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A REVIEW OF THE EURASIAN FOSSIL SPECIES OF THE BEE *APIS*

by A. NEL, X. MARTÍNEZ-DELCLÒS, A. ARILLO and E. PEÑALVER

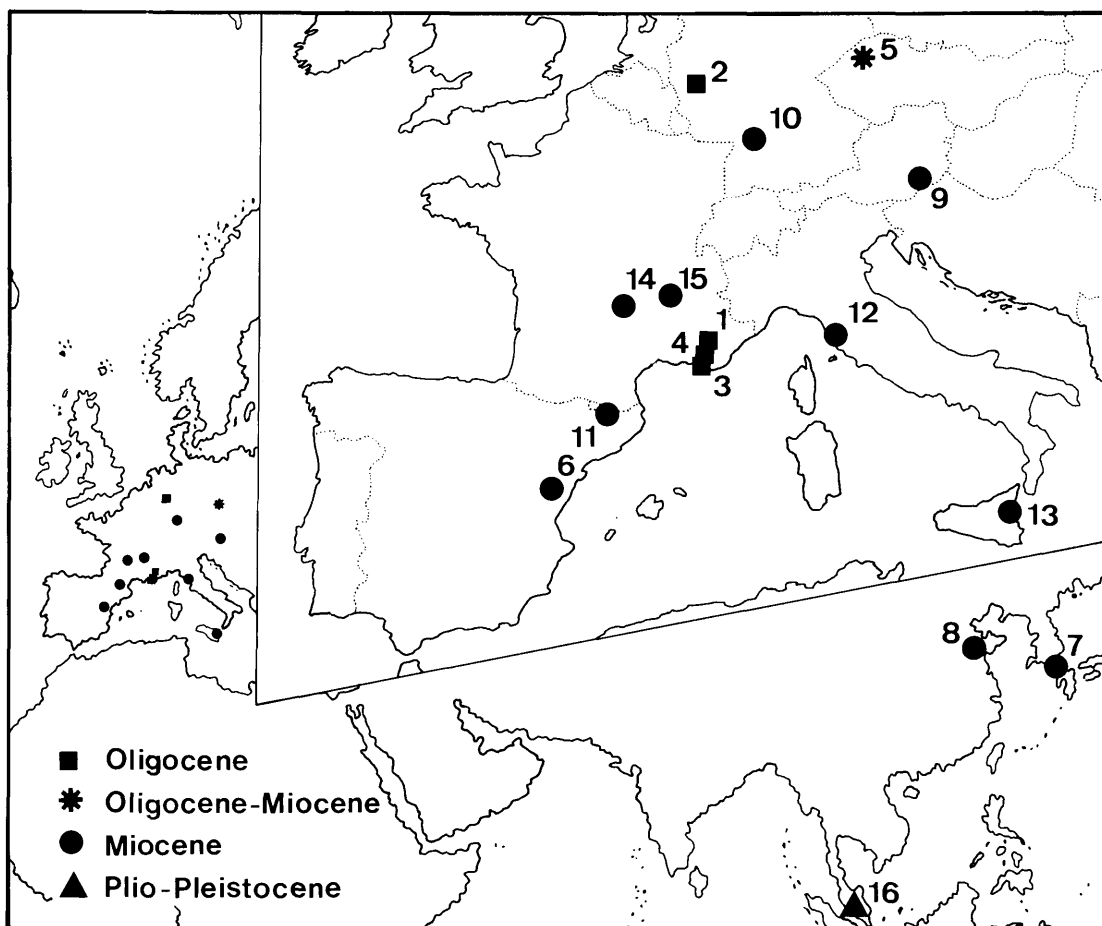
ABSTRACT. Fossil *Apis* species from the Oligocene, Miocene and Plio-Pleistocene of Eurasia are described and their relationships with Recent species are discussed. Several new populations of fossil bees are reported from the Oligocene and Miocene of France and Spain, including *Apis aquisextusensis* sp. nov. The present state of knowledge of fossil bee systematics is poor because of the general lack of preserved characters. Some of the problems, and items requiring further investigation, are identified.

