

TEXT-FIG. 4. A-I, *Apis aquisextusensis* sp. nov.; Upper Oligocene, Aix-en-Provence, Bouches-du-Rhône, France. A-B, holotype MNHN R.08381; A, right forewing; B, left hindwing. C-E, H, paratype R.08382; C, right forewing; D, right hindwing; E, left hind leg; H, detail of the junction between hind tibia and basitarsus. F-G, paratype MNHN R.10421; F, hind leg; G, apex of the abdomen; I, left forewing. Scale bars represent 1 mm (A-G) or 0.5 mm (H). Drawings made using a *Camera lucida*.

Even if these bees have dimensions similar to *A. henshawi* from the Oligocene of Rott, Germany, their narrow cell 2Rs is different and it is obviously impossible to identify them as *A. henshawi*. They probably belong to a new species but their fragmentary state of preservation does not allow us to name them specifically, because no obvious autapomorphic character can be established. More material is needed.

Bees from the Upper Oligocene of Aix-en-Provence, Bouches-du-Rhône, France

Apis aquisextusensis sp. nov.

Plate 1, figures 3–4; Text-figure 4

Derivation of name. After the latin name *Aquae Sextus* for Aix-en-Provence, the type locality.

Material. Holotype MNHN-LP-R.08381 (a nearly complete insect (part and counterpart) in dorsal view; four wings well preserved; pilosity not visible; body partly deformed; organic matter replaced by calcium carbonate; no coloration preserved; only median parts of antenna preserved); paratypes R.08382 (part and counterpart of a nearly complete bee in the same state of preservation) and R.10421 (impression of a nearly complete bee in dorsal view); Upper Oligocene, Upper Chattian; Aix-en-Provence, Bouches-du-Rhône, France.

Diagnosis. Body length 12.7–12.8 mm. Forewing 8.5 mm long. A little smaller than worker *Apis mellifera*. Metathoracic leg structures (tibia and basitarsus) similar to those of worker *A. mellifera* but metathoracic basitarsus shorter and narrower. Eyes appear bare. Cell 2R of forewing distally narrow and vein 1cu-a in prefurcal position. Forewing cell 2Rs not widened. Hindwing crossveins 1cu-a and 1A nearly make right angle. Cells Rs and M of hindwing well separated.

Description. Holotype: Head 2 mm long, 3.2 mm wide, deformed and covered with long hairs which cannot be determined as either simple or plumose. Eyes 1.2 mm long and 0.7 mm wide, probably bare (no visible trace of pilosity). Thorax 4.3 mm long, 3.9 mm wide, covered with small hairs. Thoracic structures not well preserved. Abdomen elongate, 6.5 mm long, 4.5 mm wide, dorsally rather densely covered with hairs. Sternites not visible. Prothoracic and mesothoracic legs not well preserved. A metathoracic leg well preserved. Metathoracic tibia widened, 3 mm long, 0.95 mm wide, covered with hairs along outer margin. Rastellum (*sensu* Snodgrass 1956) on distal apex and no spur. Hind basitarsus widened, covered with hairs along outer margin and with well-defined pollen press (*sensu* Snodgrass 1956). Forewing 8.5 mm long and 2.8 mm wide (Text-fig. 4A). Cell 2R very elongate (3.2 mm long, 0.3 mm wide in distal half and 0.45 mm in proximal half), distally closed and clearly narrowed at distal end. Cell R 3.4 mm long. Cell 1R 1.4 mm long and 0.5 mm wide. Cell 1Rs 1.6 mm long and 0.38 mm wide. Cell 2Rs not widened, 1.4 mm long and 0.38 mm wide. XY 0.5 mm, VS 0.6 mm, ratio XY/VS 0.83. Crossvein 1m-cu meets cell 1Rs near its base. NO 0.35 mm, OS 1.2 mm (*sensu* Louis 1966). Costal margin of cell 1Rs distinctly shorter than posterior margin. WX 0.4 mm, NS 1.6 mm. Vein 1cu-a clearly prefurcal, 0.2 mm from branching of M and CuA. Vein cu-a of hindwing (Text-fig. 4B) nearly makes right angle with vein 1A. Cells Rs and M clearly separated by abscissa of M. Hamuli not preserved.

