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Cover: Late meraspid pygidium of the Lower Cambrian eodiscid trilobite *Shizhudiscus longquanensis*, from Pengshui, Sichuan, South China, preserved by phosphatic incrustation; × 252 (see Zhang and Clarkson 1993: *Palaeontology*, **36**, 785–806).

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.

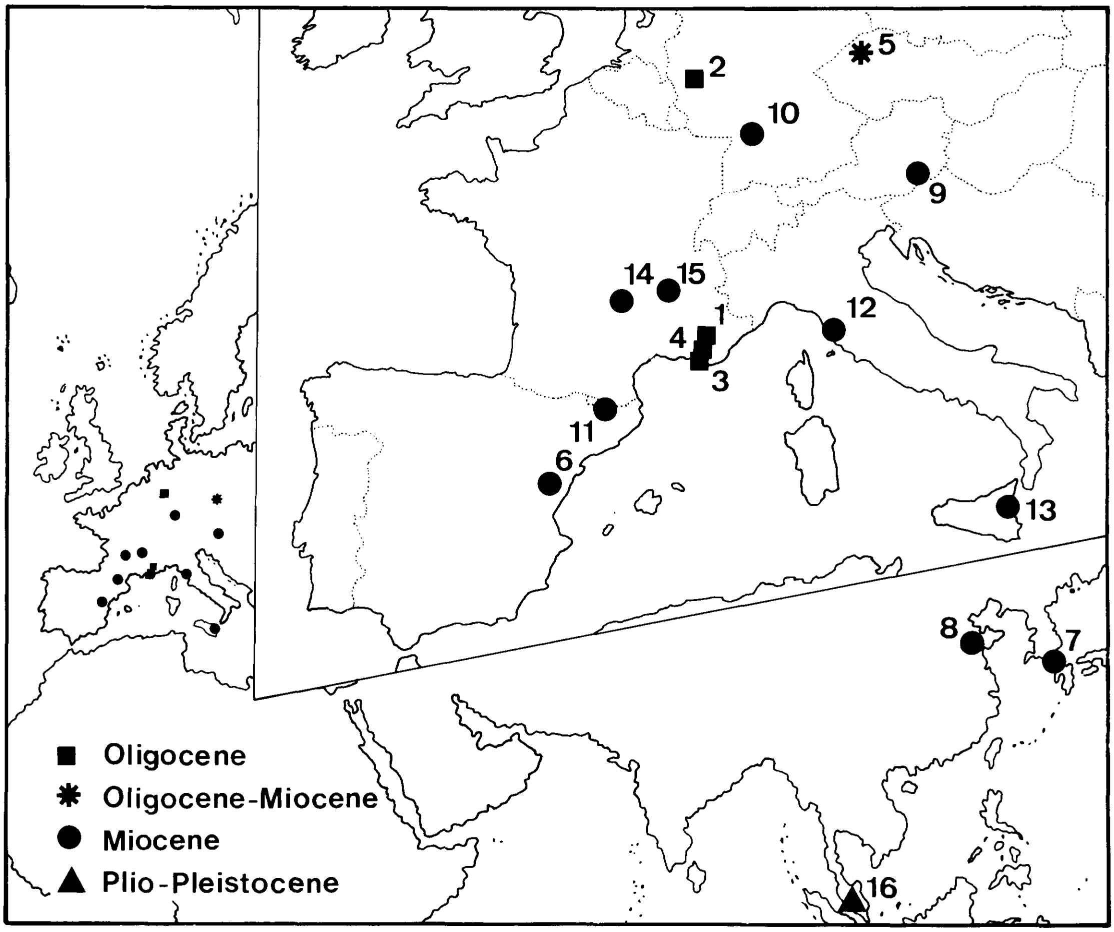
MAA (1953) divided Recent *Apis* into three genera, *Megapis* Ashmead, 1904, *Apis* Linnaeus, 1758 and *Micrapis* Ashmead, 1904, which Michener (1944) had earlier regarded as subgenera of *Apis*. To these three, Zeuner and Manning (1976) added the fossil subgenus *Synapis* Cockerell, 1907 from the Upper 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°/<45°; (3), angle (SVY) of forewing: >45°/<45°; (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

[Palaeontology, Vol. 42, Part 2, 1999, pp. 243–285, 2 pls]



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 PALAEONTOLOGY

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.

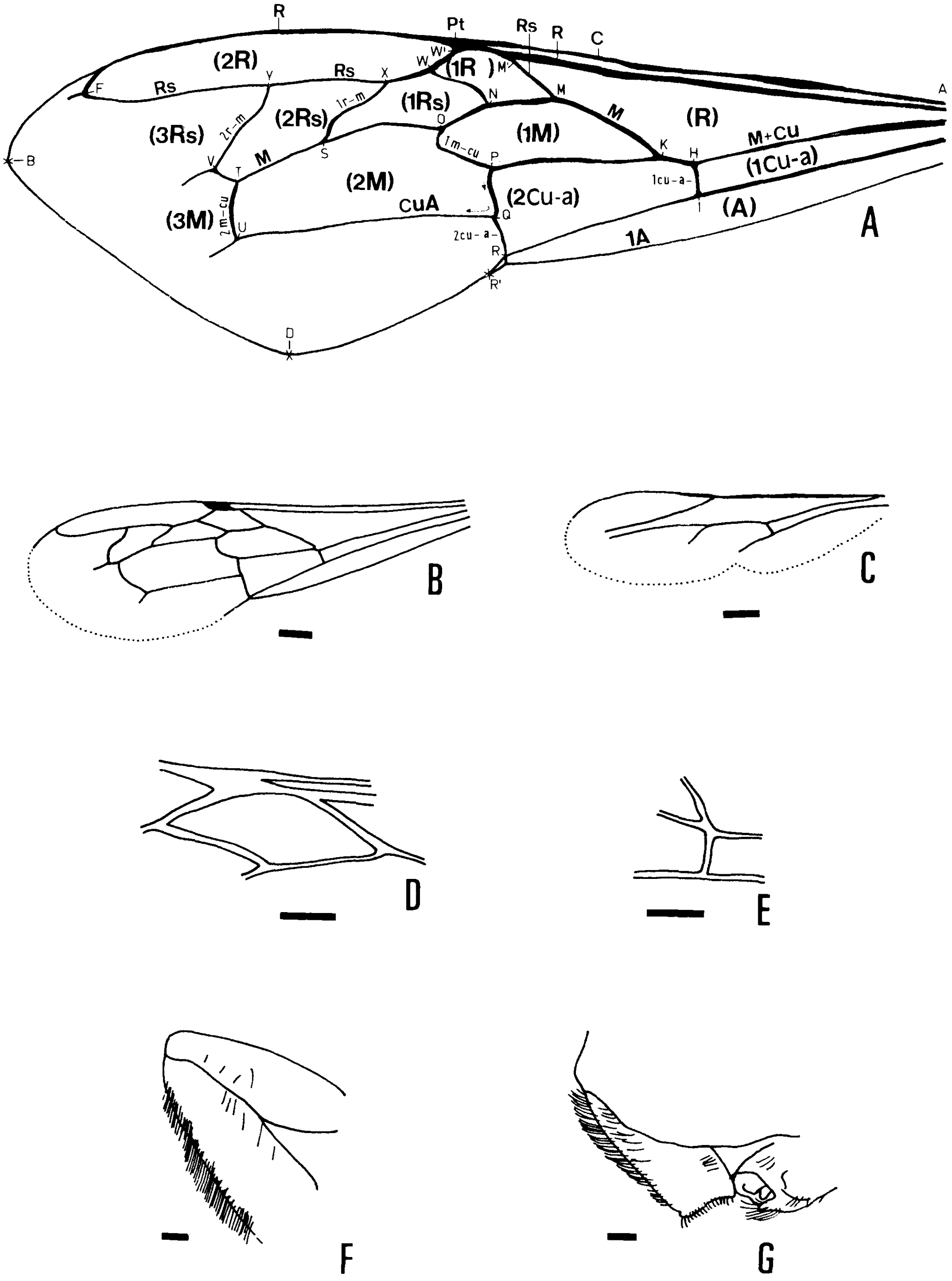
Type locality. Céreste, Vaucluse, France.

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).

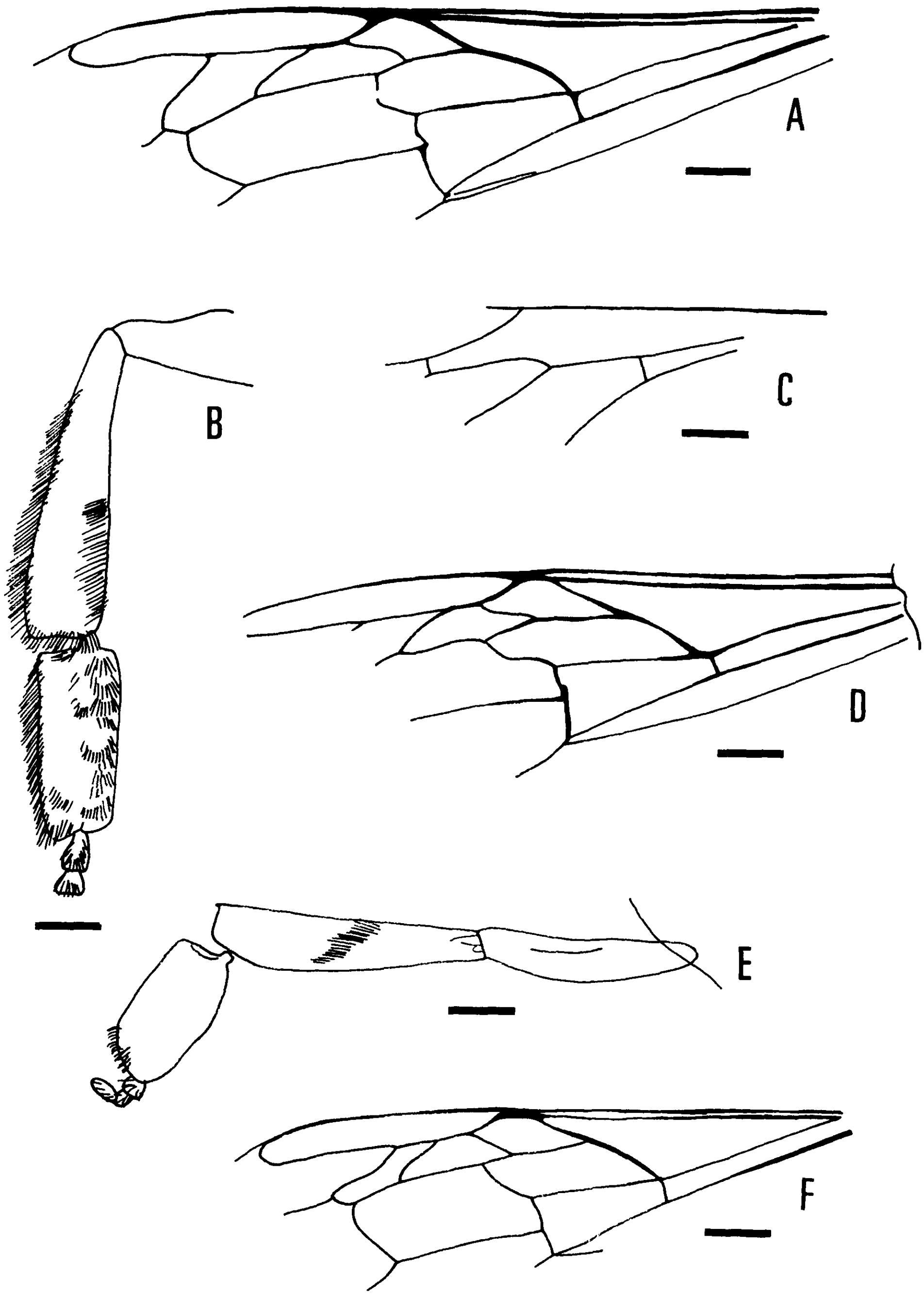
Description. The original description of Théobald (1937, p. 401) is not very precise so, we give some additional details below.

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*) *henshawi* 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*) *henshawi 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*) *henshawi henshawi* Cockerell, 1907

1907 *Synapis henshawi* Cockerell, p. 229.
1915 *Apis oligocenica* Meunier, p. 210.
1934 *Synapis henshawi* Cockerell; Statz, p. 5, figs 1, 4–7.
1942 *Synapis henshawi* Cockerell; Statz, p. 1, figs 2–4.
1943 *Synapis henshawi* Meunier, Cockerell; Statz, pp. 103, 109, two unnumbered text-figs.
1952 *Apis* (*Synapis*) *henshawi* Cockerell; Manning, pl. 1, fig. 3.
1973 *Synapis henshawi* (Cockerell); Sphon, p. 55.
1976 *Apis* (*Synapis*) *henshawi* Cockerell; Zeuner and Manning, p. 240.
1978 *Apis henshawi* Cockerell; Burnham, p. 118, fig. 4, p. 122.
1983 *Apis henshawi* 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.
1969*a*	*Synapis dormitans* Cockerell; Kelner-Pillault, p. 92, fig. B (p. 90), fig. B (p. 91).
1969*b*	*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 seens 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.*) *henshawi kaschkei*, based on only one specimen, but is not very plausible for the numerous specimens of *A.* (*S.*) *henshawi 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.

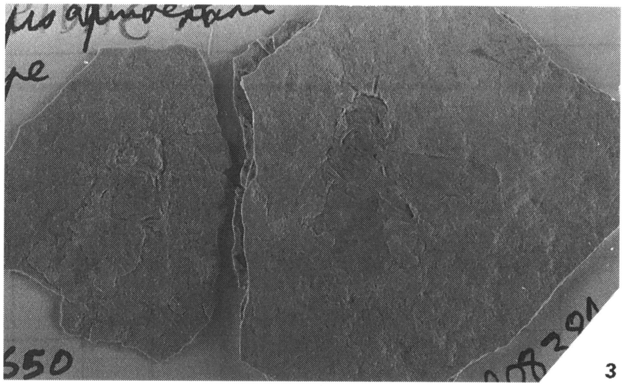
R.08385: Thorax 3 mm long and 4 mm wide. Abdomen 6 mm long and 4·8 mm wide. Hind tibia 2·2 mm long and 0·9 mm wide. Length of hind basitarsus unknown, width 0·9 mm. Tibia and hind basitarsus widened but structure not determinable. Forewing venation similar to R.08384, except that crossvein 1cu-a is in 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 1

Fig. 1 *Apis* (*Synapsis*) *cuenoti* Théobald, 1937; MNHN R.08383; forewing length 12·6 mm; ×2.
Fig. 2. *Apis* (*Synapsis*) *henshawi kaschkei* (Statz, 1931)[redacted]rewing 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.