MAA (1953) divided Recent *Apis* into three genera, *Megapis* Ashmead, 1904, *Apis* Linnaeus, 1758 and *Micrapis* Ashmead, 1904, which Michener (1944) had earlier regarded as subgenera of *Apis*. To these three, Zeuner and Manning (1976) added the fossil subgenus *Synapis* Cockerell, 1907 from the Upper Oligocene of France and Germany. We follow the subgeneric classification of Michener (1944) rather than the generic classification of Maa (1953) because there is no good reason to consider *Synapis* as a separate genus. It is not well-characterized and is almost a 'melting-pot' for the bees of the Oligo-Miocene with plesiomorphic characters in their wing venation. The use of the subgenus *Synapis* is still convenient for naming some Oligo-Miocene bees but is of little significance in a phylogenetic classification. Since Zeuner and Manning's (1976) work on fossil *Apis*, which omitted a species described by Riha (1973) from Bohemia, some new species have been discovered in China and Japan. In addition, we have recently found numerous specimens of fossil bees in the Oligocene of Provence, southern France and the Miocene of central France and Cerdanya in Lleida, Spain. We have also restudied the holotype of *Synapis cuenoti* Théobald, 1937. Our friend Mr P. Brisac has discovered well preserved fossil *Apis* in the Miocene of Ardèche, France and one of us has recovered two bees in the Miocene of Rubielos de Mora, Teruel, Spain. Localities which have yielded fossil *Apis* are shown on Text-figure 1.

We follow an amended venational nomenclature after Michener (1944), Eickwort (1969), Wootton (1979) and Alexander (1991), but not Maa (1953, p. 538). For the names of points of intersections of veins, we follow the nomenclature of Louis (1963, 1966, 1971) (see Text-fig. 2A and Table 5). The first article of the hind tarsus is here called the basitarsus (*sensu* Snodgrass 1956) (= metatarsus *sensu* Ruttner 1988).

Although phylogenetic studies of Recent *Apis* have been undertaken by Alexander (1991), Garnery *et al.* (1991), and Willis *et al.* (1992), summarized in Engel and Schultz (1997), it is nearly impossible to integrate fossil bees with these because of the lack of preserved characters. For example, following Alexander's (1991) study, we attempted to make a list of characters that could be examined in nearly all fossil material. We discovered only seven, as follows: (1), compound eyes hairy: present/absent; (2), angle (OSX) of forewing: $>45^\circ/<45^\circ$; (3), angle (SVY) of forewing: $>45^\circ/<45^\circ$; (4), distal abscissa of hindwing vein M: present/absent; (5), cell 2R: distally narrowed/not distally narrowed; (6) desclerotization of vein 1m-cu in the middle (forewing): on distal side only/on both sides; (7), cubital index: $>3/<3$. The cubital index is usually named Ci (= CB/CA = a/b *sensu* Ruttner 1988, p. 42, fig. 4.7, p. 72, fig. 6.8) (= TS/TV *sensu* Louis 1971) (see Text-fig. 2A). As we have more fossil taxa than characters, it is hopeless trying to construct a phylogeny. Other characters used by Alexander (1991) or Garnery *et al.* (1991) are too delicate and usually not preserved in the available material. Construction of a phylogeny will only be possible after the discovery of further specimens and a careful revision of all the known material, especially the fossil bees which were described by Statz (1931, 1934, 1942, 1943) and Armbruster (1938).

The following measurements, based on Ruttner (1988), give an idea of how intraspecific variation



TEXT-FIG. 1. Localities with fossil *Apis*. 1, Céreste, France; 2, Rott, Germany; 3, Camoins-les-Bains, France; 4, Aix-en-Provence, France; 5, Kundratice, Czech Republic; 6, Rubielos de Mora, Spain; 7, Iki Island, Japan; 8, Shanwang, China; 9, Parschlug, Austria; 10, Randecker Maar, Germany; 11, Bellver de Cerdanya, Spain; 12, Gabbro, Italy; 13, Catania, Italy; 14, Saint-Reine, France; 15, Montagne d'Andance, France; 16, Kuala Lumpur, Malaysia.

within the Recent species of *Apis* can be relatively great: (1) for *Apis cerana* Fabricius, 1793, the forewing length varies between 7.5 and 8.9 mm, the forewing width varies between 2.6 and 2.7 mm, and the mean value of the cubital index is 4.40; (2) for *Apis mellifera* Linnaeus, 1758, the forewing length varies between 7.64 and 9.75 mm (worker), the forewing width varies between 2.64 and 3.31 mm, and the mean value of the cubital index is 2.30 with a variation between 1.53 and 3.60; (3) for the Recent species of the *Apis dorsata* Fabricius, 1793 group, the forewing length varies between 12.5 and 14.5 mm; (4) for *Apis koschevnikovi* (Buttel-Reepen, 1906), the forewing length varies between 8.5 and 8.8 mm, the forewing width varies between 2.9 and 3.1 mm, and the cubital index between 5.6 and 9.5 (Ruttner *et al.* 1989); (5) for *Apis florea* Fabricius, 1787, the forewing length varies between 6.5 and 7.0 mm (see Text-fig. 13).