Paratype R.08382: Head 2.2 mm long, 3.2 mm wide, covered with long hairs. Eyes without hairs. Thorax 4.2 mm long, 4.1 mm wide, deformed but covered with hairs. Abdomen 6.3 mm long and 4.6 mm wide. A well preserved hind leg (Text-fig. 4E, H). Hind tibia widened (2.8 mm long, 0.8 mm wide), densely covered with long hairs along outer edge, with shorter hairs along inner edge, without any spur but with rastellum. Hind basitarsus widened (1.85 mm long, 0.9 mm wide), covered with long hairs and with well-developed pollen-press. Forewing 8.5 mm long and 2.8 mm wide. Dimensions and structures of wings identical to those of holotype (Text-fig. 4C–D).

Paratype R.10421: Head *c.* 2 mm long, 3 mm wide, covered with long hairs. Eyes without hairs. Thorax 4 mm long, 4 mm wide, deformed but covered with hairs. Abdomen 8 mm long and 5 mm wide (Text-fig. 4G). A well preserved hind leg (Text-fig. 4F). Hind tibia widened (2.8 mm long, 0.8 mm wide), densely covered with long hairs along outer edge, and shorter hairs along inner edge, rastellum but no spur. Hind basitarsus widened (1.85 mm long, 0.9 mm wide), covered with long hairs, and with well-developed pollen-press. Forewing 8.6 mm long and about 3 mm wide. Dimensions and structures of four wings identical to those of holotype (Text-fig. 4I).

Remarks. The structures of the four wings and the hind legs clearly show that these fossils belong to the

genus *Apis*. The dense pilosity of the hind legs suggests that they are workers (Snodgrass 1956). The venation and the very similar dimensions demonstrate that the described specimens belong to the same species.

Apis aquisextusensis sp. nov. could be related to the subgenus *Micrapis* Ashmead, 1904 because its cell 2R is distally narrowed. Also, its cu-a in the hindwing makes closer to a right angle with 1A than in *Micrapis florea*. Nevertheless, it differs from the subgenus *Micrapis* in its greater dimensions and having the hindwing cell Rs well-separated from cell M.

The structure of the hindwing would suggest some affinities with *Apis* and *Megapis* but the structure of the forewing cell 2R is different from these subgenera. Vein 1cu-a of the forewing, which is in a prefurcal position, differs from the subgenus *Synapis* but the bare eyes suggest affinities with *A. (S.) henschawi*. The wing venation, especially the non-widened cell 2Rs, shows that *A. aquisextusensis* sp. nov. is a very different species.

Apis sp. B.

Text-figure 5A-B

Material. MNHN-LP-R.10429 (part and counterpart of a nearly complete bee, in dorsal view; wing venation only partly preserved, apical parts of the wings having been destroyed); Upper Oligocene, Upper Chattian; Aix-en-Provence, Bouches-du-Rhône, France.

Description. Head 2.1 mm long, 3.5 mm wide, covered with long hairs. Eyes without hairs. Thorax 5 mm long, 5 mm wide, deformed but covered with hairs. Abdomen 7.5 mm long and 5 mm wide. Legs absent or not well preserved. Hind leg visible. Hind tibia and basitarsus widened, covered with long hairs, and with a well-developed pollen-press. Forewing c. 11.9 mm long (Text-fig. 5A), longer and slightly broader than wing of *Apis aquisextusensis* sp. nov. Vein 1cu-a in furcal position. Cell 2Rs 1.7 mm long and 0.9 mm wide. XY 1 mm, VS 0.8 mm, ratio XY/VS 1.25. Cell 2R distally narrowed, 3.3 mm long, proximal width 0.4 mm, distal width 0.3 mm. Hindwing not well preserved (Text-fig. 5B) but vein ab M, separating cells Rs and M, apparently present. Vein cu-a makes right angle with 1A.

Remarks. The main differences between this bee and *A. aquisextusensis* sp. nov. are: (1), its forewing is longer, about 12 mm long compared to 8.5 mm for *A. aquisextusensis*; (2), cell 2Rs is widened, broader than in *A. aquisextusensis*; (3), vein 1cu-a of forewing is in a furcal position. They share the basally widened cell 2R of the forewing and vein cu-a of the hindwing making a right angle with vein 1A.

It is difficult to determine whether the visible differences between this fossil and *A. aquisextusensis* are due to intraspecific variations or because they are different species. More material is required before this can be resolved although we believe that they are probably the same species.

