

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; Linqou 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; Linqou 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; Linqou 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; Linqou 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 (1969a, 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.

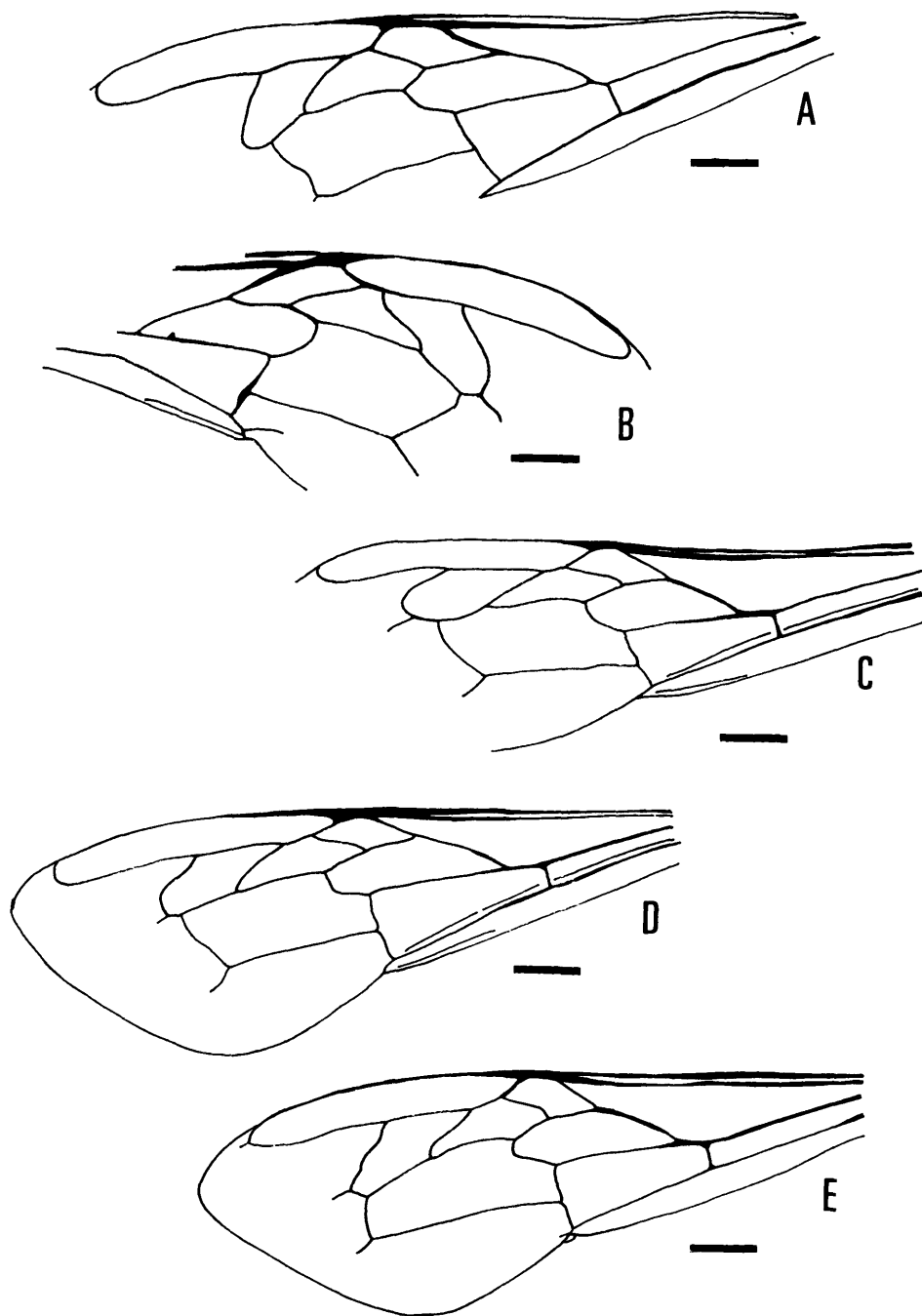
1976 '*Apis*' *styriaca* Pongracz; Zeuner and Manning, p. 251.