It is difficult to establish the limits of any intraspecific variations in fossil *Apis* species. Comparisons with Recent taxa, based on biometrical analyses similar to those proposed by Ruttner (1988) or Ruttner and Tassencourt (1978), are impossible to make on the basis of the few available specimens. Furthermore, there is no guarantee that a phylogenetic classification could be constructed on the basis of such phenetic analyses (Penny 1982; Darlu and Tassy 1993). We prefer to use open nomenclature for many of the fossil

bee populations described herein because of difficulties of comparison with previously described species. The definition of several populations named herein species A, B, etc., is as informative as giving new species names and more realistic in view of the poor present state of knowledge of fossil bee systematics. In the following systematic descriptions of Eurasian fossil *Apis*, the taxa are ordered chronostratigraphically from old to young.

Repositories of specimens. The following abbreviations are used: EFN (Ecole Nationale des Eaux et Forêts, Nancy), LACM (Los Angeles County Museum), MNCN (Museo Nacional de Ciencias Naturales, Madrid), MNHN (Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris), MPV (Museo Paleontológico, València), NHM (The National History Museum, London).

SYSTEMATIC PALAEOLOGY

Order HYMENOPTERA Linnaeus, 1758

Family APIDAE Latreille, 1802

Tribe APINI Latreille, 1802

Genus APIS Linnaeus, 1758

Bees from the Upper Oligocene of Cereste, Vaucluse, France

Apis (*Synapis*) *cuenoti* Théobald, 1937

Text-figures 2B–G, 3A–E; Plate 1, figure 1

- 1937 *Apis cuenoti* Théobald, p. 401, pl. 8, fig. 16; pl. 28, fig. 8.
 1953 '*Apis*' *cuenoti* Théobald; Maa, p. 631.
 1969*b* *Apis cuenoti* Théobald; Kelner-Pillault, p. 525.
 1976 *Apis* (*Synapis*) *cuenoti* (Théobald); Zeuner and Manning, p. 240.
 1978 *Apis cuenoti* Théobald; Burnham, p. 122.
 1984 *Apis cuenoti* Théobald; Lutz, p. 13, pl. 4, figs 15–16.

Type horizon. Upper Oligocene, Upper Stampian, lacustrine laminites.