1



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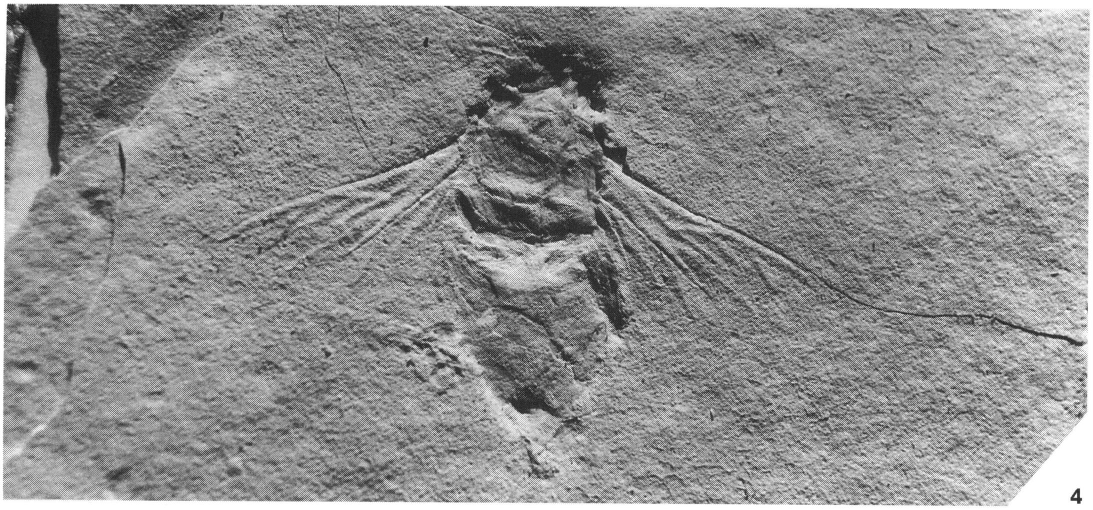
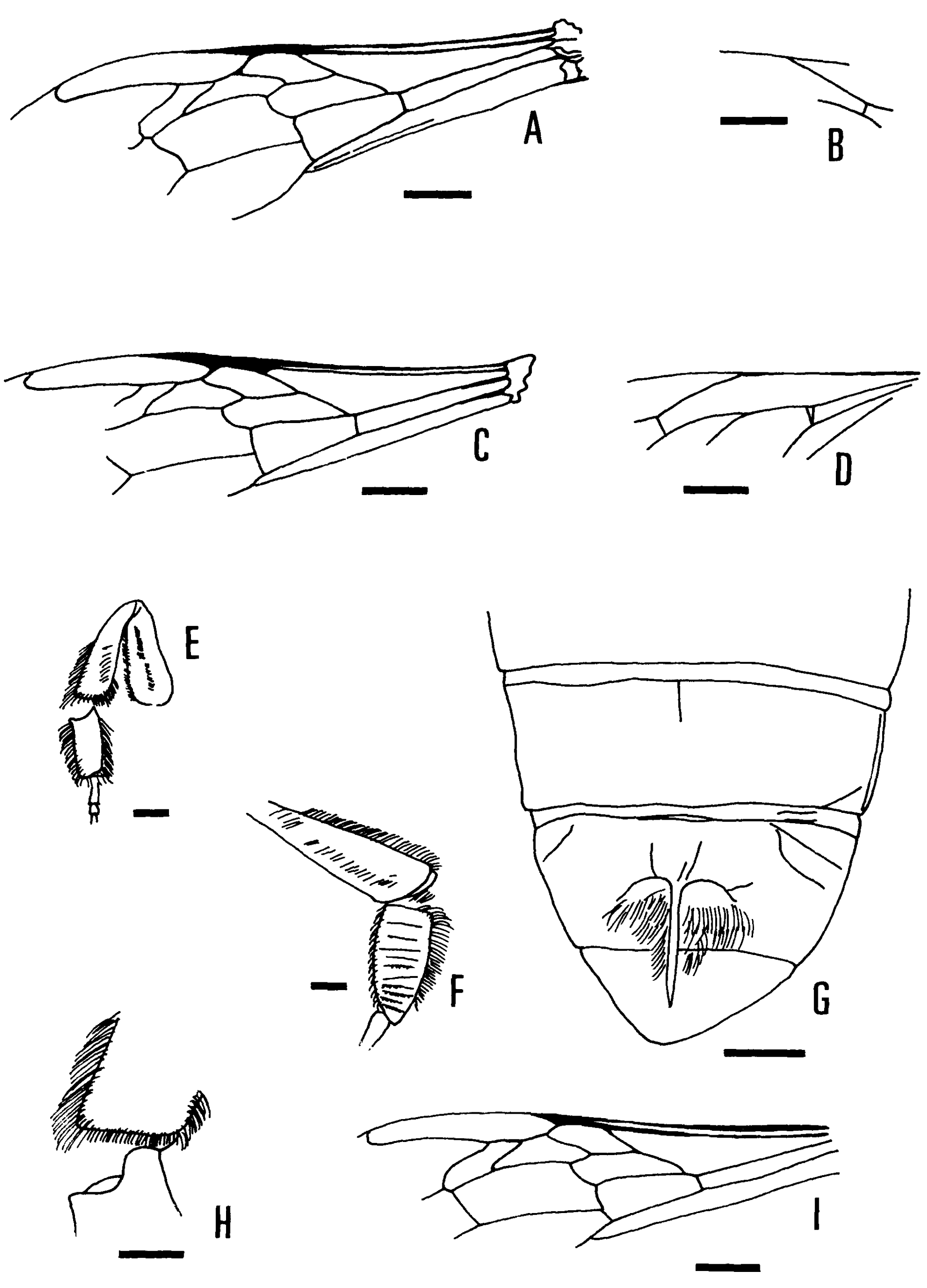


4

NEL *et al.*, *Apis*



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.*) *henshawi*. 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.

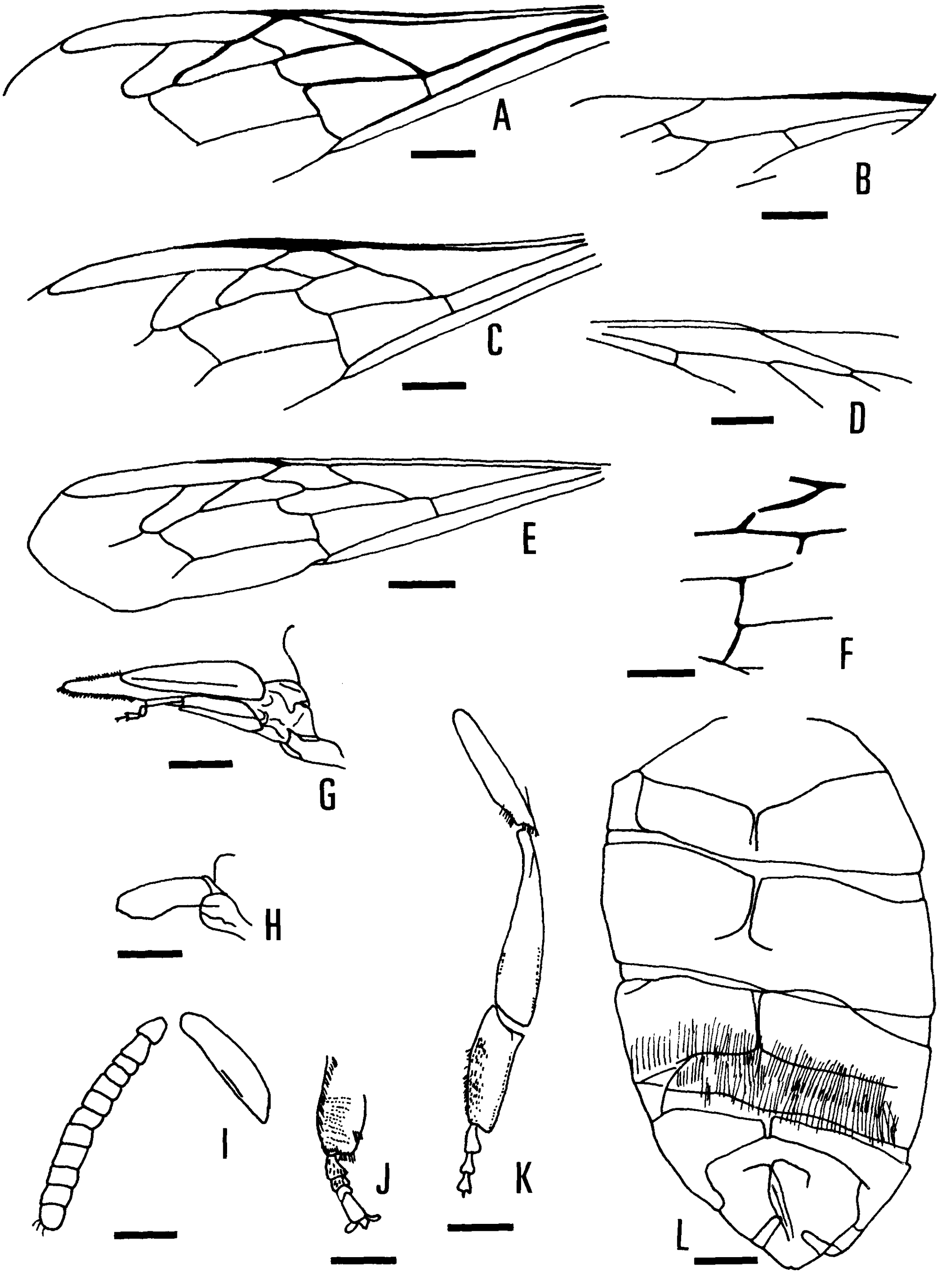
Apis sp. C

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.
1969*b* *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-Pl-7418 (? worker); Middle Miocene, diatomitic palaeolake; Chôjabaru Formation, Iki Island, Japan.

Remarks. Although Fujiyama (1970) did not describe this bee, he indicated that it is possibly an *Apis sensu stricto*. The fossil, which is not cited in Zeuner and Manning (1976), needs restudy.

Bees from the Upper Miocene of Shanwang, Shandong Province, China

Apis miocenica Hong, 1983

1983 *Apis miocenica* Hong, p. 10, pl. 2, fig. 3.
1985 *Apis miocenica* Hong; Hong and Wang, p. 11, fig. 7.
1985 *Apis miocenica* Hong; Hong, p. 62, text-fig. 44.
1989 *Apis miocenica* Hong; Zhang, p. 322, text-figs 324–326, pl. 83, figs 1–3.
1990 *Apis miocenica* Hong; Zhang, p. 91, fig. 4.

Material. Holotype, Shandong Provincial Museum, China, no. 79040; Miocene, Shanwang Formation; Linqu County, Shandong Province, China.

Apis longitibia Zhang, 1990

1990 *Apis longitibia* Zhang, p. 85, p. 91, text-fig. 3, pl. 1, figs 5–6.
1994 *Apis longitibia* Zhang; Zhang, Sun and Zhang, p. 185, text-fig. 170, pl. 33, fig. 4.

Material. Holotype, Shandong Provincial Museum, China, no. 82773; Miocene, Shanwang Formation; Linqu County, Shandong Province, China.

Apis fota Zhang, 1989

1989 *Apis fota* Zhang, p. 323, text-figs 327–329, pl. 83, figs 4–6.

Material. Shandong Provincial Museum, China, holotype no. 830072, paratypes nos 820036 and 820126; Miocene, Shanwang Formation; Linqu County, Shandong Province, China.

Apis shandongica Zhang, 1989

1989 *Apis shandongica* Zhang, p. 325, text-figs 330–331, pl. 83, fig. 5.

Material. Holotype, Shandong Provincial Museum, China, no. 820158; Miocene, Shanwang Formation; Linqu County, Shandong Province, China.

Remarks. Using Zhang's (1989) illustrations of *A. miocenica*, *A. fota* and *A. shandongica*, it is difficult to differentiate them on the basis of wing venation alone. Their wing dimensions are also similar. A revision of these three species is clearly necessary. Zhang (1990) compared *A. miocenica* and *A. longitibia* and differentiated them using the following characters: (1), *A. longitibia* has its forewing vein 1cu-a in a furcal position, while in *A. miocenica* it is prefurcal; (2), cell 2R of *A. longitibia* is distinctly narrower than in *A. miocenica*; (3), the forewing basal part of vein M is curved in *A. longitibia* whereas it is straight in *A. miocenica*; (4), the hindwing distal part of vein M is Y-shaped in *A. longitibia* whereas it is more-or-less straight in *A. miocenica*.

Character (1) suggests that *A. longitibia* is close to the *Synapis* group and that *A. miocenica* would be representative of the more Recent groups of *Apis*. However, as already stated, vein 1cu-a in a furcal position is a plesiomorphic character which is little help in the determination of the phylogenetic position of an *Apis*.

According to Zhang's (1989) illustrations, both *A. longitibia* and *A. miocenica* have no abscissa of vein M in their hindwing, but according to Hong's (1985) figure, the hindwing of *A. miocenica* has a long abscissa of vein M.

Zhang (1990) also indicated a rather strange character for an *Apis*: *A. longitibia* has a very long and narrow hind tibia, twice the length of the basitarsus. This character appears to be unique within the genus *Apis* and it looks like the hind tibia of *Electrapis apoides* Manning, 1960 (Upper Eocene, Baltic amber) as figured in Kelner-Pillault (1969*a*, pl. 4, fig. A). It is somewhat strange that an *Apis* with a very Recent wing venation could have such a plesiomorphic structure in the proportions of its hind leg. This very interesting character needs confirmation. *Apis* (*Synapis*) *henshawi kaschkei* (Statz, 1931) from Rott, Germany, and specimen R.08396 of *Apis cuenoti* from Céreste, France, also show a short basitarsus and a comparatively very long hind tibia. *A. longitibia* could possibly be a drone or a female of *A. miocenica*. According to Hong (1983), the hind tibia of *A. miocenica* is not well preserved. Both *A. longitibia* and *A. miocenica* have forewings 10·0–11·7 mm long.

Bees from the Upper Miocene of Parschlug, Austria

Apis sp. E

Text-figure 6A–B

Material. MNHN-LP-B.31781 (impression of nearly complete forewing; no preserved coloration; extreme base and posterior margin of apex missing); MNHN-LP-B.31782 (impression of apical half of forewing, without any trace of coloration); Miocene, 'Unterer Horizont' (Beier 1952); Parschlug, Steiermark, Austria.

Description. B.31781 (Text-fig. 6A): Wing 11·5 mm long, 3·7 mm wide. Venation similar to that of Recent *Apis*. Cell 2R closed, 4·1 mm long and 0·6 mm wide in both distal and proximal parts. Cell R 5 mm long. Vein 1cu-a in prefurcal position (distance from 1cu-a to separation between M and CuA 0·2 mm). Cell 1R 1·6 mm long, 0·6 mm wide. Cell 1Rs 0·8 mm long, 0·6 mm wide. Cell 2Rs 2 mm long, 0·7 mm wide. XY 1·2 mm, VS 1 mm, ratio XY/VS 1·2. Cell 2Rs widened. Vein 1m-cu begins near base of cell 1Rs (NO 0·45 mm, OS 1·5 mm). Costal margin of 1Rs distinctly shorter than posterior one (WX 0·4 mm, NS 1·8 mm). Pterostigma similar to that of Recent *Apis*.

B.31782 (Text-fig. 6B): Structures and dimensions similar to specimen B.31781.

Remarks. These two wings belong to *Apis sensu lato*. It is impossible to attribute them to a precise Recent subgenus, and the sex and caste of these bees are undetermined. Giving a specific name to these fossils is inappropriate, even if they definitely belong to the same species. The wings are similar to those of fossil bees from the Upper Miocene of La Montagne d'Andance (France) described below; they show nearly the same proportions and dimensions of the forewing. However, the fragmentary state of preservation of the material from Parschlug prevents any conclusion being drawn concerning the conspecificity of these different bee populations. It is also difficult to compare them with *A. armbrusteri* Zeuner, 1931 (Upper Miocene of Germany).