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, Stuttgart, 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, Stuttgart-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.

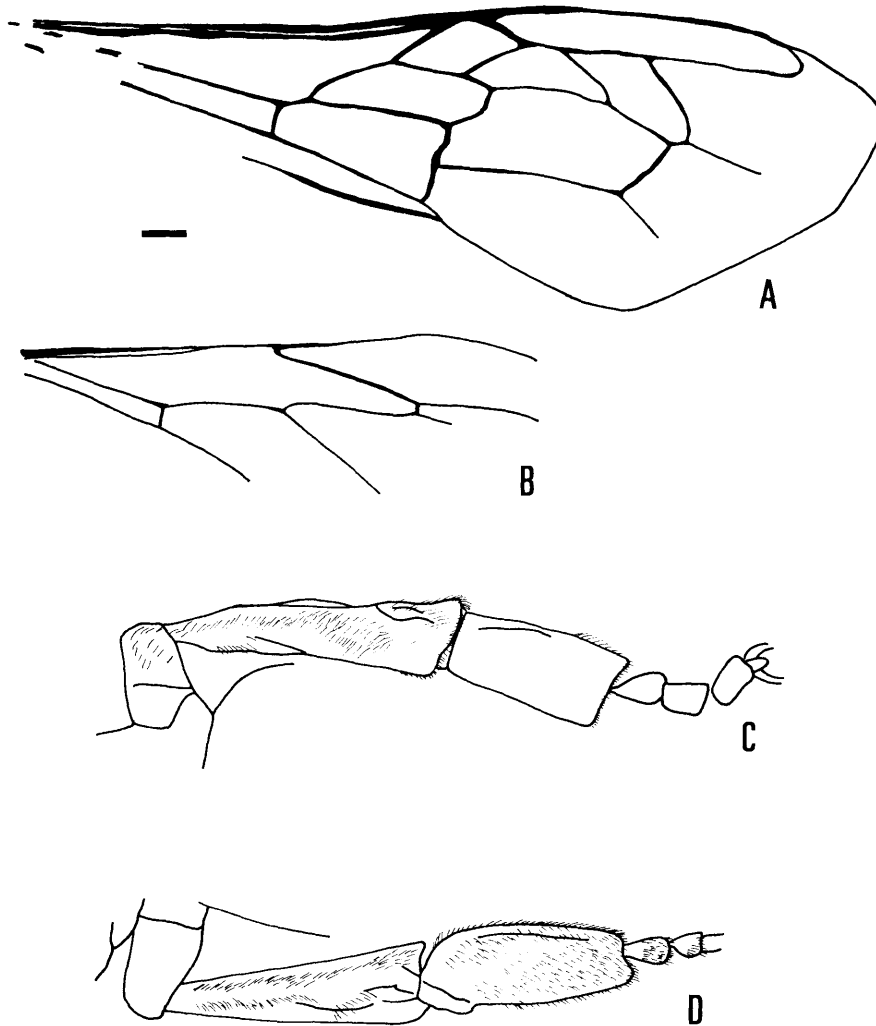
The ‘subspecies’ *A. armbrusteri scharmanni* and *A. armbrusteri scheeri* have about the same dimensions as Recent *A. mellifera* but *A. armbrusteri scheuthlei* is larger. The subspecies *A. armbrusteri armbrusteri* is known from bodies of bees fossilized as negative impressions (holes) in a travertine. 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*.