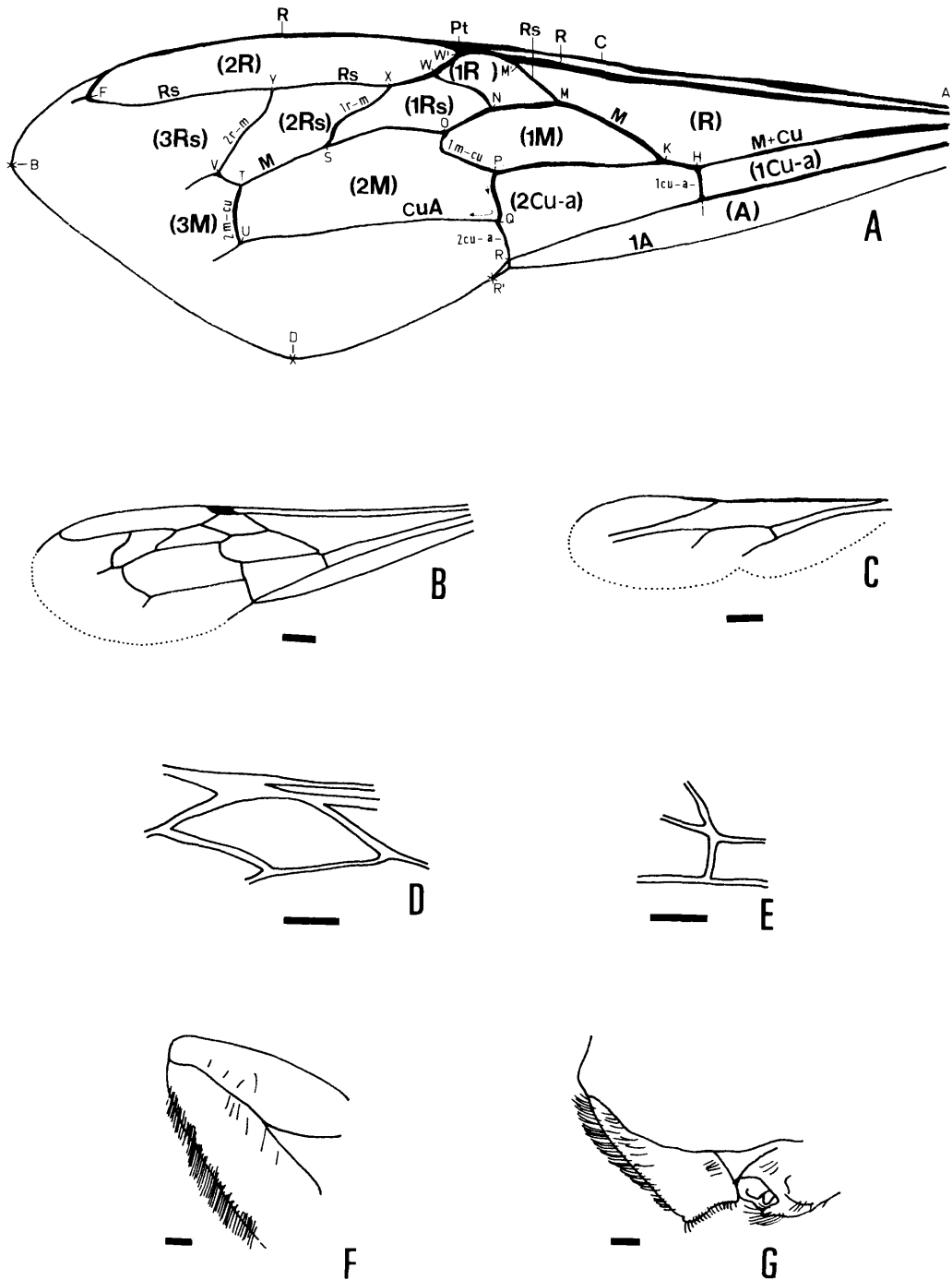
Type locality. Céreste, Vaucluse, France.

Material. Holotype EFN no. 173 (nearly complete mummy; only distal half of abdomen, antenna and fore- and median legs missing; head deformed). MNHN-LP-R.08383 (part and counterpart of thorax with a hind leg, a forewing, a hindwing and abdomen preserved connected), MNHN-LP-R.08396 (state of preservation not good enough for detailed description); also a specimen figured by Lutz (1984).

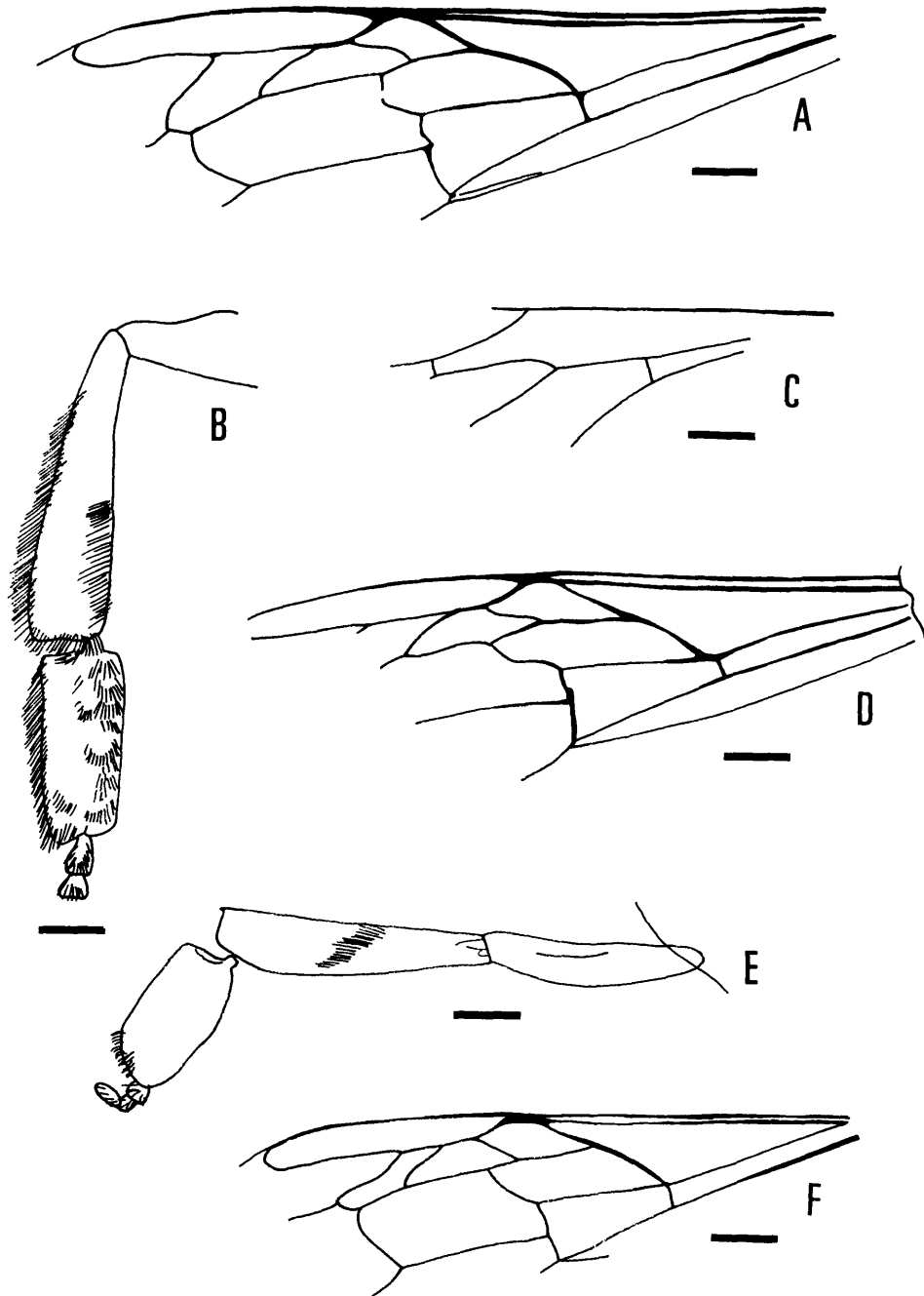
Description. The original description of Théobald (1937, p. 401) is not very precise so, we give some additional details below.

