti* THÉOBALD, 1937 (Upper Oligocene, France) could be a junior synonym of *Apis henshawi* COCKERELL, 1907. Nel et al., in a paper submitted to the Palaeontology in 1996 but published in 1999, revised *A. cuenoti* and indicated that it differs from *A. henshawi* in its hairy eyes, after its revision of Zeuner and Manning (1976). But, after Engel's (1998) last revision of *A. henshawi*, this latter species has hairy eyes. Thus, there is no more argument to separate the two species. In consequence, we follow Engel (1999) who decided to synonymize the two species, but without further argument.

(3) Arillo et al. (1996) described a specimen of *Apis* from the Oligocene of Alava (Spain) and attributed it to '*Apis aquisextiana* NEL et al., in press'. The description of the type specimen (from Aix-en-Provence, France) of this species was in press in the review Palaeontology at that time, but it was only published in 1999, with a name emendation into '*Apis aquisextuensis*' due to suggestion of an editor of the review. The designation of the type material of this species was made in the paper of Nel et al. (1999), from the Upper Oligocene of Aix-en-Provence (France). Meanwhile, Engel (1998, 1999) synonymized both material from Spain and France with *Apis* (*Synapis*) *henshawi*, because he misinterpreted the main diagnostic character of *Apis aquisextuensis*: Engel considered that Arillo et al. and Nel et al. separated *A. aquisextuensis* on the basis of 'the slightly distal position of forewing basal vein' but this was not the diagnostic character of this species, which is 'the distally narrowed cell 2R'. This character is not shared by *A. henshawi* (Arillo et al. 1996: 62, Nel et al. 1999a: 253, Engel 1998: figs 5–6). Engel (1998, 1999) ignored this character in his discussion on *Apis aquisextuensis*.

Furthermore, Engel (1999) characterized the two fossil subgenera *Cascapis* ENGEL, 1999 and *Synapis* COCKE-RELL, 1907 (including *A. (S.) henshawi*) by the angle of postero-apical margin of first submarginal cell (sic, in fact the third cell (3Rs), see Engel, 1998) much greater than 45°, and the more recent subgenera *Apis* LINNAEUS, 1758, *Megapis* ASHMEAD, 1904 and *Micrapis* ASHMEAD, 1904 by this angle less than 45°. Engel's definition of this angle is mathematically strange because if one uses the tangencies to the two concerned curved veins to estimate it, this angle cannot be less than 45° in *Apis*. Nevertheless, if one uses the angle YVS defined by the three remarkable points Y, V and S of *Apis* wing venation (see definitions in Nel et al., 1999: text-fig. 2A), this agrees with Engel's characters. With this last definition, *Apis aquisextuensis* has an angle of 35°. Thus it does not fall into *Cascapis* or *Megapis* and greatly differs from *A. henshawi*. In conclusion, we propose to restore *Apis aquisextuensis* as a genuine species.

(4) Nel et al. (1999) described several populations of *Apis* from the Upper Miocene outcrops from France. They left them in open nomenclature but noted that, in both outcrops of Sainte Reine and Montagne d'Andance, there were two 'types' of *Apis*, i.e. a large one with long wings (mean length 11.9 mm) and with an abscissa of M in hindwing, and a small one with shorter wing (mean length 8.8 mm) and without abscissa of M. Engel (1999: 186) denied any possibility of specific difference between these populations because he said they are 'based on minor morphometric differences in wing venation and size'. But, in the same paper, Engel (1999: 170, 176) characterized the subgenera *Apis* and *Megapis* on the basis of the same characters. The same characters cannot be of minor importance and at the same time sufficient to characterize subgenera. Thus, we consider that there are two 'types' of *Apis* in these outcrops, as well as in those we study now.

(5) Nel et al. (1999) noted that it is hopeless to try to

make a phylogenetic analysis of the fossil *Apis* species because there are more species than available characters. Engel (1999) denied any value to this remark, noting that Buttel-Reepen (1906), Statz (1931), and Engel (1998) already made such attempts. But the analyses of Buttel-Reepen (1906) and Statz (1931) are not based on the cladistic method, which was not available at their times. Thus they cannot be qualified as 'phylogenetic analyses'. The 'analysis' of Engel (1998: fig. 13, 1999: fig. 1) was originally labelled as 'hypothesis of phylogenetic relationships', with no character list supporting it. Furthermore, nearly all the fossil *Apis* spp. fall in an unresolved polytomy in Engel's hypothesis, except for *A. vetusta*. This exactly supports Nel et al. (1999) remark.