'Apis' styriaca Pongracz, 1931

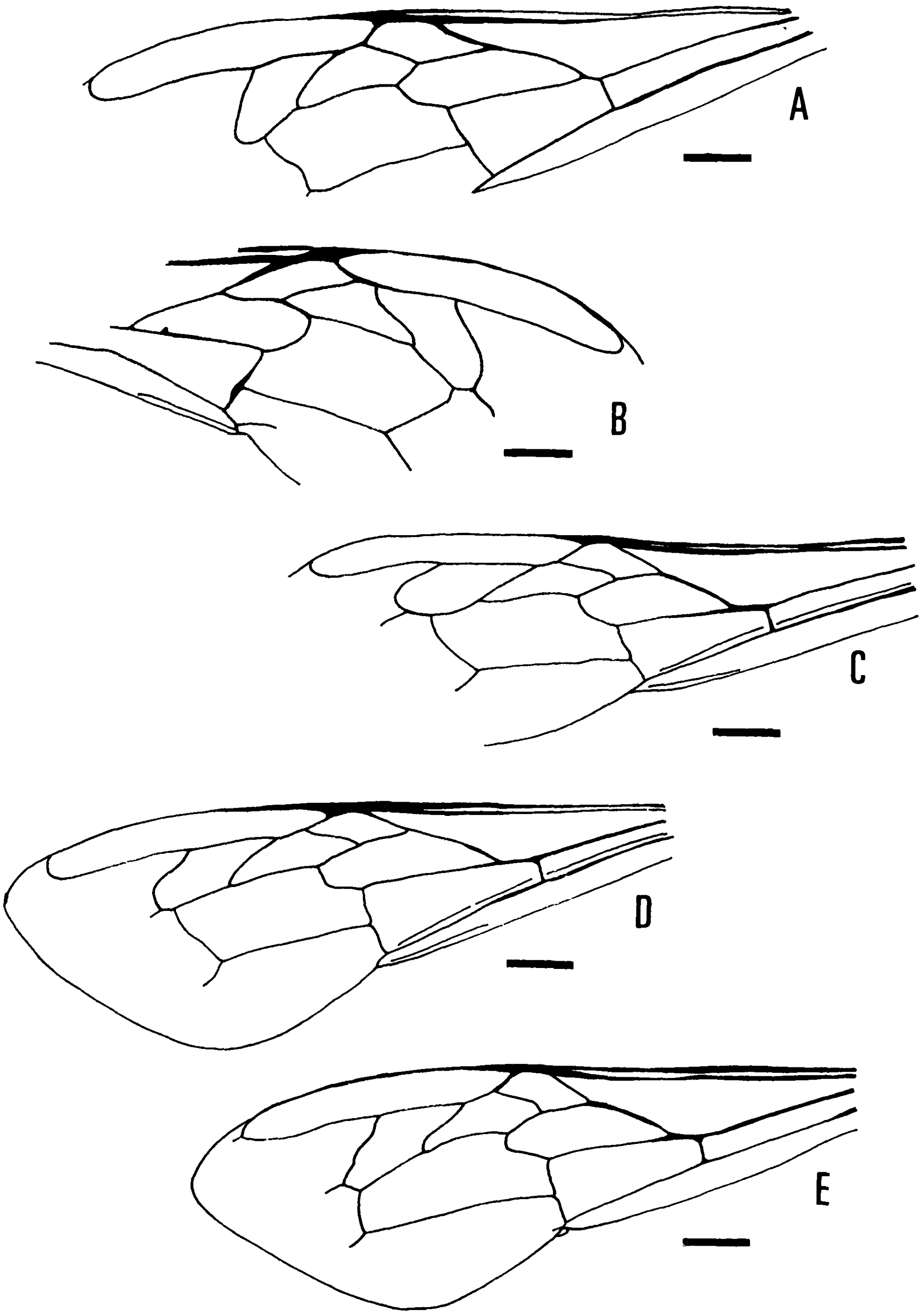
1931 *Apis styriaca* Pongracz, p. 105.
1938 *Apis styriaca* Pongracz; Armbruster, p. 88.
1976 *'Apis' styriaca* Pongracz; Zeuner and Manning, p. 251.

Type horizon. Miocene, 'Unterer Horizont' (Beier 1952).

Type locality. Parschlug, Steiermark, Austria.

Material. Whereabouts of holotype unknown.

Remarks. Zeuner and Manning (1976, p. 251) considered *Apis styriaca* to be a *nomen nudum* because Pongracz (1931) did not describe his specimen. The discovery of the two new wings (*Apis* sp. E above) shows the presence of genuine *Apis* at the Parschlug site.



TEXT-FIG. 6. A–B, *Apis* sp. E; Upper Miocene, Parschlug, Austria; A, MNHN B.31781; right forewing; B, MNHN B.31782; right forewing. C–E, *Apis* sp. F; Upper Miocene, Bellver, Spain; C, MNHN R.08386, left forewing; D, MNHN R.10425, left forewing; E, MNHN R.10422, left forewing. Scale bars represent 1 mm. Drawings made using a *Camera lucida.*

Bees from the Upper Miocene of the Randecker-Maar, Böttingen, Germany

Apis armbrusteri Zeuner, 1931

Remarks. Zeuner (1931) and later Armbruster (1938) and Zeuner and Manning (1976) described four 'subspecies' of this fossil bee, from two neighbouring outcrops: the Upper Miocene of the Randecker Maar and the 'Böttinger Marmor'. Ruttner (1988) used these subspecific divisions without comment.

Apis armbrusteri armbrusteri Zeuner, 1931

1931 *Apis armbrusteri* Zeuner, p. 292, fig. 21, pl. 8, fig. 1.
1934 *Apis armbrusteri* Zeuner; Statz, p. 7.
1938 *Apis armbrusteri* Zeuner; Armbruster, pp. 16, 45.
1976 *Apis armbrusteri armbrusteri* Zeuner, Zeuner and Manning, p. 244.
1983 *Apis armbrusteri* Zeuner, Culliney, p. 33.
1988 *Apis armbrusteri* Zeuner; Rutter, p. 26.

Material. Holotype and paratypes in the Württembergische Naturliensammlung, Stüttgart, coll. Böttingen; Upper Miocene, Sarmatian; Böttingen, Swabian Alb, Württemberg, Germany.

Apis armbrusteri scharmanni (Armbruster, 1938)

1938 *Hauffapis scharmanni* Armbruster, pp. 44, 113, fig. 78.
1976 *Apis armbrusteri scharmanni* (Armbruster); Zeuner and Manning, p. 246.

Material. Holotype, figured by Armbruster (1938, fig. 78), in the private collection of Hauff, Holzmaden (current whereabouts unknown); Upper Miocene, Sarmatian; Randecker Maar (Bleich 1988), Württemberg, Germany.

Apis armbrusteri scheeri (Armbruster, 1938)

1938 *Hauffapis scheeri* Armbruster, p. 43, 92, figs 50, 52, 62, 66, 69, 71, 73.
1976 *Apis armbrusteri scheeri* (Armbruster); Zeuner and Manning, p. 247.

Material. Lectotype selected by Zeuner and Manning (1976), figured in Armbruster (1938, fig. 71), in the private collection of Schempp, Stüttgart-Weil (Germany) (current whereabouts unknown); Upper Miocene, Sarmatian; Randecker Maar, Württemberg, Germany.

Apis armbrusteri scheuthlei (Armbruster, 1938)

1938 *Hauffapis scheuthlei* Armbruster, p. 43, figs 63, 65, 67, 70, 72, 76–77, 79.
1976 *Apis armbrusteri scheuthlei* (Armbruster); Zeuner and Manning, p. 247.

Material. Lectotype selected by Zeuner and Manning (1976), figured in Armbruster (1938, fig. 63), in the private collections of Schempp and Hauff (see above); Upper Miocene, Sarmatian; Randecker Maar, Württemberg, Germany.

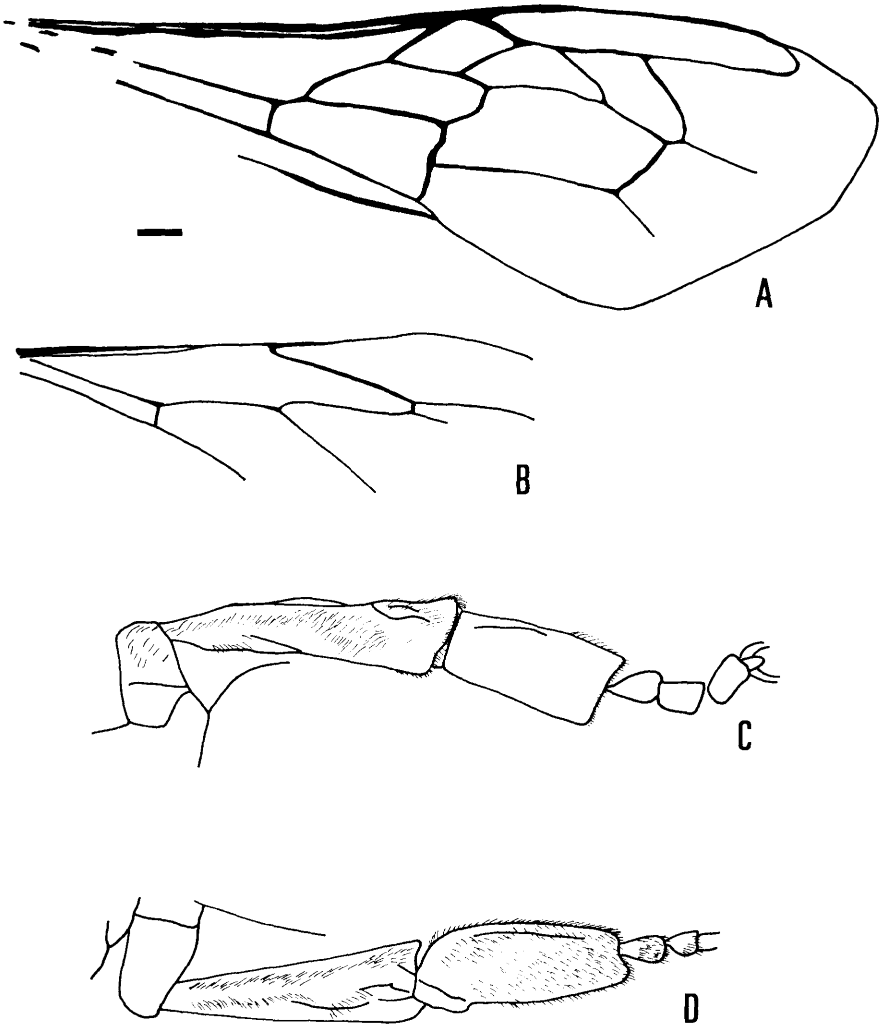
Remarks. As with *A. henshawi*, the presence of several subspecies of the same bee in the same outcrop (Randecker Maar) is unusual. The real status of these 'forms' is still to be determined; they could represent intraspecific variation of workers, sexual castes (but not according to Zeuner and Manning), different species, or maybe a combination of these. Zeuner and Manning (1976) maintained the subspecies merely for convenience in naming the different forms.

The 'subspecies' *A. armbrusteri scharmanni* and *A. armbrusteri scheeri* have about the same dimensions as Recent *A. mellifera* but *A. armbrusteri scheuthlei* is larger. The subspecies *A. armbrusteri armbrusteri* is known from bodies of bees fossilized as negative impressions (holes) in a travertine. Their wing venations are unknown. By contrast, the bodies of the specimens of the other 'subspecies' are less well known than their wings because they are fossilized as impressions or mummies in laminites. Comparison between the type material of *A. armbrusteri armbrusteri* and the forms from the Randecker Maar is obviously difficult. Ruttner (1988, p. 27) indicated that *A. armbrusteri* is very similar to the Recent species *A. dorsata*, but specimens of the latter are broader and have longer wings.

Apis cf. *armbrusteri scheuthlei* (Armbruster, 1938)

Text-figure 7A–D

Material. Bayerische Staatssammlung für Palaeontologie und Historische Geologie, specimen 1982 XIV (impression of nearly complete specimen in very fine state of preservation); Upper Miocene, Sarmatian; Randecker Maar, Württemberg, Germany.



TEXT-FIG. 7. *Apis* cf. *armbrusteri scheuthlei* Zeuner, 1931; Bayerische Staatssammlung für Palaeontologie und Historische Geologie, no. 1982 XIV; A, right forewing; B, right hindwing; C, right hind leg; D, left hind leg. Scale bars represent 1 mm. Drawings made using a *Camera lucida*.

Description. Forewing 9·7 mm long, 3·2 mm wide. Cell 2R 3·4 mm long, 0·4 mm wide in both proximal and distal halves and well closed. 1cu-a in clearly praefurcal position, distance between 1cu-a and point of separation of M and CuA 0·3 mm. Cell 1R 1·3 mm long, 0·5 mm wide. Cell 1Rs 1·5 mm long, 0·5 mm wide. Cell 2Rs 1·5 mm long, 0·5 mm wide, broadened. Vein 1m-cu joins 1Rs near its base (NO 0·3 mm; OS 1·3 mm). XY 0·9 mm, VS 0·9 mm. Pterostigma small, similar to that of *A. mellifera*. Cells Rs and M of hindwing clearly separated by long abscissa of M (Text-fig. 7B). Hamuli not preserved. Vein cu-a nearly perpendicular to vein 1A. Head 2 mm long and 3·5 mm wide. Eyes visible but impossible to determine if hairy. Thorax 4·5 mm long and 4 mm wide, appears bare but hairs may have been destroyed. Abdomen elongate, 8·5 mm long and 5 mm wide. Structures of different segments very deformed. Sting apparatus not visible but its insertion on ventral surface of abdomen clearly visible. Two hind legs very well preserved (Text-fig. 7C–D). Hind tibia and basitarsus comparatively elongate (left tibia 2·9 mm long, 0·8 mm wide, ratio length/width 3·6; right tibia 3·1 mm long, 0·9 mm wide, ratio length/width 3·4; left basitarsus 2·3 mm long, 0·9 mm wide, ratio length/width 2·5; right basitarsus 1·9 mm long, 0·9 mm wide, ratio length/width 2·1. Elongations of hind tibia and basitarsus partly consequence of deformation due to cleavage. Hairs bordering tibia and basitarsus few and short.

Remarks. This specimen is from the same outcrop as *A. armbrusteri scharmanni*, *A. armbrusteri scheeri* and *A. armbrusteri scheuthlei*. The broad cell 2Rs, the large wing and body dimensions and the slender legs suggest some affinities closer to *A. armbrusteri scheuthlei* than the two other forms, but also with Recent bees of the *A. dorsata* group rather than *A. mellifera*. The presence of a sting demonstrates that it is a female or a worker. The hind legs are very similar to those of the specimen from Rubielos de Mora (*Apis* sp. D, specimen MPV-91-RM).

Bees from the Upper Miocene of Bellver de Cerdanya, Lleida, Spain

Apis sp. F

Text-figures 6C–E, 8A–F; Plate 2, figure 1

Type horizon. Middle to Upper Vallesian, Upper Miocene (Roca and Santanach 1986).

Type locality. Bellver de Cerdanya, Lleida, Spain.

Material. MNHN-LP-R.08386 (196 Bellver, Nel coll.), MNHN-LP-R.10425, MNHN-LP-R.10422, MNHN-LP-R.10423, MNHN-LP-R.10424, MNHN-LP-R.10432, MNHN-LP-R.10431; MNCNI 21614 and MNCNI 21615. All are impressions (and often counterparts) of single forewings without any preserved trace of coloration. The extreme base of each wing is often broken. R.10431 is a nearly complete bee preserved in part and counterpart. All of the specimens, except R.10431, R.10432 and MNCNI 21615, come from the locality called coll de Saig, along the road between Bellver and Prats. R.10431 comes from the locality named San Salvador, near the coll de Saig. R.10432 comes from an outcrop along the road between Bellver and Casa Vilella. MNCNI 21615 comes from the outcrop called Baltargar, near Beders.