Holotype: Body dark brown; abdomen black. Head 2.4 mm long, 3.6 mm wide. Diameter of eye 1.2–1.5 mm. Distance between eyes 0.9 mm. Eyes have some little hairs; head hairy. Ocelli not visible. Thorax very hairy, deformed, 5.5 mm long, 5 mm wide. Abdomen very hairy; length of its preserved part 7.5 mm, width 5.5 mm. Wings hyaline. Forewing 12.6 mm long, 3.7 mm wide. Cell 2R 4.5 mm long, 0.6 mm wide, distally closed but not distally narrowed. Cells 1R and 1Rs similar to those of Recent *Apis* (Text-fig. 2B) but cell 2Rs clearly widened. Costal side of cell 1Rs distinctly shorter than posterior side (WX 0.5 mm, NS 2.1 mm). Vein 1m-cu begins near base of cell 1Rs. Pterostigma (Text-fig. 2D) similar to Recent *Apis*. Crossvein 1cu-a opposite branching of M and CuA, in furcal position (Text-fig. 2E). Hindwing 9.5 mm long. Cells Rs and M well-separated by abscissa of vein M, and vein cu-a nearly makes right angle with 1A (Text-fig. 2C). Hind legs are not well preserved (Text-fig. 2F–G) but clearly without any spurs on their tibiae. Hind basitarsus 3.2 mm long, 1.2 mm wide. Femora 3 mm long, 0.7 mm wide. Tibiae 3.5–4 mm long, 1.2 mm wide. Hind tibiae covered with long hairs along outer margins.

R.08383: Body brown, wings hyaline. Thorax and abdomen hairy and only slightly deformed, visible in dorsal view.



TEXT-FIG. 2. A, Forewing of an *Apis* sp., showing the cells, veins and node nomenclature. B-G, *Apis* (*Synapis*) *cuenoti* Théobald, 1937; holotype EFN no. 173; Upper Oligocene, Céreste, Vaucluse, France. B, right forewing; C, right hindwing; D, detail of the right forewing pterostigma; E, detail of the forewing vein cu-a; F, left hind leg; G, right hind leg. Scale bars represents 1 mm (B-C, F-G) or 0.05 mm (D-E). Drawings made using a *Camera lucida*.



TEXT-FIG. 3. A-E, *Apis (Synapis) cuenoti* Théobald, 1937. A-C, MNHN R.08383; A, left forewing; B, left hind leg; C, left hindwing; D-E, MNHN R.08396; D, left forewing; E, left hind leg. F, *Apis* sp. A; MNHN R.08384; Upper Oligocene, Camoins-les-Bains, Marseille Basin, France; left forewing. Scale bars represent 1 mm. Drawings made using a *Camera lucida*.