### Tribus **Bombini** LATREILLE, 1802

#### Genus **Bombus** LATREILLE, 1802

##### **Bombus** sp. indet.

Pl. 1, figs 7; text-fig. 5

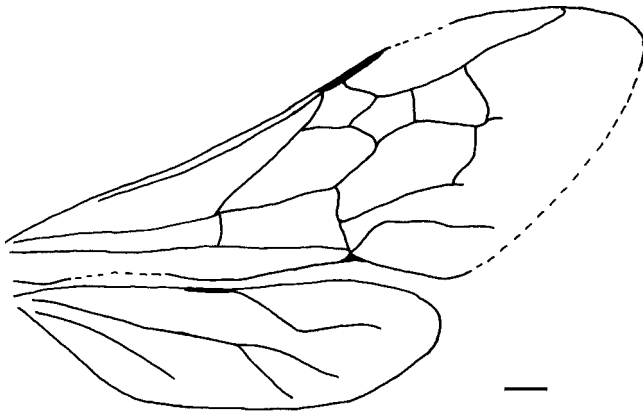
**Material.** ZD0003 (coll. Bílina mine), well-preserved forewings and hindwings; pilosity and wing coloration well preserved; body completely deformed.

**Age and Horizon.** Lower Miocene (Eggenburgian/Ottagnian), Clayey Superseam Horizon, Bílina mine, Czech Republic.

**Description.** Wings elongate, distally papillate, densely pilose, and black. Forewing 14.6 mm long and 5.1 mm wide; cell [2R] very elongate, 5.1 mm long and 1.1 mm wide, distally closed and strongly narrowed in distal part; cell [R] 7.4 mm long and 1.2 mm wide; three closed submarginal cells present; cell [1R] 0.9 mm long and 1.0 mm wide; cell [1Rs] 1.3 mm long and 0.9 mm wide; part of vein Rs between cell [1R] and [2R] sigmoidal; cell [2Rs] 1.6 mm long and 1.2 mm wide; pterostigma rather reduced but present, as broad as prestigma; prestigma long, 0.8 mm long; cross-vein 1m-cu ending on vein M nearly midway between vein Rs and cross-vein 2r-m; posterior margin of cell [1Rs] strongly angled; hindwing 9.4 mm long and 2.6 mm wide; jugal lobe of hindwing much shorter than anal lobe.

**Discussion.** This fossil could have been an Apidae: Xylocopini because of the very reduced pterostigma and the long prestigma (Michener 2000). But its angled posterior margin of cell [1Rs] and its cross-vein 1m-cu well basal of 2r-m exclude affinities with this group. Its wing venation is strikingly similar to that of an extant genus *Bombus* (tribe Bombini), especially in the shape of sigmoidal vein Rs, long cell [2R], relative positions of 1m-cu and 2r-m, long basal part of M. It is not possible to attribute this fossil to a precise subgenus of *Bombus* because all of them are based on body characters not available here.

It is impossible to compare this fossil with the very numerous recent *Bombus* spp. Fossil representatives of this genus are known from the Miocene (Zhang 1990, Rasnitsyn and Michener 1991, Zhang et al. 1994). The Oligocene



Text-fig. 5. *Bombus* sp. indet., Lower Miocene (CSH), Bílina mine, forewing venation (ZD0003, coll. Bílina mine). Scale 1 mm.

species are much more uncertain (Cockerell 1931, Zeuner and Manning 1976).

*Bombus vetustus* RASNITSYN et MICHENER, 1991 (Miocene, Russian Far East) and *Bombus florissantensis* (COCKERELL, 1906) (Eocene-Oligocene of Florissant, Colorado, USA) have hyaline wings. *Bombus proavus* Cockerell, 1931 (Miocene of Washington state, USA) has hyaline, slightly brownish wings. *Bombus luianus* ZHANG, 1990 (Miocene of Shandong Province, China) has shorter brown wings, instead of being longer and black in our fossil (forewing 13.8 mm long instead of 14.6 mm). *Bombus anacolus* ZHANG et al., 1994 (Miocene of Shandong Province, China) has hyaline wings with the apical region punctured. *Bombus dilectus* ZHANG et al., 1994 (Miocene of Shandong Province, China) has longer wings than our fossil (15.5 mm long).