Description. R.08386 (Text-fig. 6C): Forewing 9·6 mm long, 3·2 mm wide. Cell 2R well closed, 4·1 mm long, 0·4 mm wide in both proximal and distal halves. 1cu-a in clearly praefurcal position, distance between 1cu-a and point of separation of M and CuA 0·5 mm. Cell 1R 1·5 mm long, 0·6 mm wide. Cell 1Rs 2 mm long, 0·5 mm wide. Cell 2Rs 2 mm long, 0·8 mm wide. Vein 1m-cu joins near base of 1Rs (NO 0·6 mm, OS 1·5 mm). XY 1·4 mm, VS 1·1 mm. Pterostigma small, similar to that of *A. mellifera*.

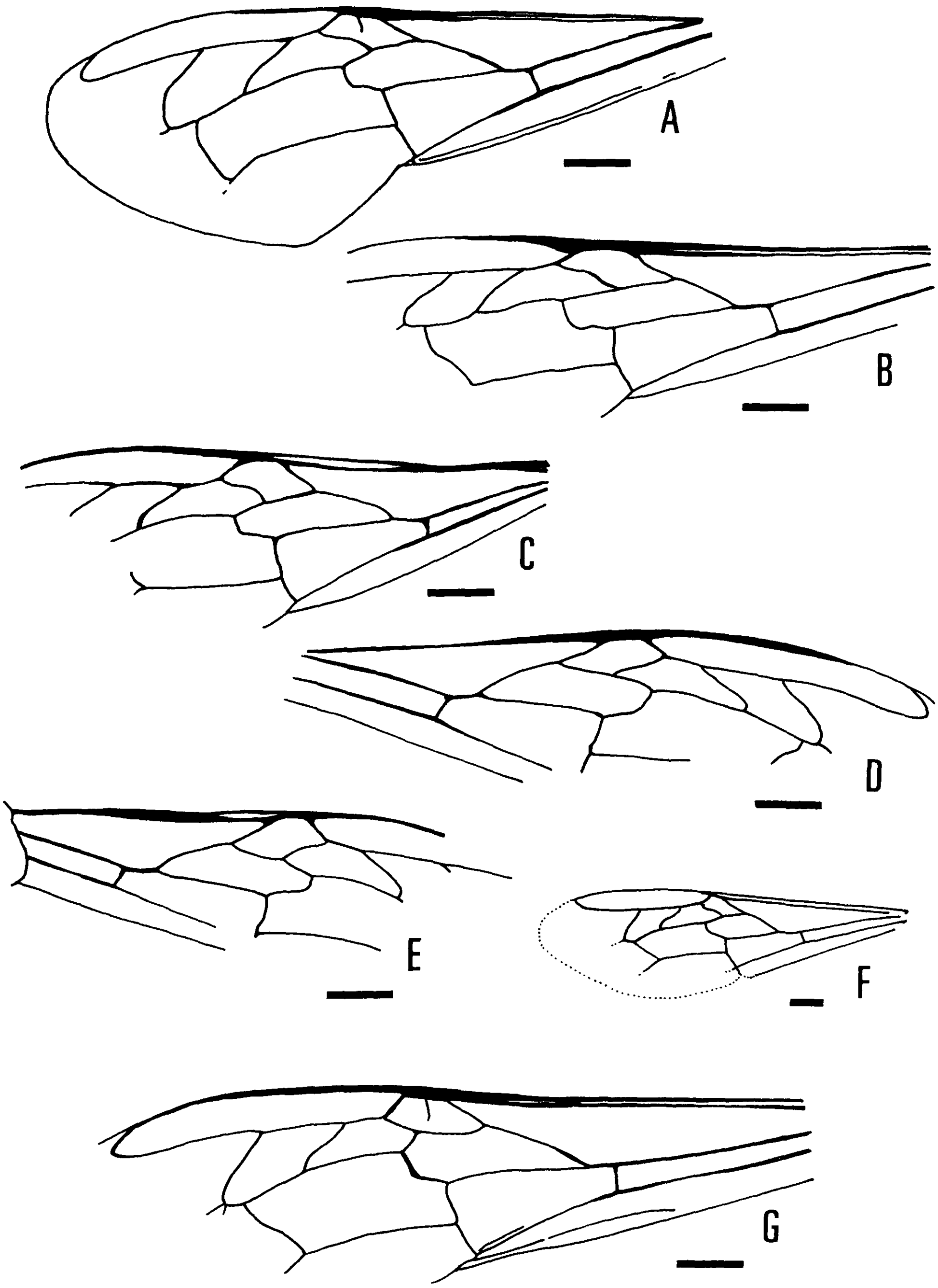
All the other specimens have forewing venations very similar to specimen R.08386. Specimen R.10423 has small supplementary veinlet in cell 1R.

R.10425 (Text-fig. 6D): Forewing 10·7 mm long, 3·6 mm wide. Cell 2R 4·4 mm long, 0·5 mm wide. Cell 1R 1·5 mm long, 0·5 mm wide. Cell 1Rs 2 mm long, 0·5 mm wide. Cell 2Rs 2 mm long, 0·9 mm wide. XY 1·3 mm, VS 1·1 mm.

R.10422 (Text-fig. 6E): Forewing 10·8 mm long, 3·7 mm wide. 2R 4·2 mm long, 0·5 mm wide. 1R 1·3 mm long, 0·6 mm wide. 1Rs 1·8 mm long, 0·6 mm wide. 2Rs 2 mm long, 1·1 mm wide. XY 1·3 mm, VS 1·2 mm.

R.10423 (Text-fig. 8A; Pl. 2, fig. 1): Forewing 10·5 mm long, 3·6 mm wide. 2R 4·1 mm long, 0·4 mm wide. 1R 1·3 mm long, 0·5 mm wide. 1Rs 1·9 mm long, 0·7 mm wide. 2Rs 2·1 mm long, 1·1 mm wide. XY 1·3 mm, VS 1·3 mm.

R.10424 (Text-fig. 8B): Forewing c. 10·4 mm long, width unknown. 2R 3·8 mm long, 0·5 mm wide. 1R 1·7 mm long, 0·6 mm wide. 1Rs 2·1 mm long, 0·5 mm wide. 2Rs 1·9 mm long, 0·8 mm wide. XY 1 mm, VS 1 mm.



TEXT-FIG. 8. A–F, *Apis* sp. F; A, MNHN R.10423; left forewing; B, MNHN R.10424; left forewing; C, MNHN R.10431; left forewing; D, MNHN R.10432; right forewing; E, MNHN R.10431; right forewing; F, MNCNI-21614; left forewing. G, *Apis* sp. G; MNHN R.08389; Upper Miocene, Sainte-Reine, Cantal, France; right forewing. Scale bars represent 1 mm. Drawings made using a *Camera lucida*.

R.10432 (Text-fig. 8D): Forewing 10·4 mm long, width unknown. 2R 4·3 mm long, 0·4 mm wide. 1R 1·5 mm long, 0·6 mm wide. 1Rs 2 mm long, 0·5 mm wide. 2Rs 2·1 mm long, 0·8 mm wide. XY 1·2 mm, VS 1·2 mm.

R.10431 (Text-figs 8C, E): Forewing *c*. 10 mm long, width unknown. 2R 3·9 mm long, 0·5 mm wide. 1R 1·3 mm long, 0·6 mm wide. 1Rs 1·9 mm long, 0·6 mm wide. 2Rs *c*. 2 mm long and *c*. 1 mm wide. XY 1·1 mm, VS unknown. Body not well preserved and impossible to determine if eyes hairy. Structures of hind legs not well preserved but hind tibiae widened and hairy, *c*. 2 mm long and 1 mm wide. Head of unknown length, 4 mm wide. Pronotum 5 mm long, 5 mm wide. Abdomen 9 mm long, 6 mm wide. One hindwing partly preserved.

MNCNI 21614 (Text-fig. 8F): Forewing 10 mm long, *c*. 3 mm wide. 2R 3·9 mm long, 0·5 mm wide. 1R 1·3 mm long, 0·5 mm wide. 1Rs 1·9 mm long, 0·6 mm wide. 2Rs 1·8 mm long, 0·9 mm wide. XY 1·1 mm, VS 1 mm.

MNCNI 21615 not well preserved.

Mean length of forewings 10·4 mm.

Remarks. The small amount of variation between these wings is compatible with intraspecific diversity, and the specimens probably all belong to the same species. They are similar to *A. mellifera* but all are bigger than that species, with longer forewings and broader 2Rs cells. They have a very similar venation to *Apis* sp. E (Parschlug), *A.* sp. I (Montagne d'Andance) and *A.* sp. G. (Sainte-Reine), but they are smaller (their forewing length varies from 9·8 to 10·5 mm with a mean of 10·4 mm compared with 11–12·4 mm, with a mean of 11·9 mm for the population of Montagne d'Andance and 11–12·6 mm with a mean of 11·8 mm for the population of Sainte-Reine). It is highly probable that the population from Bellver belongs to a different species or subspecies. Comparison with *Apis armbrusteri* is difficult because wing length variation of the latter species is unknown, but their wing venations are very similar. Until a revision of *A. armbrusteri* has been undertaken, it is not advisable to name this new population.

Bee from the Upper Miocene of Gabbro, Toscana, Italy

Apis (*Apis*) *melisuga* (Handlirsch, 1908)

1908	(Apidae) *melisuga* Handlirsch, p. 893.
1969*b*	*Apidae melisuga* Handlirsch; Kelner-Pillault, p. 525.
1976	*Apis* (*Apis*) *melisuga* (Handlirsch, 1908); Zeuner and Manning, p. 248.
1988	[Apidae] *melisuga* Handlirsch; Ponomarenko and Schultz, p. 19.

Material. Holotype, Geologisch-Paläontologischen Abteilung, Naturhistorischen Museum Wien, 1984/32/264; Upper Miocene, Messinian; Gabbro, Toscana, Italy.

Remarks. Zeuner and Manning (1976) considered this fossil bee to be a genuine *Apis*, even subgenus *Apis*, but also noted that it resembled *A.* (*Megapis*) *dorsata*, and that new material would be necessary for definite determination.

'Bee' from the Upper Miocene of Catania, Sicily, Italy

'Apis' catanensis Roussy, 1960

1960	*Apis catanensis avolii* Roussy, p. 8, fig. 2.
1969*b*	*Apis catanensis avolii* Roussy; Kelner-Pillault, p. 524.
1976	*Apis catanensis* Roussy; Zeuner and Manning, p. 257.
1989	Isoptera; Kohring and Schlüter, pp. 49, 52.

Material. Holotype in the private collection of A. and G. Avolio, jewellers of Sicily; Upper Miocene, Messinian; Simetite, Sicily, Italy.

Remarks. Roussy (1960) thought that this fossil belonged to the *A. dorsata* group but Kohring and Schlüter (1989) indicated that it appears to be an Isoptera.

Bees from the Upper Miocene (Upper Messinian) of Sainte-Reine, Cantal, France

First group: larger bees with longer wing and widened cell 2Rs

Apis sp. G

Text-figures 8G, 9

Material. MNHN-LP-R.08388, MNHN-LP-R.08389, MNHN-LP-R.08390. All are more or less deformed although their forewings are well preserved; Upper Miocene, Upper Messinian (Roiron 1991; Serieyssol and Gass 1991); Sainte-Reine, Murat, Cantal, France.

Description. Bees with typical venation of Recent *Apis*, with crossvein 1cu-a prefurcal. Forewing mean length 11·8 mm.

R.08389 (Text-figs 8G, 9A–C): Forewing with impression of thorax. Wing hyaline, similar to that of *A. mellifera.* Forewing 12 mm long, 3·7 mm wide. Cell 2R 4·4 mm long, 0·6 mm wide. Cell 1R 1·5 mm long, 0·6 mm wide. Cell 1Rs 1·7 mm long, 0·6 mm wide. Cell 2Rs widened, 2·1 mm long, 1 mm wide. XY 1·2 mm, VS 1·3 mm, ratio XY/VS 0·92. Abnormal veinlet in cell 1R. Cells Rs and M clearly separated in hindwing.

R.08388 (Text-fig. 9D–F): Body with remains of two forewings and hindwings, identical to those of R.08389. Forewing *c.* 12·6 mm long, *c.* 4 mm wide. 2R 4·4 mm long, 0·6 mm wide. 1R 1·7 mm long, 0·7 mm wide. 1Rs 1·9 mm long, 0·7 mm wide. 2Rs widened, 2 mm long, 1·1 mm wide. XY 1·6 mm, VS 1·2 mm. Hindwing Rs and M clearly separated and cu-a nearly perpendicular to vein 1A.

R.08390 (Text-fig. 9G–H): Body covered by ? iron oxide with forewing identical to those of R.08388. Costal half of 2R darker than rest of wing. Forewing 11 mm long, 3·8 mm wide. 2R 4 mm long, 0·6 mm wide. 1R 1·5 mm long, 0·6 mm wide. 1Rs 2 mm long, 0·6 mm wide. 2Rs widened, 2 mm long, 1·1 mm wide. XY 1·4 mm, VS 1 mm.

Remarks. Even if these specimens are somewhat smaller than the bees from the Upper Miocene of Montagne d'Andance (see below), they are very similar in wing venation and coloration. The best preserved specimen (R.08390) even shows the same dark border of cell 2R as in the best preserved specimens from Andance (R.54922 and R.54926). It is still impossible to decide whether these two fossil populations are conspecific. The difference in age of the strata at the two quarries (5·34 ± 0·3 Ma for Sainte-Reine and 10·3–5·9 Ma for Montagne d'Andance) suggests that they may belong to different species or subspecies but, if so, they must be very closely related.