Thorax *c.* 6 mm long and 5 mm wide. Abdomen 11.5 mm long, 5.5 mm wide. Forewing 12.6 mm long, 3.8 mm wide. Venation similar to that of holotype (Text-fig. 3A). Cell 2R 4.6 mm long, 0.6 mm wide. Cell R 4.9 mm long. Cell 1R 1.8 mm long, 0.6 mm wide. Cell 1Rs 2.2 mm long, 0.6 mm wide. Cell 2Rs 2.3 mm long, 0.8 mm wide. XY 1.5 mm, VS 1.5 mm, ratio XY/VS 1. WX 0.5 mm, NS 2.2 mm. Vein 1cu-a in a furcal position, below branching of M and CuA. Hindwing similar to that of holotype (Text-fig. 3C). Vein cu-a nearly makes right angle with 1A. One hind leg well preserved (Text-fig. 3B); visible structures similar to those of leg of Recent *Apis*: row of long hairs present along outer margin of tibia, corbicula present on tibia, rastellum at apex of tibia, tibia without any spurs, basitarsus widened, with long hairs aligned in ten rows along outer margin and with well-developed pollen press. Hind tibia 4.2 mm long, 1.2 mm wide. Hind basitarsus 3 mm long, 1.3 mm wide. Basitarsus obviously longer and broader than that of Recent *Apis mellifera* (Ruttner and Tassencourt 1978). Number of rows of bristles on basitarsus not determinable.

R.08396: Thorax 6.7 mm long, 5.6 mm wide. Forewing *c.* 11 mm long and 3.6 mm wide. Venation not well preserved but all visible parts strictly similar to those of holotype and R.08383 (Text-fig. 3D). Cell 1R 1.9 mm long, 0.5 mm wide. Cell 1Rs 2 mm long, 0.5 mm wide. Cells 2R and 2Rs not completely preserved but probably similar to those of R.08383. Vein cu-a in somewhat prefurcal position, 0.2 mm before fork of M + CuA. Hind basitarsus 2.4 mm long, 1.2 mm wide. Femora 3.3 mm long, 0.7 mm wide. Tibiae 4.2 mm long, 0.9 mm wide. Hind tibia 1.75 times longer than hind basitarsus. Basitarsus distinctly shorter than that of R.08383 and holotype; pilosity comparatively reduced (Text-fig. 2E). Mean of forewing length of three specimens 12 mm.

Remarks. The structure and hind leg pilosity show that R.08383 and the holotype are workers (Snodgrass 1956). Maa (1953) and Zeuner and Manning (1976) attributed *Apis cuenoti* to the subgenus *Synapis* and considered that it could not be identified as *Apis (Synapis) henschawi* Cockerell, 1907 because of its eye pilosity and its very long wings. Although they considered that 'upon reexamination, the specimen may turn out to resemble this species more closely than is at present apparent', our study indicates that the two species are very different. *A. cuenoti* is close to Recent *Apis* because of the hairy eyes but resembles *Synapis* in having the forewing vein 1cu-a opposite the fork of vein M + CuA. This last character, shared by numerous Bombini, is probably plesiomorphic within the tribe Apini.

Despite the opinion of Théobald (1937, p. 402), *A. cuenoti* has no clear phylogenetic affinities with *Apis (Megapis) dorsata*, from which it clearly differs in its venation. *A. cuenoti* is also clearly different from the *Apis* from Aix-en-Provence and Camoins-les-Bains, France (see below) because of its greater size.

R.08396 has nearly the same venation as other specimens but its hind leg is very different, with a shorter basitarsus and reduced pilosity. It probably belongs to the same species but it could be a drone or a queen. The only known specimen of *Apis (Synapis) henschawi kaschkei* (Statz, 1931) from the Oligo-Miocene of Rott (Germany) also has a short basitarsus, and could also represent a different caste (drone or queen?).