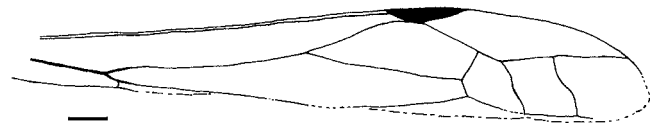
*Bombus pristinus* Unger, 1867 (Miocene, Euboea Island, Greece) is based on a hyaline forewing, strikingly different from those of fossil and extant *Bombus* in its very broad pterostigma, shape of vein Rs, elongate cell [1Rs] (Unger 1867). It is probably not a *Bombus*. *Bombus abavus* HEER, 1867 (Miocene, Öhningen, Germany) and *Bombus crassipes* NOVAK, 1877 (Lower Miocene, Mokřina, Czech Republic) are based on poorly preserved fossils that cannot be compared with our material (Zeuner and Manning 1976). Our fossil is probably a new species, but we lack too many characters to accurately compare it to the extant *Bombus*, thus naming it would not add any information. We prefer to maintain it in open nomenclature.

## Family Vespidae LEACH, 1815

### Vespinæ vel Polistinae gen. et sp. indet.

Pl. 1, figs 8,9,11; text-fig. 6

**Material.** JP0004 (coll. Bílina mine), nearly a complete insect (part and counterpart) in dorsal view; plaited forewings preserved but venation not well preserved; body partly deformed; mesothoracic and metathoracic legs poorly preserved.



Text-fig. 6. Vespidae: ?Polistinae gen. et sp. indet., Upper Oligocene, Veselíčko, anterior part of forewing venation (VE0101, coll. Bílina mine). Scale 1 mm.

ZD0005 (coll. Bílina mine), an isolated plaited forewing with only anterior half of venation preserved; coloration not preserved.

VE0101 (coll. Bílina mine), an isolated plaited forewing; venation well preserved.

BE001 (coll. J. Valíček), nearly a complete insect (part and counterpart) in dorsal view, plaited forewings preserved in medio-apical part; wing venation distinct in anterior part; head and thorax poorly preserved, abdomen with segmentation preserved.

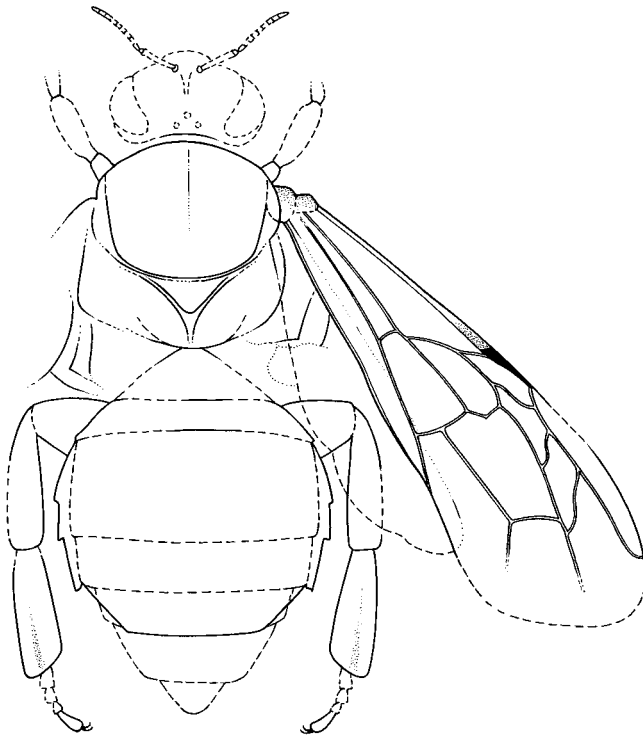
**Age and Horizon.** BE001 Lower Oligocene (Rupelian), Středohoří Complex, Bechlejovice, Czech Republic; VE0101 Lower/Upper Oligocene (Rupelian/Chattian), Středohoří Complex, Veselíčko, Czech Republic; JP0004, ZD0005 Lower Miocene (Eggenburgian/Ottngian), Clayey Superseam Horizon, Bílina mine, Czech Republic

**Description.** BE001: Body length 19.2 mm; head and thorax poorly preserved; abdomen about 13.2 mm long and 7.7 mm wide; forewing about 13.9 mm long and about 2.3 mm wide (wing is folded); pterostigma about 9.4 mm from wing base, 1.5 mm long and 0.4 mm wide; discoidal cell [M] elongated, 7.0 mm long and 1.2 mm wide; cell [1R] 3.2 mm long and 1.1 mm wide; marginal cell [2R] distally pointed onto costa, not appendiculate, about 3.2 long and 1.3 mm wide; cell [1Rs] 1.3 mm long and 1.2 mm wide; veins 1m-cu and 2m-cu received at the same submarginal cell [1Rs]; cross-vein 1cu-a straight, very short, just distal of base of vein M.