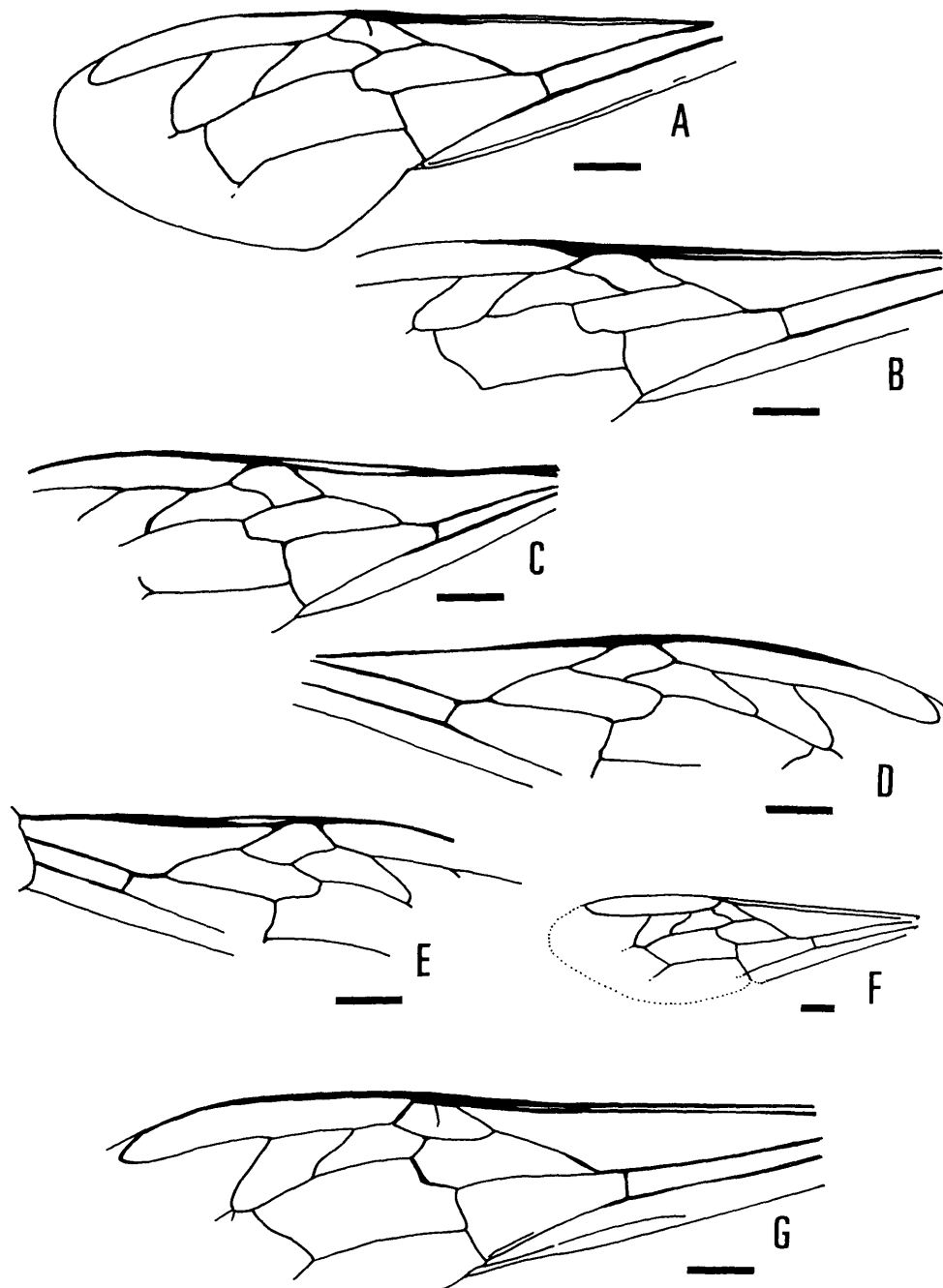
All the other specimens have forewing venations very similar to specimen R.08386. Specimen R.10423 has small supplementary veinlet in cell 1R.

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.

1969b *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.

1969b *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; Simitite, 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; Serieyssel and Gasse 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