Bees from the Upper Oligocene–Lower Miocene of Rott, Rheinland, Germany

Apis (Synapis) henschawi henschawi Cockerell, 1907

- 1907 *Synapis henschawi* Cockerell, p. 229.
- 1915 *Apis oligocenica* Meunier, p. 210.
- 1934 *Synapis henschawi* Cockerell; Statz, p. 5, figs 1, 4–7.
- 1942 *Synapis henschawi* Cockerell; Statz, p. 1, figs 2–4.
- 1943 *Synapis henschawi* Meunier, Cockerell; Statz, pp. 103, 109, two unnumbered text-figs.
- 1952 *Apis (Synapis) henschawi* Cockerell; Manning, pl. 1, fig. 3.
- 1973 *Synapis henschawi* (Cockerell); Sphon, p. 55.
- 1976 *Apis (Synapis) henschawi* Cockerell; Zeuner and Manning, p. 240.
- 1978 *Apis henschawi* Cockerell; Burnham, p. 118, fig. 4, p. 122.
- 1983 *Apis henschawi* Cockerell; Culliney, p. 32, fig. 1.

Type horizon. Upper Oligocene–Lower Miocene.

Type locality. Rott, near Bonn, Germany.

Material. Holotype in collection of Museum of Comparative Zoology, Harvard University, number unknown (Zeuner

and Manning 1976); LACM 3919 (Sphon 1973). The holotype of *Apis oligocenica* Meunier, 1915 is in the Heimatmuseum, Siegburg an der Lahn, Germany.

Apis (Synapis) henshawi dormiens Zeuner and Manning, 1976

- 1907 *Apis dormitans* (nec Heyden 1862); Cockerell, p. 228.
 1908 *Apis dormitans* Cockerell; Handlirsch, p. 1357.
 1931 *Synapis dormitans* Cockerell; Statz, p. 47, figs 1–9.
 1931 *Synapis dormitans* (Cockerell); Statz, pp. 42, 46, figs 1a, 2b, 3c, 4a, 5–9.
 1932 *Synapis dormitans* (Cockerell); Alfonsus, p. 275, unnumbered fig.
 1933 *Synapis dormitans* (Cockerell); Watson, p. 48, unnumbered fig.
 1934 *Synapis dormitans* (Cockerell); Statz, p. 1, figs 2, 8, 10.
 1942 *Synapis dormitans* Cockerell; Statz, p. 1, figs 1, 5–6, 8–13, 20–21.
 1943 *Synapis dormitans* (Cockerell); Statz, pp. 101, 105 and 108, three unnumbered text-figs.
 1959 *Synapis dormitans* (Cockerell); Furst, p. 48, unnumbered fig.
 1969a *Synapis dormitans* Cockerell; Kelner-Pillault, p. 92, fig. B (p. 91).
 1969b *Synapis dormitans* Cockerell; Kelner-Pillault, p. 528, figs 6, 9.
 1973 *Synapis dormitans* (Heyden, 1862); Sphon, p. 55.
 1976 *Apis (Synapis) henshawi dormiens* Zeuner and Manning, p. 241.
 1978 *Apis henshawi dormitans* (Cockerell); Burnham, p. 122.
 1989 *Apis (Synapis) henshawi dormiens* Zeuner and Manning; Lutz, p. 37, fig. 4.8.

Type horizon. Upper Oligocene–Lower Miocene.

Type locality. Rott, near Bonn, Germany.

Material. Holotype LACM 3915 and others in LACM (Statz coll.; listed by Sphon (1973) under the name *Synapis dormitans*); one specimen in Museum of Comparative Zoology, Harvard University, number unknown (Zeuner and Manning 1976); NHM In. 59634 and In. 36655.

Apis (Synapis) henshawi kaschkei (Statz, 1931) ♂

Plate 1, figure 2

- 1931 *Synapis kaschkei* Statz, p. 50, figs 10–11.
 1934 *Synapis kaschkei* Statz; Statz, p. 3, figs 3, 9.
 1942 *Synapis kaschkei* Statz; Statz, p. 2, fig. 7.
 1973 *Synapis kaschkei* Statz; Sphon, p. 55.
 1976 *Apis (Synapis) henshawi kaschkei* (Statz, 1931); Zeuner and Manning, p. 243.
 1978 *Apis henshawi kaschkei* (Cockerell); Burnham, p. 122.

Material. Holotype LACM 3920 (Sphon, 1973), Statz coll.; Upper Oligocene–Lower Miocene; Rott, near Bonn, Germany.