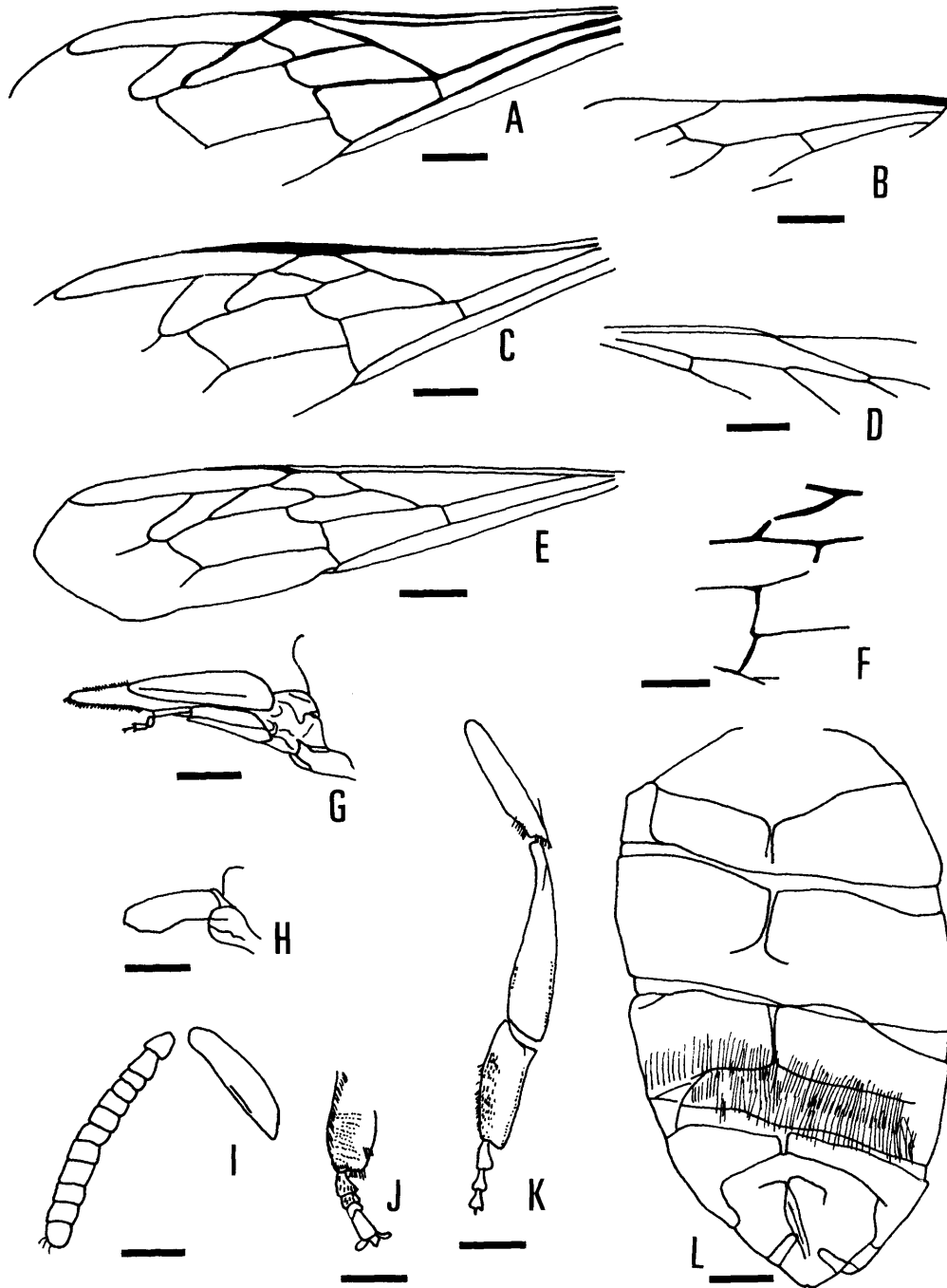
Apis sp. C

Text-figure 5c

Material. MNHN-LP-R.10426 (impression of nearly complete bee, in dorsal view; wing venation only partly preserved, apical parts of wings destroyed); Upper Oligocene, Upper Chattian; Aix-en-Provence, Bouches-du-Rhône, France.

Description. Head 2.0 mm long, 3.0 mm wide, covered with long hairs. Eyes not clearly visible but apparently without hairs. Thorax 4.0 mm long, 4.0 mm wide, deformed but covered with hairs. Abdomen 6 mm long and 5 mm wide. Legs poorly preserved. Forewing c. 10.0 mm long and 3.0 mm wide (Text-fig. 5c). Cell 2R 3.7 mm long and 0.3 mm wide. Cell 2Rs 1.5 mm long and 0.9 mm wide. XY 0.8 mm, VS 1 mm, ratio XY/VS 0.8.

Remarks. This specimen differs from *Apis* sp. B in the non-distally narrowed cell 2R and its crossvein 1cu-a which is clearly in a praefurcal position, but the two forms share a relatively large forewing and very similar proportions of other cells.