Second group: smaller bees with shorter wing and cell 2Rs not widened

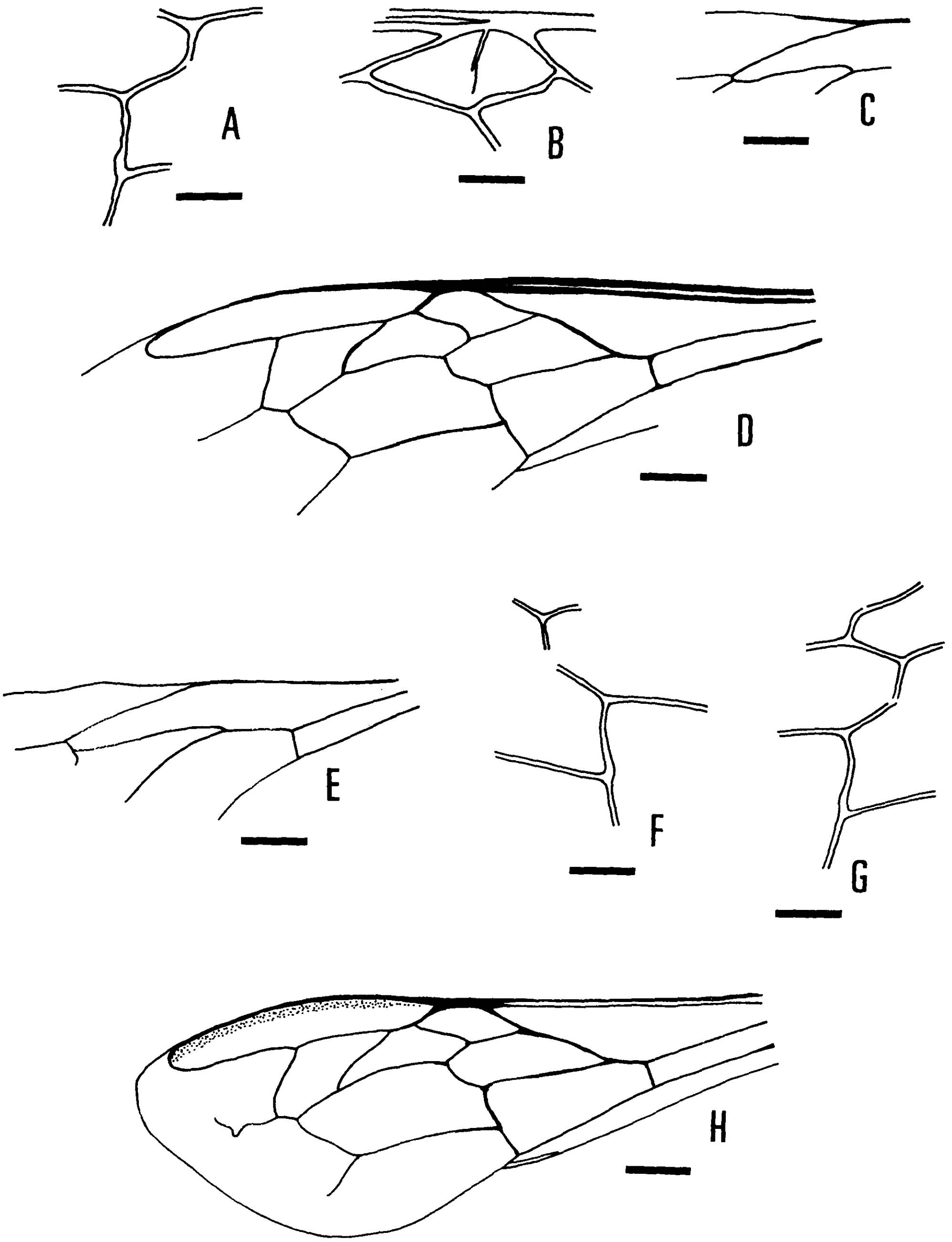
Apis sp. H

Text-figure 10A–D

Material. MNHN-LP-R.08391 and MNHN-LP-R.08392 (specimens more or less deformed; forewings in good state of preservation); Upper Miocene (Roiron 1991; Serieyssol and Gasse 1991); Sainte-Reine, Murat, Cantal, France.

Description. Venation typical of Recent *Apis*, with crossvein 1cu-a prefurcal. Forewing mean length 8·5 mm. R.08391 (Text-fig. 10A–C): Body with forewing. Forewing 8·5 mm long, width unknown. 2R 2·8 mm long, 0·3 mm wide. 1R 1·1 mm long, 0·4 mm wide. 1Rs 1·5 mm long, 0·5 mm wide. 2Rs not widened, 1·4 mm long, 0·7 mm wide. XY 0·7 mm, VS 0·7 mm, ratio XY/VS 1. Pterostigma abnormal. R.08392 (Text-fig. 10B, D): Body with two forewings. Forewing 8·6 mm long, width unknown. 2R 3·2 mm long, 0·4 mm wide. Length and width of 1R unknown. 1Rs 1·7 mm long, 0·5 mm wide. 2Rs not widened, 1·4 mm long, 0·9 mm wide. XY 0·6 mm, VS 0·5 mm, ratio XY/VS 1·2.

Remarks. The fossil bees of Sainte-Reine can be separated into two groups on the basis of the forewing dimensions and structure of cell 2Rs. These differences could be of specific or sexual origin. If the latter,



TEXT-FIG. 9. A–H. *Apis* sp. G; A–C, MNHN R.08389; A, detail of the centre of the wing; B, pterostigma; C, left hindwing; D–F, MNHN R.08388; D, left forewing; E, left hindwing; F, detail of the left forewing centre; G–H, MNHN R.08390, detail of the centre of the wing; H, right forewing. Scale bars represent 1 mm (C–E, H) or 0·5 mm (A–B, F–G). Drawings made using a *Camera lucida*.

the smallest bees could be workers and the biggest drones or females(?). Such differences can be seen in different castes of *Apis mellifera*. Although the presence of so many females and/or drones would be very strange, more specimens are necessary before any final conclusion can be reached. Nevertheless, the possibility that these two groups of bees represent two different species is more likely because the same phenomenon occurs in the Upper Miocene of Montagne d'Andance.

Bees from the Upper Miocene of Montagne d'Andance, Ardèche, France

First group: larger bees with longer wing and widened cell 2Rs

Apis sp. I

Text-figures 10E-H, 11–12; Plate 2, figures 2–4

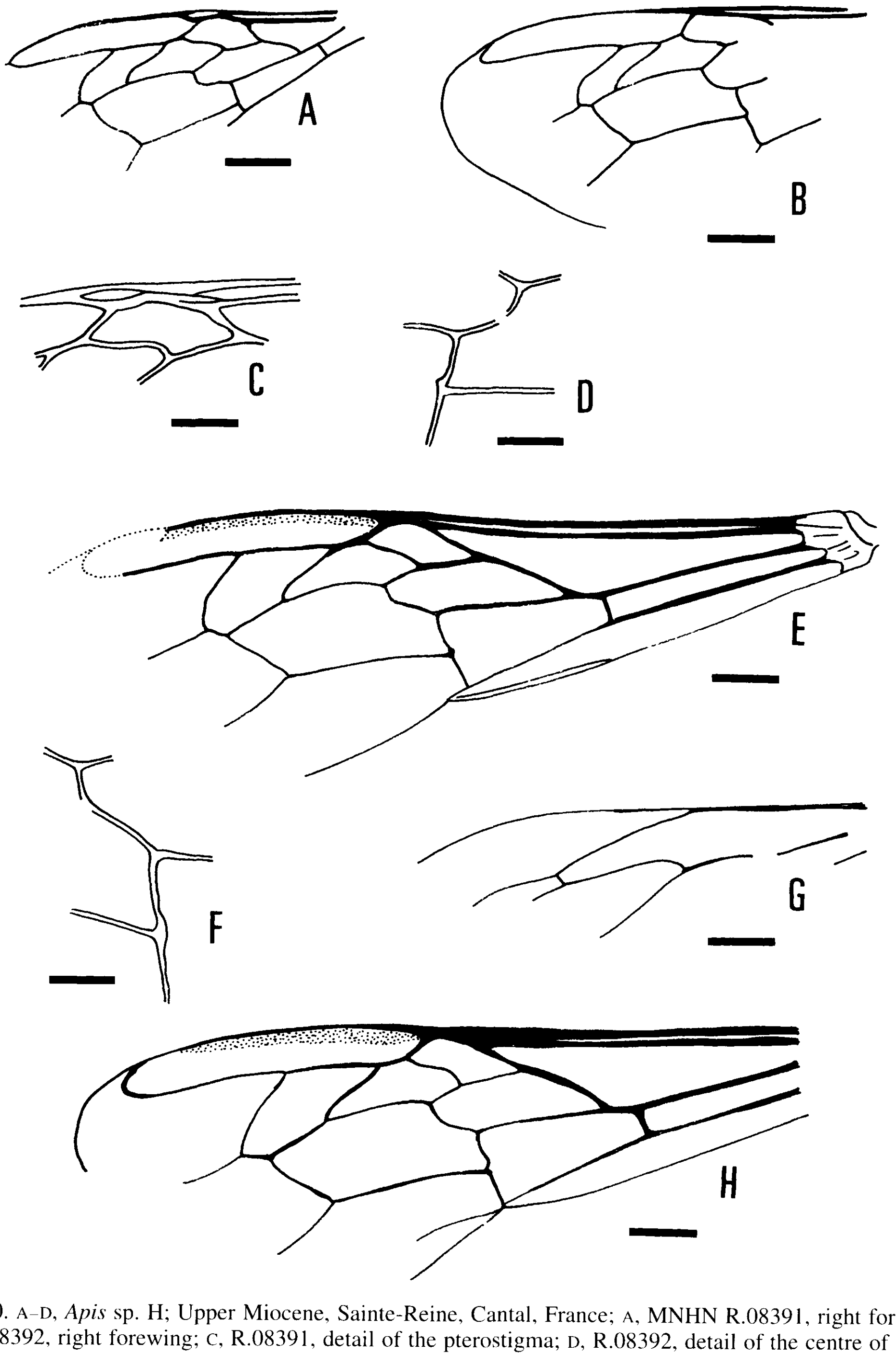
Material. MNHN-LP-R.54926, R.54921 (both in dorsal view, bodies black), R.54922 (in lateral position, with forewing 5 mm away, body black), R.54924; R.55166 and R.55206 (both coalified impressions, parts and counterparts, fossilized in dorsal view), R.55167 (coalified impression fossilized in lateral view) and R.55169; Upper Miocene, Lower Turolian (Demarcq *et al.* 1989; Serieyssol and Gasse 1991); Montagne d'Andance, Saint Bauzile, Ardèche, France.

Description. All specimens have darker costal margin along cell 2R, least visible in R.54924 and R.54921.

R.54922 (Text-fig. 10E, G): head 5 mm long, deformed, laterally visible, covered with long hairs but not possible to determine whether these are simple or plumose. No visible trace of pilosity on eyes. Thorax 5·5 mm long, covered with small hairs. Thoracic structures not well preserved. Abdomen dorsally rather densely covered with hairs, rather rounded, 12 mm long, with sternites not visible. Prothoracic and mesothoracic legs not well preserved. A metathoracic leg well preserved. Metathoracic tibia widened, 3 mm long and 1·6 mm wide, covered with hairs along outer margin with rastellum on distal apex and no spur. Hind basitarsus widened, 2·8 mm long and 1·5 mm wide, covered with hairs along outer margin. Very well-defined pollen press (*sensu* Snodgrass 1956) on hind basitarsus. Forewing *c.* 12 mm long and 3·7 mm wide. Cell 2R very elongate, distally closed with costal margin darker, 4·6 mm long and 0·4 mm wide in both distal and proximal halves. 1R 1·6 mm long, 0·6 mm wide. 1Rs 2 mm long, 0·5 mm wide. 2Rs 2·1 mm long, 1·2 mm wide. Vein 1m-cu meets 1Rs near its base. NO 0·5 mm, OS 1·5 mm. Costal margin of 1Rs distinctly shorter than posterior margin. WX 0·5 mm, NS 2·1 mm. Cells 1R, 1Rs, 2Rs and pterostigma similar to those of *A. mellifera* except that 2Rs widened (XY 1·5 mm, VS 1·3 mm, ratio XY/VS 1·15). Vein 1cu-a clearly prefurcal as in *A. mellifera*. 1cu-a 0·5 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Vein cu-a of hindwing not well preserved but makes nearly a right angle with 1A. Hindwing cells Rs and M clearly separated by abscissa of M. Hamuli not preserved.

R.54926 (Text-figs 10H, 11A): head not well preserved, length not determinable, deformed, dorsally visible, covered with long hairs; not possible to determine whether hairs simple or plumose. No visible trace of pilosity on eyes. Thorax *c.* 5 mm long, covered with small hairs. Thoracic structures not well preserved. Abdomen dorsally rather densely covered with hairs, rather rounded, 11 mm long with sternites not visible. Prothoracic and mesothoracic legs not visible. A metathoracic leg present but not well preserved, similar to that of R.54922. Forewing venation identical to that of R.54922. Forewing 11·2 mm long and *c.* 4 mm wide. 2R 4·6 mm long, 0·4 mm wide both in distal and proximal halves. 1R 1·6 mm long, 0·7 mm wide. 1Rs 2 mm long, 0·6 mm wide. 2Rs distinctly widened, 2·2 mm long, 1·1 mm wide. NO 0·5 mm, OS 1·5 mm. WX 0·5 mm, NS 2·1 mm, XY 1·4 mm, VS 1·4 mm, ratio XY/VS 1. 1cu-a clearly prefurcal, 0·5 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Vein cu-a of hindwing nearly makes right angle with vein 1A. Hindwing cells Rs and M clearly separated by abscissa of M. 15 hamuli clearly visible.

R.54921 (Text-fig. 11D): head not well preserved, length not determinable, deformed, ventrally visible, covered with long hairs; not possible to determine whether hairs simple or plumose. No visible trace of pilosity on eyes. Antenna well preserved. Thorax *c.* 5 mm long, covered with small hairs. Thoracic structures not well preserved. Abdomen dorsally rather densely covered with hairs, rather rounded, 12 mm long, with sternites not visible. Prothoracic and mesothoracic legs not visible. A metathoracic leg present but not well preserved, similar to that of R.54922. Forewing venation identical to that of R.54922, 12·4 mm long and *c.* 4·6 mm wide. 2R 4·6 mm long, 0·6 mm wide both in distal and proximal halves. 1R 1·7 mm long, 0·7 mm wide. 1Rs 2 mm long, 0·6 mm wide. 2Rs widened, 2·3 mm long, 1·2 mm wide. NO 0·6 mm, OS 1·6 mm. WX 0·6 mm, NS 2·1 mm. XY 1·6 mm, VS 1·6 mm, ratio XY/VS 1.



TEXT-FIG. 10. A–D, *Apis* sp. H; Upper Miocene, Sainte-Reine, Cantal, France; A, MNHN R.08391, right forewing; B, MNHN R.08392, right forewing; C, R.08391, detail of the pterostigma; D, R.08392, detail of the centre of the wing. E–H, *Apis* sp. I; Upper Miocene, Montagne d'Andance, Ardèche, France; E–G; MNHN R.54922; E, left forewing; F, centre of the wing; G, left hindwing; H, MNHN R.54926; left hindwing. Scale bars represent 1 mm (A–B, E, G–H) or 0·5 mm (C–D, F). Drawings made using a *Camera lucida*.

1cu-a clearly prefurcal, 0·5 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Hindwing identical to that of R.54926.

R.54924 (Text-fig 11c): head not well preserved, length not determinable, deformed, only ventral side visible, covered with long hairs and not possible to determine whether hairs simple or plumose. No visible trace of pilosity on eyes. Thorax *c.* 5·5 mm long and 6 mm wide, covered with small hairs. Thoracic structures not well preserved. Abdomen dorsally rather densely covered with hairs, rather rounded, 10 mm long and 8 mm wide, with sternites not visible. Legs not well preserved. Forewing venation identical to R.54922, 11 mm long and about 4 mm wide. 2R nearly 4·5 mm long, 0·5 mm wide in both distal and proximal halves. 1R 1·6 mm long, 0·6 mm wide. 1Rs 2 mm long, 0·6 mm wide. 2Rs distinctly widened, 2·2 mm long, 1·1 mm wide. NO 0·4 mm, OS 1·6 mm. WX 0·5 mm, NS 2·1 mm, XY 1·3 mm, VS 1·3 mm, ratio XY/VS 1. 1cu-a clearly prefurcal, 0·6 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Hindwing identical to that of R.54926. Twenty-one hamuli clearly visible.

R.55166 (Text-fig. 11b, e): Although complete, body not well preserved. Head 2 mm long, 3·5 mm wide. Thorax 6 mm long, 5 mm wide. Abdomen 11 mm long, 7·5 mm wide, well-rounded. Whole body black and covered with rather dense pilosity but impossible to determine whether eyes covered with hair. Wings especially well preserved. Forewing 12·4 mm long, 4·2 mm wide. 2R 4·5 mm long, 0·6 mm wide in both distal and proximal halves. 1R 1·6 mm long, 0·8 mm wide. 1Rs 2·1 mm long, 0·7 mm wide. 2Rs widened, 2·3 mm long, 1·2 mm wide. NO 0·5 mm, OS 1·7 mm. WX 0·5 mm, NS 2·2 mm. XY 1·5 mm, VS 1·5 mm, ratio XY/VS 1. 1cu-a clearly prefurcal, 0·6 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Vein cu-a of hindwing nearly makes right angle with 1A. Hindwing cells Rs and M clearly separated by abscissa of M which is 0·5 mm long. Some hamuli visible. Hindwing 8·2 mm long, 2·5 mm wide.