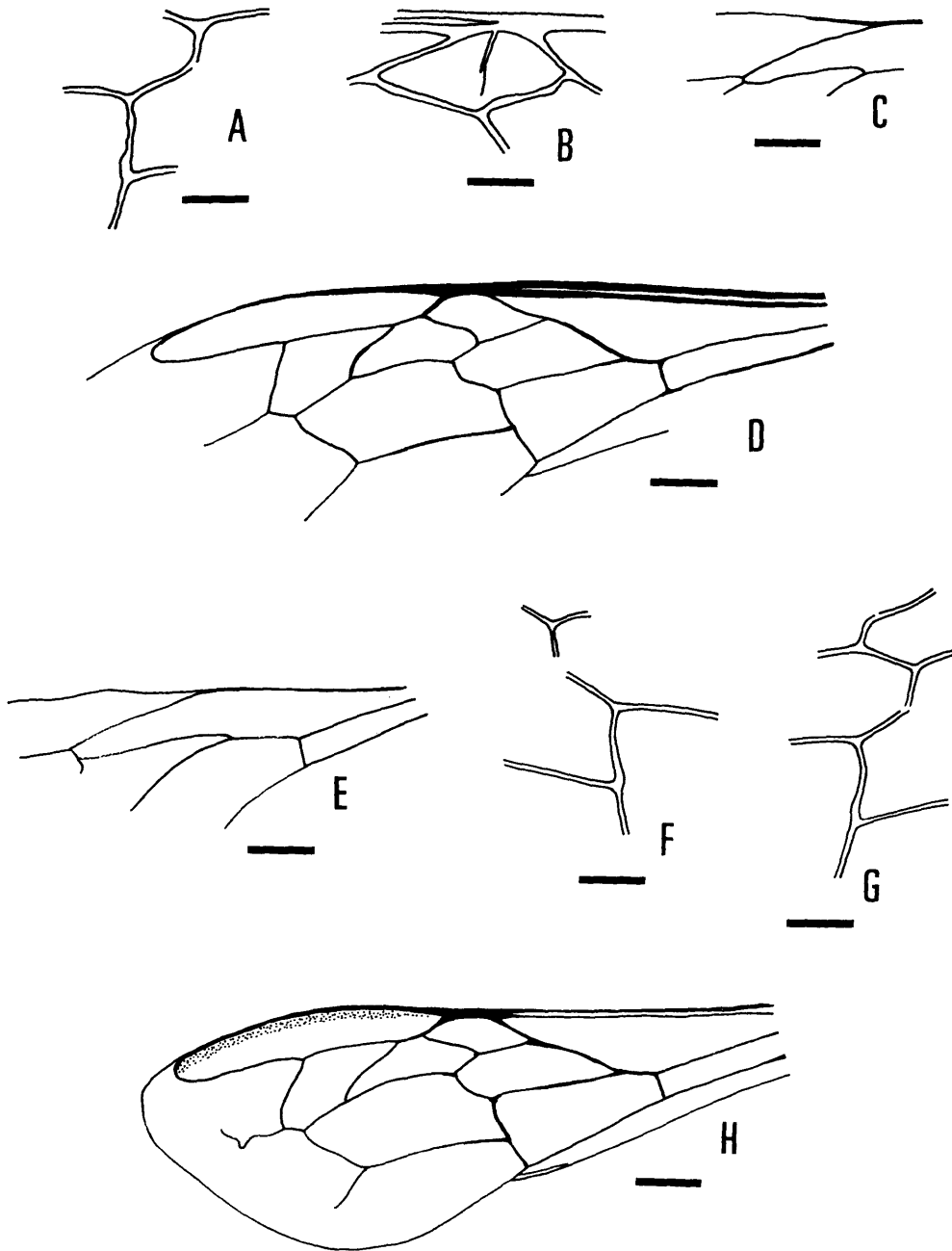
Apis sp. H

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; Serieyssel 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