JP0004: Body 17.4 mm long; head and thorax not well preserved; abdomen 6.6 mm long and 9.0 mm wide; metathoracic tibia 4.2 mm long and 1.2 mm wide; metathoracic tarsus elongated, 9.3 mm long, basitarsus 4.8 mm long; forewing 14.6 mm long and about 3.0 mm wide (wing plaited).

ZD0005: Forewing about 16 mm long and 2.5 mm wide (wing plaited); veins 1m-cu and 2m-cu received in the same submarginal cell; apex of marginal cell not separated from anterior margin of wing.

VE0101: Forewing about 20 mm long and 3.5 mm wide (wing plaited); pterostigma about 12 mm from base of wing, 1.9 mm long and 0.3 mm wide; discoidal cell [M] elongated, 9.4 mm long and 1.3 mm wide; cell [1R] 4.5 mm long and 1.3 mm wide; cell [2R] distally pointed onto costa, not appendiculate, 5.4 long and 1.2 mm wide; cells [1Rs] 1.4 mm long and 1.2 mm wide, [2Rs] 1.4 mm long and 1.6 mm wide, [3Rs] 2.2 mm long and 1.5 mm wide; veins 1m-cu and 2m-cu received in the same submarginal cell.



**Text-fig. 7.** *Apis* sp. indet., Lower Miocene (CSH), Bílina mine, reconstruction of examined specimen (ZD0001, coll. Bílina mine) by Miss Zuzana Čadová (scientific illustrator, Charles University, Praha).

**Discussion.** The venation is typical for the family Vespidae with a very long cell [M] and three submarginal cells in forewing. The plaited forewings, with 1m-cu and 2m-cu received in the same submarginal cell and the apex of marginal cell not separated from anterior margin of wing, and the very short and straight cross-vein 1cu-a exclude affinities with the subfamilies Stenogastrinae, Euparagiinae, and Masarinae (Brothers and Fynnmore 1993). The marginal cell not appendiculate and distally pointed onto costa is an apomorphy present in Vespinae and Polistinae, but not in Eumeninae (Carpenter 1982, Carpenter and Cumming 1985).

The venation of the forewing anterior part is nearly constant among recent genera of Vespinae and Polistinae (Snelling 1981). Thus we cannot discriminate the two subfamilies and we leave all these specimens in open nomenclature. However, specimen JP0004 probably belongs to subfamily Vespinae because of the distinct long pilosity on thorax, last tarsal segment simple without claw and small pterostigma. On the other hand all other specimens resemble more the subfamily Polistinae because of the pterostigma pointed and prominently enhanced. Despite the fact that the specimen BE001 is attributed on the basis of its wing venation closer to Polistinae, its body habitus is clearly similar to those of Vespinae. Also the ZD0005 probably belongs to the Polistinae because of its large pointed pterostigma and the shape of the submarginal and discoidal cells.

The first record of the family Vespidae is from the Lower Cretaceous with two described subfamilies (Carpenter and Rasnitsyn 1990). There are four genera described in fossil record from Paleocene to Recent, i.e. *Vespa* LINNÉ, 1758, *Palaeovespa* COCKERELL, 1906, *Polistes* LATREILLE, 1802, and *Polybia* LEPELETIER, 1836 (Piton 1940, Carpenter 1992). Vespid wasps are rather frequent in Cenozoic outcrops but nearly always in poor condition to allow correct subfamilial and generic attributions. These several findings represent the first record of the family in the Tertiary deposits of the Czech Republic.

### Conclusions and palaeoecological significance for pollination of Tertiary flowers

All of these new finds demonstrate a unique abundance of the fossil entomofaunas in the North Bohemian Tertiary (see Prokop 2003). Because of the limits of biometrical analysis of advanced hymenopterans such as bees, we do not establish any new species in the present study. The material is more interesting from palaeoecological point of view. It extends the palaeogeographical distribution of the genus *Apis* and *Bombus*. All herein described bees are significant specialized pollinating taxa. Beside these Hymenoptera, there are several other pollinating insects present in the Tertiary of northern Bohemia, i.e. Coleoptera, Diptera and Lepidoptera (Prokop 2003). They are ranging from facultative to obligate nectar and pollen feeders like the bees described herein. In general aspect, the associations between these insects and flowers were probably highly similar to those of modern ecosystems. But they probably differ in the palaeogeographical evolution of both groups. Thus, we have to be prudent in the use of actuo-palaeontological approaches to determine the relationships between fossil plants and insects.