R.55206 (Text-figs 11f, 12a–b): Although complete, body not well preserved. Head 3 mm long, 4 mm wide. Thorax 6 mm long, 5 mm wide. Abdomen well-rounded, 12 mm long, 8 mm wide. Whole body black and covered by rather dense pilosity but impossible to determine whether eyes were covered with hair. Wings well preserved. Forewing 12·4 mm long, width unknown. 2R 4·3 mm long, 0·6 mm wide in both distal and proximal halves. 1R 1·6 mm long, 0·7 mm wide. 1Rs 2·2 mm long, 0·9 mm wide. 2Rs distinctly widened, 1·9 mm long, 1·3 mm wide. NO 0·7 mm, OS 1·6 mm. WX 0·6 mm, NS 2·2 mm. XY 1·3 mm, VS 1 mm, ratio XY/VS 1·3. 1cu-a clearly prefurcal, 0·6 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Vein cu-a of hindwing makes nearly a right angle with vein 1A. Hindwing cells Rs and M clearly separated by abscissa of M which is 0·3 mm long. Few hamuli visible. Length and width of hindwing unknown.

R.55167 (Text-fig. 12c): Incomplete body not well preserved. Head 3 mm long, width unknown. Thorax 6 mm long, width unknown. Abdomen well-rounded, 12 mm long, 8 mm wide. Whole body black and covered with a rather dense pilosity but impossible to determine whether eyes were covered with hair. Wings well preserved. Forewing 12·4 mm long, width unknown. 2R 4·5 mm long, 0·6 mm wide both in distal and proximal halves. 1R 1·6 mm long, 0·7 mm wide. 1Rs 2 mm long, 0·7 mm wide. 2Rs distinctly widened, 2·2 mm long, 1·3 mm wide. NO 0·6 mm, OS 1·5 mm, WX 0·6 mm, NS 2 mm. XY 1·3 mm, VS 1·4 mm, ratio XY/VS 0·9. 1cu-a clearly prefurcal, 0·6 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Hindwing not preserved.

R.55169 (Text-fig. 12d–e): Incomplete body not well preserved. Head 3 mm long, 4 mm wide. Thorax 6 mm long, 6 mm wide. Abdomen well-rounded, 11 mm long, 8 mm wide. Whole body black and covered with rather dense pilosity but impossible to determine whether eyes were covered with hair. Wings well preserved. Forewing 12·6 mm long, 4·2 mm wide. 2R 4·6 mm long, 0·6 mm wide both in distal and proximal halves. 1R 1·6 mm long, 0·7 mm wide. 1Rs 2·1 mm long, 0·7 mm wide. 2Rs widened, 2·2 mm long, 1·2 mm wide. NO 0·6 mm, OS 1·6 mm. WX 0·6 mm, NS 1·9 mm. XY 1·3 mm, VS 1·4 mm, ratio XY/VS 0·9. 1cu-a clearly prefurcal, 0·6 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Hindwings well preserved but length and width unknown; vein cu-a nearly makes right angle with vein 1A. Hindwing cells Rs and M clearly separated by abscissa of M which is 0·9 mm long. Some hamuli visible.

Remarks. These bees are very similar to *Apis* sp. G from Sainte-Reine, especially in their dimensions

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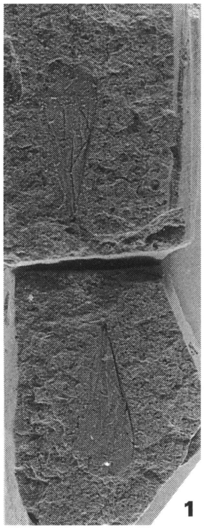
EXPLANATION OF PLATE 2

Fig. 1. *Apis* sp. F; MNHN R.10423; forewing length 10·5 mm; ×2.

Figs 2–4. *Apis* sp. I. 2, MNHN R.55166; forewing length 12·4 mm; ×2·2. 3, MNHN R.55167; forewing length 12·4 mm; ×2·4. 4, MNHN R.55169; forewing length 12·6 mm; ×3.

Fig. 5. *Apis* sp. J; MNHN R.55168; forewing length 8·8 mm; ×2·5.

PLATE 2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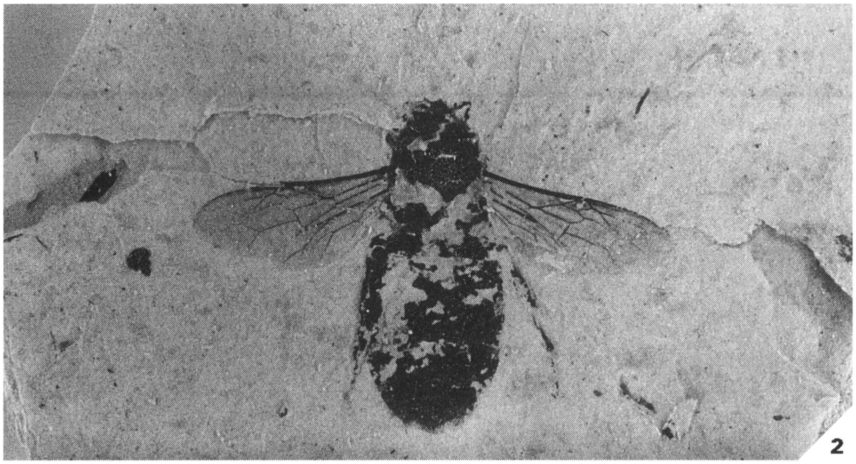
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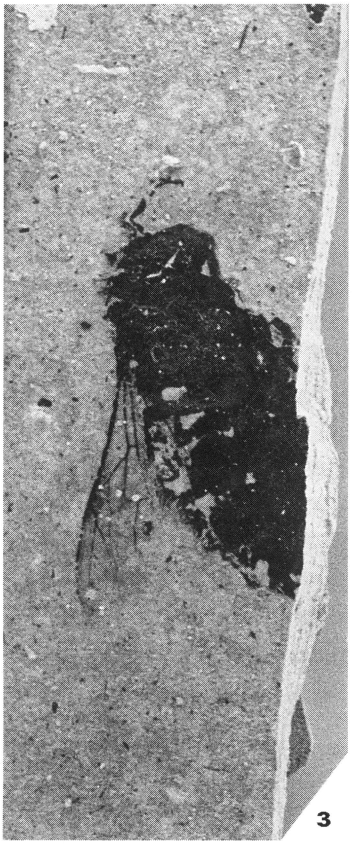
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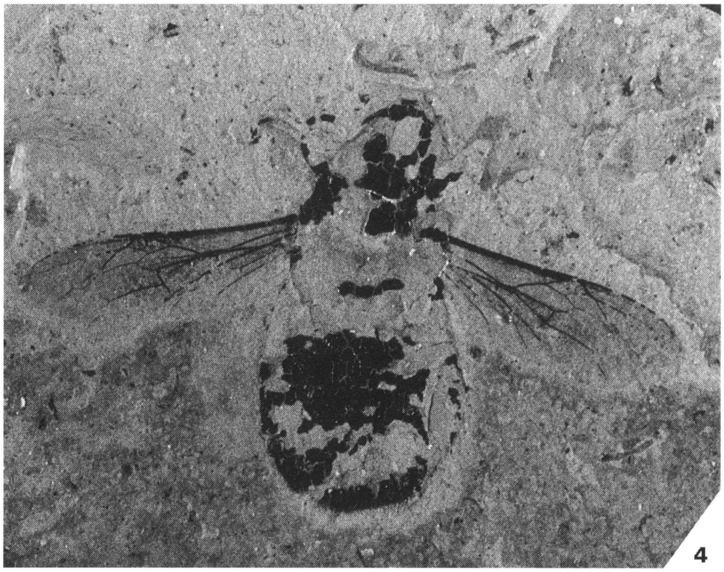
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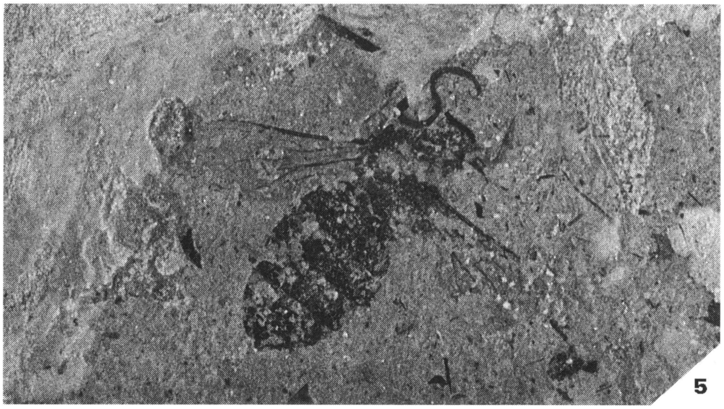
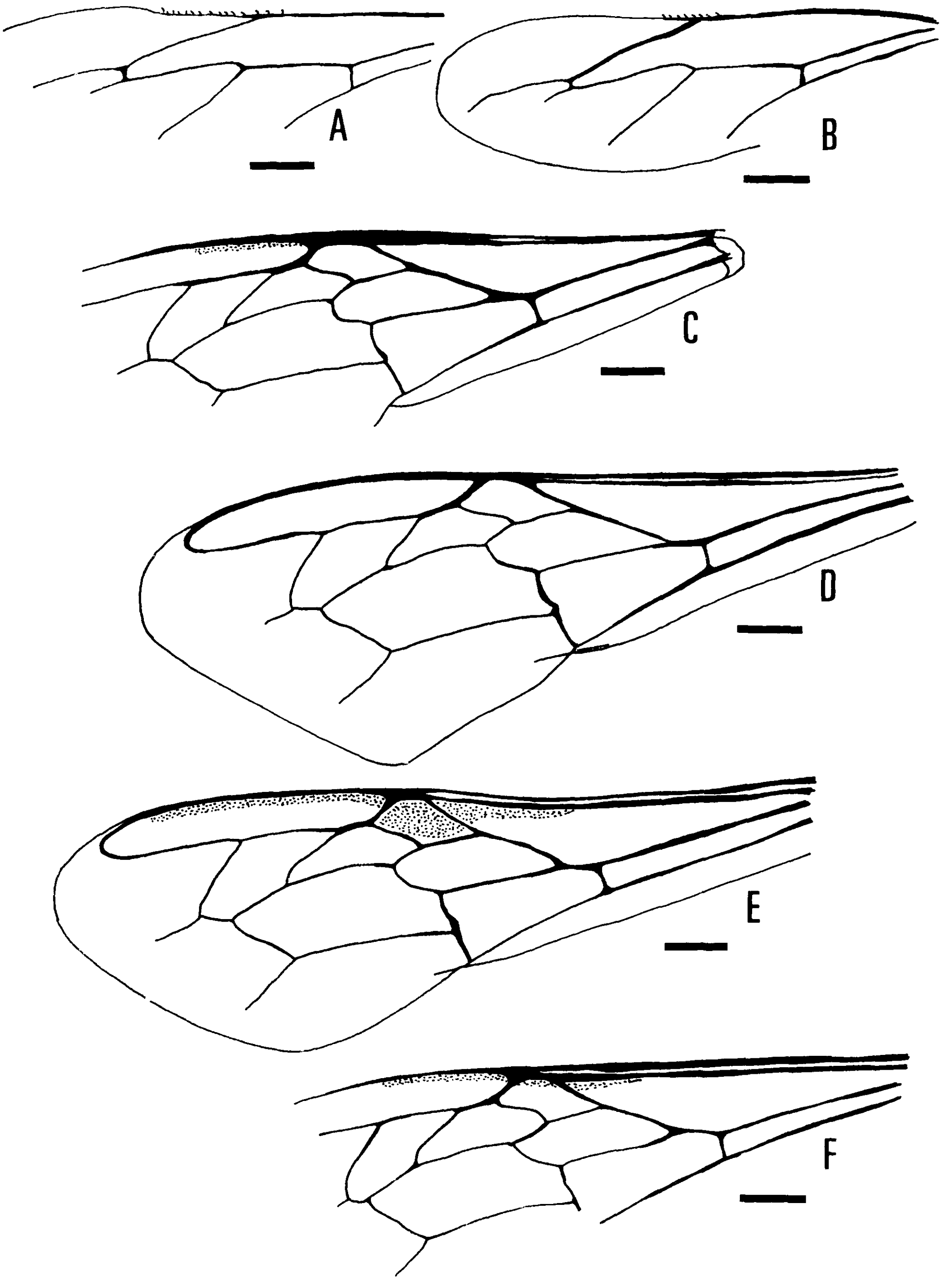
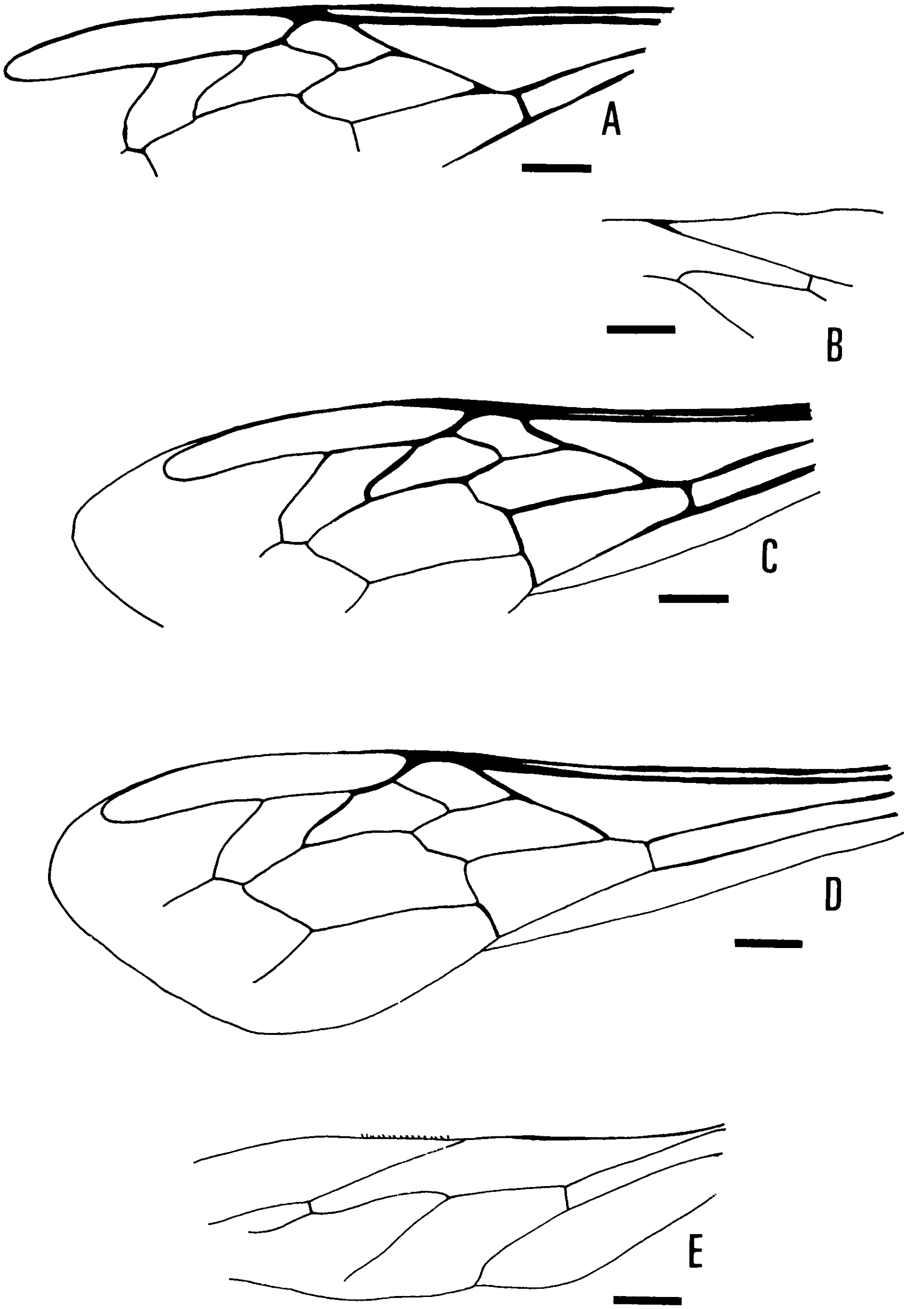

5

NEL *et al.*, *Apis*



TEXT-FIG. 11. A–F, *Apis* sp. I; A, MNHN R.54926; left hindwing; B, MNHN R.55166; left hindwing; C, MNHN R.54924; left forewing; D, MNHN R.54921; right forewing; E, R.55166; left forewing; F, MNHN R.55206; right forewing. Scale bars represent 1 mm. Drawings made using a *Camera lucida*.