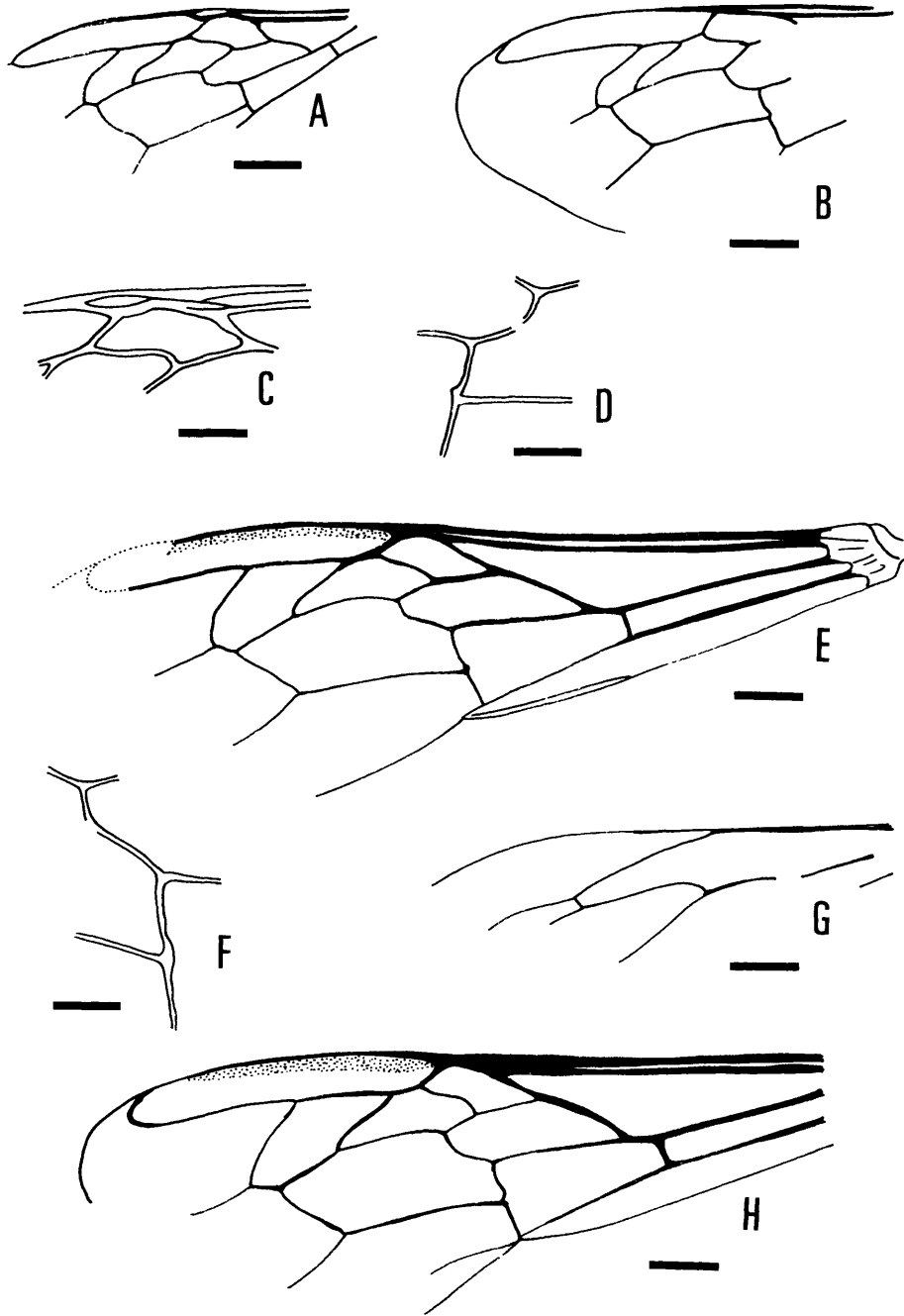
Material. MNHN-LP-R.54926, R.54921 (both in dorsal view, bodies black), R.54922 (in lateral position, with forewing 5 mm away, body black), R.54924; R.55166 and R.55206 (both coalified impressions, parts and counterparts, fossilized in dorsal view), R.55167 (coalified impression fossilized in lateral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

EXPLANATION OF PLATE 2

Fig. 1. *Apis* sp. F; MNHN R.10423; forewing length 10.5 mm; $\times 2$.

Figs 2-4. *Apis* sp. I. 2, MNHN R.55166; forewing length 12.4 mm; $\times 2$. 3, MNHN R.55167; forewing length 12.4 mm; $\times 2.4$. 4, MNHN R.55169; forewing length 12.6 mm; $\times 3$.

Fig. 5. *Apis* sp. J; MNHN R.55168; forewing length 8.8 mm; $\times 2.5$.