Status of the subspecies of *Apis (Synapis) henshawi*

A. (S.) henshawi Cockerell, 1907 is the type species of the subgenus *Synapis* Cockerell, 1907. Zeuner and Manning (1976) considered that there were at least three subspecies of *A. (S.) henshawi* in the same outcrop of the Upper Oligocene–Lower Miocene at Rott which seems unusual and surprising. Normally, three (or even two) subspecies cannot be found in the same place because of possible hybridization. The validity of the subspecific status of the three ‘forms’ of *A. (S.) henshawi* is very doubtful. There are four possibilities. (1), The three ‘forms’ might not be of exactly the same age. If so, their subspecific status is feasible. However, this seems unlikely because we have found a similar phenomenon at Céreste, with the discovery of a specimen of *A. (S.) cuenoti* which has the same hind leg characters as *A. (S.) henshawi kaschkei*. The specimen of *A. (S.) cuenoti* was found in the same layer as normally developed specimens;



the two different 'forms' lived together at Céreste, and the same situation probably occurred at Rott. (2), The three 'forms' could be castes (worker, queen and drone) of the same species. This is highly probable for *A. (S.) henschawi kaschkei*, based on only one specimen, but is not very plausible for the numerous specimens of *A. (S.) henschawi dormiens* if, as seems likely, queens and drones were as rare in the ancient forest at Rott as they are now. (3), Polymorphism could be higher in the worker caste of Oligocene bees than today. (4), One or two of the 'forms', it not all three, were different species.

At present, the choice between these hypotheses cannot be made because of insufficient information about the taphonomy at Rott and the polymorphism of Oligocene bees. More collections are needed from Rott but also from other Oligocene outcrops, like Céreste, before the problem can be solved.

'Apis' dormitans Heyden, 1862

1862 *Apis dormitans* Heyden, p. 76, pl. 10, fig. 8.

1976 *'Apis' dormitans* Heyden; Zeuner and Manning, p. 251.

Material. Holotype, NHM no. 58778; Upper Oligocene–Lower Miocene; Rott, near Bonn, Germany.

Remarks. According to Zeuner and Manning (1976), this species is an *incertae sedis*.

Bees from the Upper Oligocene of Marseille, Bouches-du-Rhône, France

Apis sp. A

Text-figure 3F

Material. MNHN-LP-R.08384 (part and counterpart of a forewing, without any preserved coloration and pilosity) and MNHN-LP-R.08385 (impression of bee in dorsal position; only thorax, abdomen, hind legs and forewings preserved; body covered by some chalk which masks details; only wings available for detailed study); Upper Oligocene, Upper Stampian, lacustrine laminites; Marseille Basin, Camoins-les-Bains, Bouches-du Rhône, France.

Description. R.08384 (Text-fig. 3F): Wing 10 mm long and 3.4 mm wide. Cell 2R 4.2 mm long, 0.5–0.55 mm wide, closed, slightly broader in proximal part than in distal part. Cell R 4.7 mm long. Cell 1R 1.6 mm long and 0.6 mm wide. Cell 1Rs 2.1 mm long and 0.5 mm wide. Cell 2Rs 1.6 mm long and 0.5 mm wide. XY 0.6 mm, VS 1 mm, ratio XY/VS 0.6. Cell 2Rs not widened. Structure of all cells identical to those of Recent *Apis*. Pterostigma small, similar to that of *A. mellifera*. Crossvein 1cu-a in furcal position, exactly opposite fork between M and CuA.

R.08385: Thorax 3 mm long and 4 mm wide. Abdomen 6 mm long and 4.8 mm wide. Hind tibia 2.2 mm long and 0.9 mm wide. Length of hind basitarsus unknown, width 0.9 mm. Tibia and hind basitarsus widened but structure not determinable. Forewing venation similar to R.08384, except that crossvein 1cu-a is in slightly prefurcal position, below division between M and CuA. Forewing about 10 mm long, width unknown. Vein cu-a of hindwing nearly perpendicular to vein 1A.

Remarks. These specimens are clearly different from *Apis aquisextusensis* sp. nov. (see below) because of the narrow cell 2R and the position of vein 1cu-a. The crossvein 1cu-a of the forewing in a furcal position is characteristic of the subgenus *Synapis*. The specimens are smaller than *A. cuenoti*, and their narrow cell 2Rs also distinguish it from the latter.

EXPLANATION OF PLATE I

Fig. 1 *Apis (Synapis) cuenoti* Théobald, 1937; MNHN R.08383; forewing length 12.6 mm; ×2.

Fig. 2. *Apis (Synapis) henschawi kaschkei* (Statz, 1931); forewing length 9.2 mm; ×6.

Figs 3–4. *Apis aquisextusensis* sp. nov. 3, holotype, MNHN R.08381; forewing length 8.5 mm; ×2. 4, paratype, MNHN R.08382; forewing length 8.6 mm; ×5.