TEXT-FIG. 5. A-B, *Apis* sp. B; MNHN R.10429; Aix-en-Provence; A, left forewing; B, left hindwing. C, *Apis* sp. C; MNHN R.10426; Aix-en-Provence; left forewing. D-L, *Apis* sp. D; MPV-91-RM; Rubielos de Mora, Spain; D, right hindwing; E, right forewing; F, detail of the median part of right forewing; G, tongue; H, right mandible; I, right antenna; J, left hind tarsi; K, right hind leg (notice the deformation); L, abdomen. Scale bars represent 1 mm (A-E, L) or 0.5 mm (F-K).

It is impossible to say whether these two specimens belong to different species. Indeed, *Apis* sp. C, *A.* sp. B and *A. aquisextusensis* are all very similar, although *A.* sp. C is distinctly longer and broader than *A. aquisextusensis* and has a distinctly broader cell 2Rs. More specimens are needed before the exact number of fossil species in the Oligocene of Aix-en-Provence can be assessed.

'Apis' aquitaniensis de Rilly, 1930

- 1930 *Apis aquitaniensis*; de Rilly [reference not traced; see Remarks].
 1931 'Abeille mellifère' Alphandéry, p. 3, text-fig.
 1938 *Apis aquitaniensis* de Rilly; Armbruster, p. 88.
 1949 *Apis aquitaniensis* de Rilly; de Rilly, p. 125.
 1953 '*Apis' aquitaniensis* de Rilly; Maa, p. 631.
 1969b *Apis aquitaniensis* de Rilly; Kelner-Pillault, p. 525.
 1976 '*Apis' aquitaniensis* de Rilly; Zeuner and Manning, p. 250.
 1978 *Apis aquitaniensis* de Rilly; Burnham, p. 122.

Material. Holotype Musée d'Histoire Naturelle of Marseille no. 5979, not traced, probably lost; Upper Oligocene, Upper Chattian; Aix-en-Provence, Bouches-du-Rhône, France.

Remarks. Maa (1953) indicated that this fossil could belong to *Synapis*, although he did not see the holotype. As already stated by Zeuner and Manning (1976), this species has never been well described. Its exact taxonomic position is uncertain but it is probably not an *Apis*, although the presence of several genuine *Apis* in the Upper Oligocene of Aix-en-Provence is now clearly demonstrated. The exact date and place of publication of '*Apis' aquitaniensis* by de Rilly remain uncertain. Zeuner and Manning (1976) indicated that it was first published by de Rilly in 1930 in the journal 'L' Apiculteur', but there is no paper by de Rilly in the issue (Vol. 74) for that or adjoining years. Alphandéry (1931) reported that the species had been studied by de Rilly and Vayssière but gave no indication that they had published a description. Zeuner and Manning (1976) noted that there could be a figure of the holotype published by de Rilly in 1924, although they did not cite the reference and we could not find any trace of such a paper. The first published description that we have seen is that of Alphandéry (1931) (as 'Abeille mellifère'). Some confusion between the various de Rilly references may have arisen because the part number of the French journal *La Nature*, in which de Rilly's 1949 paper was published is the same as an issue of the English journal *Nature* published in 1930. It is possible that until 1949, *aquitaniensis* was an MS species only.

Bee from the Oligo-Miocene of Bohemia, Czech Republic

Apis (Synapis) petrefacta Ríha, 1973

- 1973 *Synapis petrefacta* Ríha, p. 217, text-fig. 1, pl. 1, figs 1-2.
 1979 *Synapis petrefacta* Ríha; Ríha, p. 29.

Material. Holotype Paläontologischen Abteilung des Nationalmuseums, Prague, Inv-Nr. P-399/P-400 (part and counterpart); Oligo-Miocene, volcanic bituminous claystone; Kundratice, Litomerice, Bohemia, Czech Republic.

Remarks. This species is not listed in Zeuner and Manning (1976). According to Ríha (1973), the forewing length is c. 9.6 mm which is distinctly shorter than that of *A. cuenoti* (mean 12 mm). Also, if the illustration of Ríha (1973) is correct, there are differences in the structure of cells 2Rs and 1Rs between the two species. Comparison with *S. henshawi* is more difficult because of the latter's great variability.

Bees from the Lower–Middle Miocene of Rubielos de Mora, Teruel, Spain

Apis sp. D

Text-figure 5D–L

1991 Apidae aff. *Apis* Martínez-Delclòs *et al.* p. 130, text-fig. 8, pl. 2, fig. 9.

Material. Holotype MPV-91-RM (nearly complete bee; only slightly deformed by cleavage of bedding); Lower–Middle Miocene (Martínez-Delclòs *et al.* 1991). Rubielos de Mora, Teruel Province, Spain.