TEXT-FIG. 12. A–E, *Apis* sp. I; A, MNHN R.55206; left forewing; B, right hindwing; C, MNHN R.55167, left forewing; D, MNHN R.55169, left forewing; E, MNHN R.55169, left hindwing. Scale bars represent 1 mm. Drawings made using a *Camera lucida*.

(mean forewing length 11·6 mm). They show the same wing venation and coloration, and probably belong to the same species, but the difference in age makes this uncertain.

Apis sp.

Remarks. Riou (1988) figured and briefly described some fossil bees from the same outcrop as Apis sp. I which are probably the same species (apparently having the same dimensions, venation and coloration of the forewing). He assigned them to a new species, but in an unpublished thesis of the Ecole Pratique des Hautes Etudes, and it is not possible to examine his specimens as they are held in his private collection. He did not compare his 'new species' with *A. armbrusteri* and other Miocene *Apis* species and his diagnosis of his 'new' species is not clear: 'species characterized by its large size and its resemblance to bumble bees of the genus *Bombus*.' These *Apis* do not resemble the genus *Bombus* and a diagnosis of a Recent or fossil *Apis* species cannot be based only on characters such as 'resemblance' or 'large size'. Only very careful comparison with *A. armbrusteri* will perhaps allow the creation of a new species for this population from the Montagne d'Andance.

Second group: smaller bees with shorter wing and cell 2Rs not widened.

'Cf. *Apis mellifera* Linneaus, 1758' *sensu* Riou (1988)

Material. R-195, in B. Riou's private collection, La Voulte, France; Upper Miocene, Lower Turolian; Montagne d'Andance, Saint Bauzile, Ardèche, France.

Remarks. This fossil bee is considered by Riou (1988) as a worker of *Apis mellifera* but, based on his incomplete illustrations and description, it is difficult to be certain of this by comparing the dimensions of the body and forewing with Recent species. In fact, differences between some Recent species (*A. cerana* Fabricius, 1793 and *A. mellifera*) are very difficult to determine (see Ruttner 1988) and are based on comparison of genitalia, sternite and hind legs. These comparisons are still to be made with this fossil specimen, so we must consider that Riou's (1988) determination is not yet confirmed. The fossil 'Cf. *Apis mellifera* Linné, 1758' *sensu* Riou (1988) must be considered as an *incertae sedis*.

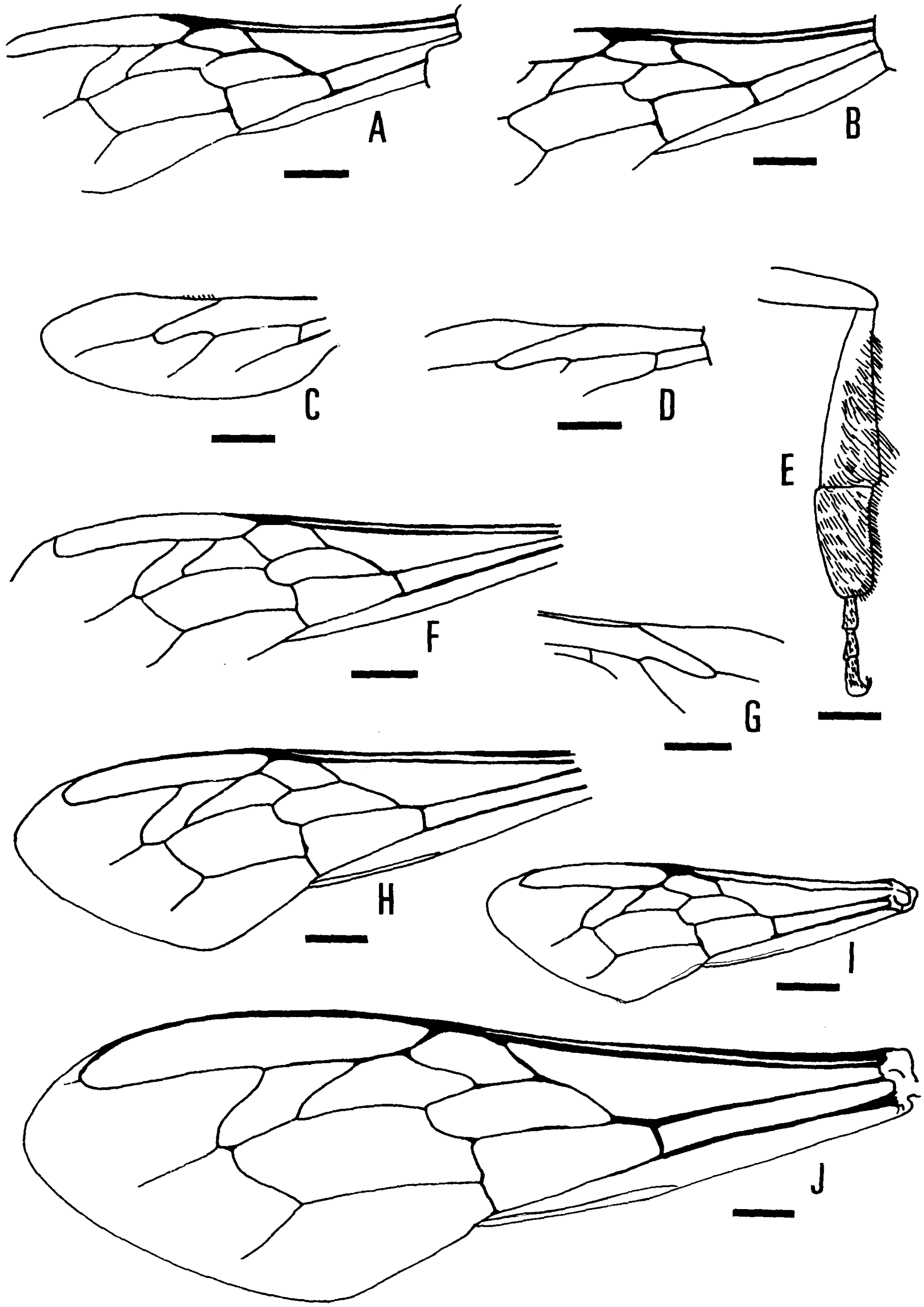
Apis sp. J

Text-figure 13A–G; Plate 2, figure 5

Material. MNHN-LP-R.55168 and R.55207 (coalified impressions and counterpart of bees fossilized in dorsal view; wings well preserved; hind leg partly preserved on R.55207 but bodies poorly preserved); Upper Miocene, Lower Turolian; Montagne d'Andance, Saint Bauzile, Ardèche, France.

Descriptions. R.55207. Although complete, body shows little detail. Head *c.* 2·5 mm long, 3 mm wide. Thorax 4 mm wide. Abdomen well-rounded, 7 mm long, 5·5 mm wide. Whole body black and covered with rather dense pilosity but not possible to determine whether eyes were covered with hair. Forewing (Text-fig. 13A–B): 8·6 mm long, 2·8 mm wide. 2R *c.* 3·1 mm long, 0·4 mm wide both in distal and proximal halves. 1R 1·1 mm long, 0·4 mm wide. 1Rs 1·4 mm long, 0·4 mm wide. 2Rs not widened, 1·4 mm long, 0·7 mm wide. NO 0·4 mm, OS 1·1 mm. WX 0·4 mm, NS 1·5 mm, XY 0·6 mm, VS 0·8 mm, ratio XY/VS 0·75. 1cu-a clearly prefurcal, 0·3 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Hindwing *c.* 5·2 mm long, 1·6 mm wide. Vein cu-a makes nearly a right angle with vein 1A (Text-fig. 13C–D). Cells Rs and M not separated because abscissa of M absent. Some hamuli visible. Only one hind leg visible but not well preserved (Text-fig. 13E). Tibia 2·8 mm long and 1 mm wide. Basitarsus 1·7 mm long and 0·9 mm wide. Ratio of length of tibia/length of basitarsus 1·6, ratio of length of basitarsus/width 1·8. Tibia and basitarsus with long hairs.

R.55168: Body poorly preserved. Thorax *c.* 4 mm long, 4 mm wide. Abdomen well-rounded, 7 mm long, 5 mm



TEXT-FIG. 13. A–G, *Apis* sp. J. A–E, MNHN R.55207; Montagne d'Andance, Ardèche, France, Upper Miocene; A, right forewing; B, left forewing; C, left hindwing; D, right hindwing; E, left hind leg showing tibia and tarsi. F–G, MNHN R.55168; F, left forewing; G, right hindwing. H, *Apis mellifera*; Recent; left forewing. I, *Apis florea*; Recent; left forewing. J, *Apis dorsata*; Recent; left forewing. Scale bars represent 1 mm. Drawings made using a *Camera lucida*.

wide. Whole body black and covered with a rather dense pilosity but impossible to dertermine whether eyes were covered with hair. Forewing 8·8 mm long, 2·8 mm wide (Text-fig. 13F; Pl. 2, fig. 5). 2R *c.* 3·2 mm long, 0·4 mm wide both in distal and proximal halves. 1R 1·2 mm long, 0·5 mm wide. 1Rs 1·3 mm long, 0·4 mm wide. 2Rs not widened, 1·3 mm long, 0·8 mm wide. NO 0·2 mm, OS 1·2 mm. WX 0·4 mm, NS 1·3 mm, XY 0·6 mm, VS 0·8 mm, ratio XY/VS 0·75. 1cu-a clearly prefurcal, 0·2 mm from branching of M and CuA. 1m-cu weakly sclerotized along distal margin. Hindwing *c.* 5·2 mm long, 1·6 mm wide (Text-fig. 13G). Vein cu-a nearly makes right angle with vein 1A. Cells Rs and M not separated because abscissa of M absent. Some hamuli visible. No legs preserved.

Remarks. These bees are distinctly smaller than *Apis* sp. I from the same outcrop. They have some important different characters: (1) there is no abscissa of vein M in the hindwing, while *A.* sp. I has a very long one; (2) the forewing is distinctly shorter (8·6–8·8 mm long), while *A.* sp. I has mean forewing length of 11·9 mm; (3) cell 2Rs is not widened, with a very closed angle YVX (15°), whereas *A.* sp. I has a more open angle YVX, mean 28°; (4) the radial index is 1·7, whereas it is about 1 in *A.* sp. I.

They belong to a species probably related to 'Cf. *Apis mellifera*' *sensu* Riou (1988) which is also based on a single specimen from the same outcrop, with similar body and wing dimensions but, as Riou's description is not very precise, it is impossible to make any closer comparisons.

The wing dimensions of *A.* sp. J are also similar to those of Recent *A. mellifera* but, as we have already noted with 'Cf. *Apis mellifera*' *sensu* Riou (1988), it is still impossible to say that these bees really belong to *A. mellifera sensu stricto*. Body and wing dimensions of *A.* sp. H (Upper Miocene of Sainte-Reine) are also very close to those of R.55207. It appears that, both at Sainte-Reine and at Andance, there were two different species of *Apis*, a larger one, similar and probably related to Recent *A. dorsata*, and a smaller one probably related to *A. mellifera*. However, it is still impossible to say that the large 'Andance bee' (*A.* sp. I) is the same as the large 'Sainte-Reine bee' (*A.* sp. G) and also that the small 'Andance bee' is the same as the small 'Sainte-Reine bee'. Further discoveries of new material are necessary before any conclusion can be made about this.

The small bees of Sainte-Reine and Andance seem to be less numerous than the large species (five 'small' specimens against 16 'large' specimens in the Nel, Brisac and privately held Riou collections for both quarries). This could be an artefact of sampling. If not, the difference in the proportions of the different species remains to be explained, and only further research will give an answer.

PLIO-PLEISTOCENE RECORDS OF *APIS*

A specimen of *Apis* (*A.*) *mellifera* Linnaeus, 1758 was reported in copal by Foord (1890). Cockerell (1909) first described a piece of amber in the collections of Cambridge University which contains two bee specimens, stating that they came from the coast of Yarmouth (England). Subsequently, he noted that the provenance of this amber (or copal) was problematical: it could be genuine English amber or African copal (Cockerell 1921). Maa (1953) was less sure of the origin. Kelner-Pillault (1969*b*) believed that it came from the Pleistocene of England, Zeuner and Manning (1976) believed that they were genuine *Apis mellifera* from East Africa. Spahr (1987) was undecided, and Ruttner (1988, p. 26) stated, without discussion, that these bees were of very Recent African origin. African copal is Pleistocene or Recent (Burleigh and Whalley 1983).

A 'Honeybee comb' was reported by Stauffer (1979) from a Plio-Pleistocene cave deposit, Batu Caves, Kuala Lumpur, Malaysia.

ORIGIN OF *APIS*

The Upper Eocene genus *Electrapis* Cockerell, 1908, which was attributed by Manning (1952), Kelner-Pillault (1969*a*, 1969*b*), Zeuner and Manning (1976) and Culliney (1983) to the Apini, and even considered to be the direct ancestor of *Apis*, is thought by Kerr and Da Cunha (1976), after a numerical taxonomic study, to be a Meliponini. As their work was not a phylogenetic analysis, the real relationships between *Apis* and *Electrapis* have not really been elucidated, as indicated by Burnham (1978). Genuine fossil Apoidea are known in the Upper Cretaceous (Cenomanian amber of New Jersey, USA; Grimaldi *et al.* 1989). Even if Apoidea is a very ancient group, as demonstrated by the discoveries in the Cretaceous, the genus *Apis* seems to have appeared 'suddenly' during the Late Oligocene. Two main theories have been proposed regarding the 'locus of origin' of the genus *Apis*: (1) *Apis* could have originated in India and South East Asia because the recent distribution of the Apini is centred in the Oriental region (Culliney 1983). (2) According to Hong and Miao's (1992) theory, the Apoidea could have originated during the late Early Cretaceous in the North China Palaeocontinent and the genus *Apis* during the Cenozoic in China.