The second part of this study was the observation of eventual presence of pollen on metathoracic legs or on other pilous structures of bees (Pl. 1, Fig. 4) using scanning electron microscopy (SEM – CAM SCAN 4). Unfortunately, we failed to find pollen in these insect structures because of the character of the claystones that is quite poor from palynological point of view, except for pollen fossilised *in situ* (Dašková 2000). This absence could be also due to the taphonomical processes or to the relatively long transport of the insects into the basin by occasional floods (Prokop 2002, 2003).

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## Nové nálezy aculeatních blanokřídých z oligocénu Českého středohoří a spodního miocénu Mostecké pánve v severních Čechách (Hymenoptera: Apidae, Vespidae)

Jakub Prokop – André Nel

V práci jsou popsány nové fosilní nálezy zástupců blanokřídých (Hymenoptera: Apocrita) pocházející z třetihorních lokalit Bechlejovice (spodní až svrchní oligocén), Veselíčko (svrchní oligocén) a důl Bílina (spodní miocén) v severních Čechách. Z hlediska systematiky náleží k dvěma čeledím Vespidae a Apidae (zastoupené v tribu Apini a Bombini). Nálezy přiřazené k rodu *Apis* sp. pravděpodobně náleží nejméně dvěma recentním podrodům *Apis* spp. a *Megapis* spp., pro jejichž jednoznačnou determinaci nejsou zachovány morfologické struktury, a proto byly ponechány v otevřené nomenklatuře na rodové úrovni. Současně větší z obou předpokládaných poddruhů vykazuje morfologickou podobnost na základě křídelní žilnatiny s dříve popsanými nálezy ze svrchního miocénu Francie a Rakouska (*Apis* 'species' E, G, I) a dále s recentním druhem *Apis dorsata* FABRICIUS, 1798 vyskytující se v Indii a dále jihovýchodní Asii. Tento fakt potvrzuje hypotézu o existenci druhu pravděpodobně příbuzného s recentním druhem *A. dorsata* v západní části palearktické oblasti v miocénu. Tribus Bombini je zastoupen jedním nálezem z rodu *Bombus* sp., u kterého není možné blíže identifikovat druhovou příslušnost vzhledem ke stupni zachování. Navíc bylo zjištěno velké množství nálezů nejasné systematické příslušnosti, např. *Bombus abavus* HEER, 1867, *Bombus crassipes* NOVÁK, 1877, které bude nutné revidovat. Dále bylo popsáno několik fragmentárních nálezů čeledi Vespidae, u nichž se nepodařilo materiál jednoznačně přiřadit k podčeledi Vespinae nebo Polistinae. I přes tuto skutečnost nálezy reprezentují vůbec první doklad této čeledi ve fosilním záznamu z našeho území.

Pokusně byla také studována potenciální přítomnost pylových zrn na metathorakálních končetinách u zástupců rodu *Apis* metodou rastrovací elektronové mikroskopie a pomocí separačních palynologických metod.

## Explanation to the plate

### PLATE 1

- 1–2. *Apis* sp. indet., Bílina mine, imprint and counterimprint (ZD0001, coll. Bílina mine, Scale 5 mm),
3. *Apis* sp. indet., Bílina mine, forewing venation (ZD0203, coll. Bílina mine, Scale 2 mm),
4. *Apis* sp. indet., Bílina mine, detail of metathoracic leg (ZD0001, coll. Bílina mine, Scale 1 mm),
5. *Apis* sp. indet., Bílina mine, detail of wing venation (ZD0001, coll. Bílina mine, Scale 1 mm),
6. Apidae gen. et sp. indet., Bílina mine, (ZD0002, coll. Bílina mine, Scale 5 mm),
7. *Bombus* sp. indet, Bílina mine, (ZD0003, coll. Bílina mine, Scale 5 mm),
8. Vespidae: Vespinae *vel* Polistinae gen. et sp. indet., Veselíčko (VE0101, coll. Bílina mine, Scale 3 mm),
9. Vespidae: Vespinae *vel* Polistinae gen. et sp. indet., Bechlejovice (BE001, coll. J. Valíček, Scale 5 mm),
10. Vespidae: Apidae gen. et sp. indet., Bílina, metathoracic leg (ZD0186, coll. Bílina mine, Scale 2 mm),
11. Vespidae: Vespinae *vel* Polistinae gen. et sp. indet., Lower Miocene (CSH), Bílina mine, (JP0004, coll. Bílina mine, Scale 5 mm).