Description. Head 3.5 mm long and 2.5 mm wide, covered with long hairs. Eyes hairy. Ocelli not visible. Not possible to determine whether eyes separated or jointed because of deformation. Antenna 3.1 mm long. Scape 1 mm long (Text-fig. 5I). 13 segments visible but base of antennal funicle not preserved. Proboscis (or maxillo-labial complex *sensu* Correia 1973) 2.1 mm long (Text-fig. 5G). Left galea partly broken. Last three segments of labial palp visible. Second segment (first visible) of labial palp longer than two apical segments. Segments of labial palp rather flattened (0.08 mm wide). Right galea 0.9 mm long and exactly covering labial palp. Glossa 1.6 mm long, longer than galeas, apically flattened and covered with small dense hairs. Prementum 0.3 mm long, less than half of length of glossa. Whole structure of proboscis similar to that of Recent *Apis mellifera* (Correia 1973, fig. 44). One mandible partly visible (Text-fig. 5H), similar to that of Recent worker *Apis*, without acute teeth (Michener and Fraser 1978). Thorax 3.0 mm long, 2.5 mm wide; apparently bare but possibly hairs destroyed. Abdomen 8.5 mm long and 5.0 mm wide (Text-fig. 5L). Structures of different segments very deformed. Whole sting apparatus pushed out of abdomen and lying near its apex. Sting barbed and sting sheath almost bare, as in Recent *Apis* sp. (Alexander 1991). One hind leg and tarsi of other legs very well preserved (Text-fig. 5J–K). Hind tibia and basitarsus comparatively elongate; tibia 3.0 mm long, 0.7 mm wide, ratio length/width 4.28; left basitarsus 2.0 mm long, 0.7 mm wide, ratio length/width 2.85; right basitarsus 1.5 mm long, 0.7 mm wide, ratio length/width 2.14; elongations of hind tibia and basitarsus probably consequence of deformation due to cleavage. Hairs which border tibia and the basitarsus not well preserved but parallel rows of setae on posterior surface of basitarsus visible. Ten rows of hairs on posterior surface of basitarsus. Forewing 9.5 mm long and 2.3 mm wide (Text-fig. 5E–F). Cell 2R very elongate, distally closed, clearly not narrowed at its distal end, 3.2 mm long, 0.3 mm wide in distal half, 0.3 mm wide in proximal half. Cell R 4.2 mm long. Cell 1R 1.4 mm long and 0.4 mm wide. Cell 1Rs 1.6 mm long, 0.4 mm wide. Cell 2Rs 1.6 mm long, 0.6 mm wide. XY 0.8 mm, VS 0.9 mm, ratio XY/VS 0.88. Crossvein 1m-cu meets 1Rs some distance distal of its base. NO 0.4 mm, OS 1.2 mm (*sensu* Louis 1966). Anterior margin of 1Rs distinctly shorter than posterior margin, WX 0.4 mm, NS 1.6 mm. Cells 1R, 1Rs, 2Rs and pterostigma similar to those of *A. mellifera*. Vein 1cu-a 0.3 mm from branching of M and CuA, clearly prefurcal as for *A. mellifera*. Hindwing vein cu-a (Text-fig. 5D) makes acute angle with vein 1A, as in *A. mellifera*. Cells Rs and M clearly separated by long abscissa of M. Hamuli not preserved.

Remarks. The structures of the forewings and the hind legs clearly show that this specimen belongs to the genus *Apis*. It had already acquired the Recent structures of the proboscis of the genus. The presence of a sting demonstrates that it is a female or a worker. Following Snodgrass (1956), the parallel rows of setae on the posterior surface of basitarsus are typical of a worker. This bee is probably a genuine worker and not a queen. Its venation is very similar to that of *Apis mellifera*. The narrow wings are a product of fossilization. This bee is related to *A. mellifera* but its exact affinities with Recent species are impossible to establish because the available characters by which differences can be gauged are very few and not preserved. Nevertheless, this specimen demonstrates the presence of genuine *Apis* clearly related to *A. mellifera* in the Early Miocene of Western Europe.

Bees from the Middle Miocene of Iki Island, Japan

'*Apis*' sp.1970 '*Apis*' sp., Fujiyama, p. 69, pl. 15, fig. 3.1978 '*Apis*' sp., Burnham, p. 119.

Material. NSM-PI-7418 (? worker); Middle Miocene, diatomitic palaeolake; Chôjabaru Formation, Iki Island, Japan.