The alleged oldest fossil 'bee' *Palaeapis beiboziensis* Hong, 1984 from the Early Cretaceous Laiyang Formation of China is probably not an Apoidea. The oldest known *Apis* are neither Chinese nor Indian but from the West Palaearctic. A biogeographical study based on a phylogenetic analysis of recent and fossil species is clearly needed.

CONCLUSIONS

The venations of the bees *Apis armbrusteri* and *A.* spp. E, F, G and I from the Upper Miocene of Western Europe (populations from Austria, south-west Germany, south-central France and Cerdanya, Spain) are very similar to that of Recent *Apis dorsata*, except for the wing dimensions; *A. dorsata* is bigger than all the others although it is virtually impossible to distinguish well-characterized species amongst these populations. Possibly, there was a 'superspecies' or a species complex of *Apis* during the Late Miocene in the region, with (sub)species, mainly characterized by their size. *Apis dorsata* is a Recent species now living in India and South-East Asia but the existence of Western Palaearctic fossil species related to *A. dorsata* suggests that this group of bees was not restricted to South-East Asia in the past. These bees also suggest that, during the Late Miocene, the palaeoclimate was warmer than that in Recent times in Western Europe, even in the mountains (Bellver de Cerdanya and Sainte-Reine are 1100 m altitude palaeolakes).

It appears that during the Late Miocene in Europe, these fossil relatives of the *dorsata* group were living with smaller bees more closely related to Recent *A. mellifera*. Our study also confirms that *Apis* (*Synapis*) spp. (very similar to Recent forms) were already present during the Late Oligocene in Western Europe together with representatives of Recent subgenera. The taxonomy of fossil *Apis* is still very confused because of the multiplicity of more or less poorly defined 'species' and 'subspecies' but mainly because of the lack, in fossil material, of many of the characters which are used in the taxonomy of Recent *Apis*. Genuine *Apis* are also present in the Miocene of Japan and China, so it appears that the genus had already colonized all the Palaearctic region at the very beginning of the Miocene if not during the Late Oligocene. Contrary to the opinion of Hong and Miao (1992), the oldest known *Apis* are from Western Europe (Germany and France), not from the Miocene of China. Late Eocene *Apis* are unknown.

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TABLE 1. Forewing nomenclature of veins. The present designation of the wing veins is based on Wootton (1979) and Mason (1990). The symbol (v) indicates that the authors consider the structure as a vein. The terminology of Eickwort (1969) is based on Michener (1944) and Lanham (1951).

Maa (1953)	Eickwort (1969)	present designation
(v) icu1	(v) cu-v	(v) 1cu-a
(v) 2A	frf (frenal fold)	frf
?	(v) V	(v) 1A
?	(v) M + Cu	(v) M + CuA
(v) mcu1	(v) M	(v) M
(v) Cu	(v) Cu	(v) CuA
(v) mcu2	(v) 1m-cu	(v) 1m-cu
?	(v) Cu2	(v) 2cu-a
?	(v) Cu1	(v) CuA
(v) mcu3	(v) 2m-cu	(v) 2m-cu
(v) M3 + 4	(v) M + Rs/M	(v) M + Rs/M
(v) M	(v) Rs	(v) Rs
(v) im1	(v) 1r-m	(v) 1r-m
(v) im2	(v) 2r-m	(v) 2r-m
(v) M1 + 2	(v) Rs	(v) Rs
?	?	Sc + R + Rs
?	(v) R1	(v) R
Pt	Stg (or Pt)	Pt
?	(v) C	(v) C
?	vf (vannal fold)	vf (+ CuP)
?	(v) r	(v) r-rs
?	smcr (submarginal crease)	smcr

TABLE 2. Forewing nomenclature of cells. The two different nomenclatures for cells proposed respectively by Michener (1944) and Eickwort (1969) do not correspond exactly with the modern nomenclature of veins, but as there is no possibility of confusion between the names of veins and those of cells, we introduce only few nomenclatural changes in order to minimize confusion in the terminology.

Maa (1953)	Michener (1944)	Eickwort (1969)	present designation
bm	R	?	cell R
1sm	1st M	?	cell 1M
2sm	2nd M	?	cell 2M
r	1st R1	1R1	cell 1R
3r	2nd R1	2R1	cell 2R
1m	1st Rs	1Rs	cell 1Rs
2m	2nd Rs	2Rs	cell 2Rs
3m	?	?	cell 3Rs
3sm	?	?	cell 3M
1a	?	?	cell A (anal cell)
?	1st Cu	?	cell 1 cu-a (1st cubito-anal cell)
?	2nd Cu	?	cell 2 cu-a (2nd cubito-anal cell)

TABLE 3. Hindwing nomenclature of veins.

Maa (1953)	Eickwort (1969)	Michener (1944)	Alexander (1991)	present designation
(v) M	(v) Rs	(v) Rs	(v) Rs	(v) Rs
?	(v) r-m	(v) r-m	?	(v) r-m
?	(v) R	(v) R	?	(v) Sc + R + Rs
(v) M1 + 2	?	?	(v) Rs	(v) Rs
(v) M3 + 4	?	?	(v) abscissa of M	(v) ab M
(v) mcu1	(v) M	(v) M	(v) M	(v) M
?	?	(v) M + Cu	(v) M + Cu	(v) M + CuA
(v) icu1	(v) m-cu	(v) cu-v	?	(v) cu-a
(v) Cu2 + 1A	(v) V	(v) V	(v) 1A	(v) 1A
(v) Cu1	?	?	(v) Cu	(v) CuA
?	jf (jugal fold)	?	(v) 2A	(v) 2A
?	smcr	?	?	smcr
?	vf (vanal fold)	?	?	vf

TABLE 4. Hindwing nomenclature of cells. We do not follow the nomenclature of Maa (1953) for the hindwing cells because it does not correspond to that for the forewing cells.

present designation	Maa (1953)
cell R (equivalent of Rc of forewing)	bm (proximal cell between R, Rs and Cu + M)
cell Rs	m (distal cell between Rs and abscissa of M)
cell M	sm (cell between CuA and M)
cell 2A (second anal cell)	jl (jugal lobe)
cell 1A (first anal cell)	vl (vanal lobe between 1A and 2A)

TABLE 5. Comparison of the names for points of intersection of wing veins. Unfortunately many workers have given different names to the points of intersection of the forewing veins of Hymenoptera (Louis 1966, 1971; Ruttner 1988; Alexander 1991). It is particularly regrettable that Ruttner and his school did not follow Louis' nomenclature which was complete but probably had the disadvantage of being written in French and not English. Note: there seems to be an error in figures 2–3 of Alexander (1991): point A in figure 2 is not the equivalent of point A in figure 3.

Louis (1971)	Alexander (1991)	Ruttner (1988)
O	A	H
S	B	B
X	C	I
V	D	A
Y	E	E
T	?	C
F	?	X
W′	?	Y (or L)!
U	?	D
W	?	M
?	?	E′
N	?	J
?	?	N
M	?	P
K	?	Q
H	?	R
I	?	O
R	?	G
Q	?	F
P	?	K

TABLE 6. Miocene fossil bees from France, Austria and Spain. Measurements are in mm. Characters of the forewing: FL, forewing length (*sensu* Ruttner 1988); FB, forewing width (*sensu* Ruttner 1988); Ci, cubital index (= CB/CA = a/b *sensu* Ruttner 1988, p. 42, fig. 4.7, p. 72, fig. 6.8) (= TS/TV *sensu* Louis 1971); Pci, Precubital index (= BJ/MH *sensu* Ruttner 1988) (= SN/WO *sensu* Louis 1971); Dbi, dumbbell index (= BA/IE *sensu* Ruttner 1988) (= SV/XY *sensu* Louis 1971); Ri, radial index (= E'X/E'Y *sensu* Ruttner 1988) (= YF'/YW' *sensu* Louis 1971); Dm, distance between vein icu-a and the point of separation between the veins M and CuA (= QR *sensu* Ruttner 1988; = HK *sensu* Louis 1971); this is positive if vein icu-a is in a proximal position relative to the point of separation between M and CuA, but otherwise negative; Lpt, length of the pterostigma (= LN *sensu* Ruttner 1988; = M'W' *sensu* Louis 1971); Wp, width of the proximal half of cell 2Rs; Wd, width of distal half of cell 2Rs; Angle YVX (*sensu* Louis 1971); Angle KIH (*sensu* Louis 1971) (= angle QOR *sensu* Ruttner 1988).

The hindwing's characters, i.e. the length of the abscissa of vein M and the number of hooks are difficult to use because the hooks of the hindwing are rarely preserved. Also, the body's characters, i.e. the length of hairs on tergite 5 = h (*sensu* Ruttner and Tassencourt 1978, fig. 1), the length and width of the basitarsus, and the length of the body, are often difficult to use because of the degree of deformation.

	F_L	F_B	Ci	Pci	Dbi	Ri	Dm	Lpt	Wp	Wd	YVX	KIH
A. mellifera	9·3	3·2	1·2	3	0·7	1·3	0·3	0·8	0·4	0·4	20°	100°
A. florea	6·8	2·2	3·6	2·2	1·3	1·7	0·2	0·8	0·3	0·2	20°	110°
A. dorsata	14·2	4·7	4·8	3	1	1·1	0·7	1·2	0·7	0·7	27°	115°
A. cuenoti												
R.08383 Céreste	12·6	3·8	3·6	3·2	1	0·9	0	0·8	0·6	0·6	29°	105°
173EFN Céreste	12·6	3·7	3·4	3	1	0·8	0	0·8	0·6	0·6	32°	105°
R.08396 Céreste	≈11	3·6	?	?	?	0·8	0·2	0·7	0·5	0·5	?	110°
Apis sp. A												
R.08384 Camoin	10	3·4	2·3	3·6	1·8	1·3	0	0·7	0·4	0·4	10°	90°
R.08385 Camoin	≈10	?	?	?	1·3	1·3	0·2	0·7	0·4	0·4	15°	105°
A aquisextusensis												
R.08381 Aix	8·5	2·8	6	2·8	1·2	1·6	0·2	0·7	0·45	0·3	15°	110°
R.08382 Aix	8·5	2·8	?	2·9	?	1·7	0·15	0·8	0·45	0·3	?	90°
R.10421 Aix	8·6	≈3	6	2·9	1·5	1·8	0·2	0·8	0·4	0·3	15°	115°
Apis sp. B												
R.10429 Aix	11·9	?	1·8	3·2	0·8	1	0	0·3	0·45	0·3	28°	105°
Apis sp. C												
R.10426 Aix	10	≈3	2	2·6	1·2	1·4	0·2	0·6	0·3	0·3	25°	110°
Apis sp. D												
MPV-91-RM	9·5	2·3	3	3·9	1·1	1·3	0·3	0·8	0·3	0·3	20°	120°
1982 XIV Mun.	9·7	3·2	4·4	2·7	1	1	0·3	0·7	0·4	0·4	30°	120°
Apis sp. E												
B.31781 Parsch.	11·5	3·7	?	2·5	0·8	1·2	0·25	1	0·6	0·6	34°	125°
B.31782 Parsch.	?	?	3·1	2·4	0·9	1·3	?	0·9	0·6	0·6	50°	?
Apis sp. F												
R.10423 Bellver	10·5	3·6	2	3	0·9	0·9	0·4	0·7	0·4	0·4	32°	110°
R.10425 Bellver	10·7	3·6	3·6	3·5	0·8	1	0·6	0·6	0·5	0·5	32°	110°
R.08386 Bellver	9·6	3·2	2	3·5	0·8	0·9	0·5	0·6	0·4	0·4	35°	105°
R.10424 Bellver	10·4	?	2·9	4	1	0·9	0·5	1	0·5	0·5	25°	105°
R.10422 Bellver	10·8	3·7	3·8	2·9	1	1	0·5	0·7	0·5	0·5	29°	110°
R.10432 Bellver	10·4	?	3·3	3·5	1	1	0·5	0·8	0·5	0·5	27°	120°
R.10431 Bellver	≈10	?	?	3·3	?	1	0·5	0·8	0·5	0·5	?	110°
MNCNI-21614	10	≈3	3	3·5	0·9	0·9	0·5	0·7	0·5	0·5	30°	110°
Apis sp. G												
R.08389 Murat	12	3·7	3·6	3	1	1	0·5	0·7	0·6	0·6	30°	90°
R.08388 Murat	12·6	≈4	2·6	2·5	0·8	0·8	0·5	0·7	0·6	0·6	44°	112°
R.08390 Murat	11	3·8	2·7	2·7	0·7	0·8	0·6	0·9	0·6	0·6	37°	115°

TABLE 6 continued.

	F_L	F_B	Ci	Pci	Dbi	Ri	Dm	Lpt	Wp	Wd	YVX	KIH
Apis sp. H												
R.08391 Murat	8·5	?	3·7	3	1	1·2	0·3	0·9	0·4	0·4	30°	105°
R.08392 Murat	8·6	?	3	3	1	1·8	?	1·2	0·4	0·4	20°	?
Apis sp. I												
R.54924 Andan.	11	≈4	2·5	2·8	1	?	0·6	1	0·5	0·5	25°	110°
R.54922 Andan.	≈12	3·7	3	2·9	0·9	≈1	0·5	0·8	0·4	0·4	35°	110°
R.54921 Andan.	12·4	4·6	2·8	2·7	1	0·8	0·6	1	0·5	0·5	30°	110°
R.54926 Andan.	11·2	≈4	2·7	2·7	1	1·1	0·5	1	0·5	0·5	25°	110°
R.55166 Andan.	12·4	4·2	2	2·8	1	0·9	0·6	0·7	0·6	0·6	29°	115°
R.55206 Andan.	12·4	?	4	2·8	0·8	1	0·6	1	0·6	0·6	32°	118°
R.55167 Andan.	12·4	?	3·2	2·7	1	1·1	0·6	1	0·6	0·6	26°	105°
R.55169 Andan.	12·6	4·2	2·3	2·8	1·1	1·1	0·6	1	0·6	0·6	25°	110°
Apis sp. J												
R.55207 Andan.	8·6	2·8	5	2·7	1·5	1·7	0·3	0·8	0·4	0·4	15°	128°
R.55168 Andan.	8·8	2·8	5	2·3	1·5	1·6	0·2	0·8	0·4	0·4	12°	112°

NOTES FOR AUTHORS

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Palaeontology

VOLUME 42 · PART 2

CONTENTS

An Early Bathonian Tethyan ammonite fauna from Argentina
ALBERTO C. RICCARDI *and* GERD E. G. WESTERMANN 193

Oelandiella, the earliest Cambrian helcionelloid mollusc from Siberia
ALEXANDER P. GUBANOV *and* JOHN S. PEEL 211

A new Carboniferous rugose coral genus from northern England
JOHN R. NUDDS 223

Using critical path method to analyse the radiation of rudist bivalves
J. R. STONE *and* M. TELFORD 231

A review of the Eurasian fossil species of the bee *Apis*
A. NEL, X. MARTÍNEZ-DELCLÒS, A. ARILLO *and* E. PEÑALVER 243

Shark and ray teeth from the Hauterivian (Lower Cretaceous) of north-east England
CHARLIE J. UNDERWOOD, SIMON F. MITCHELL *and* KEES J. VELTKAMP 287

Lower and Middle Jurassic woods of the Cleveland Basin (North Yorkshire), England
HELEN S. MORGANS 303

Gigantonoclea: an enigmatic Permian plant from North China
WANG ZI-QIANG 329

A replacement name for the trilobite *Lalax* Holloway and Lane *non* Hamilton
D. J. HOLLOWAY *and* P. D. LANE 375

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