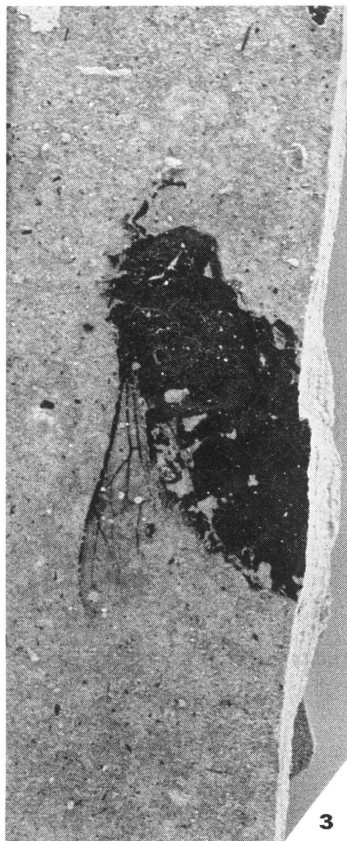
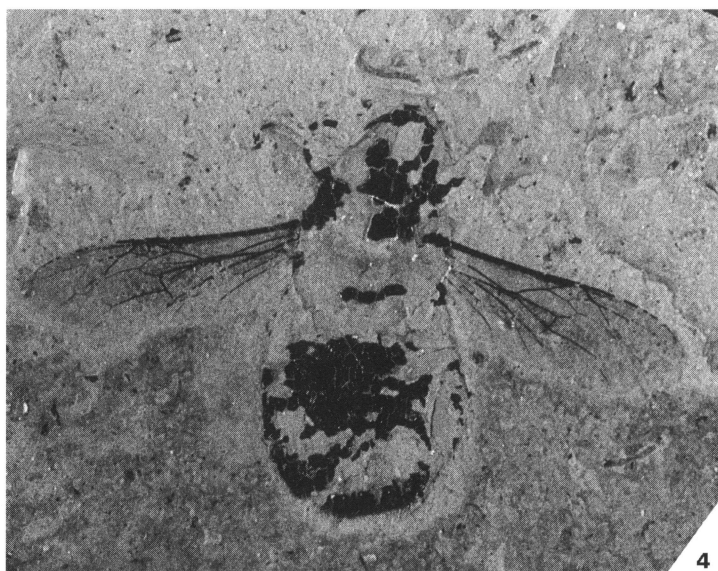


2



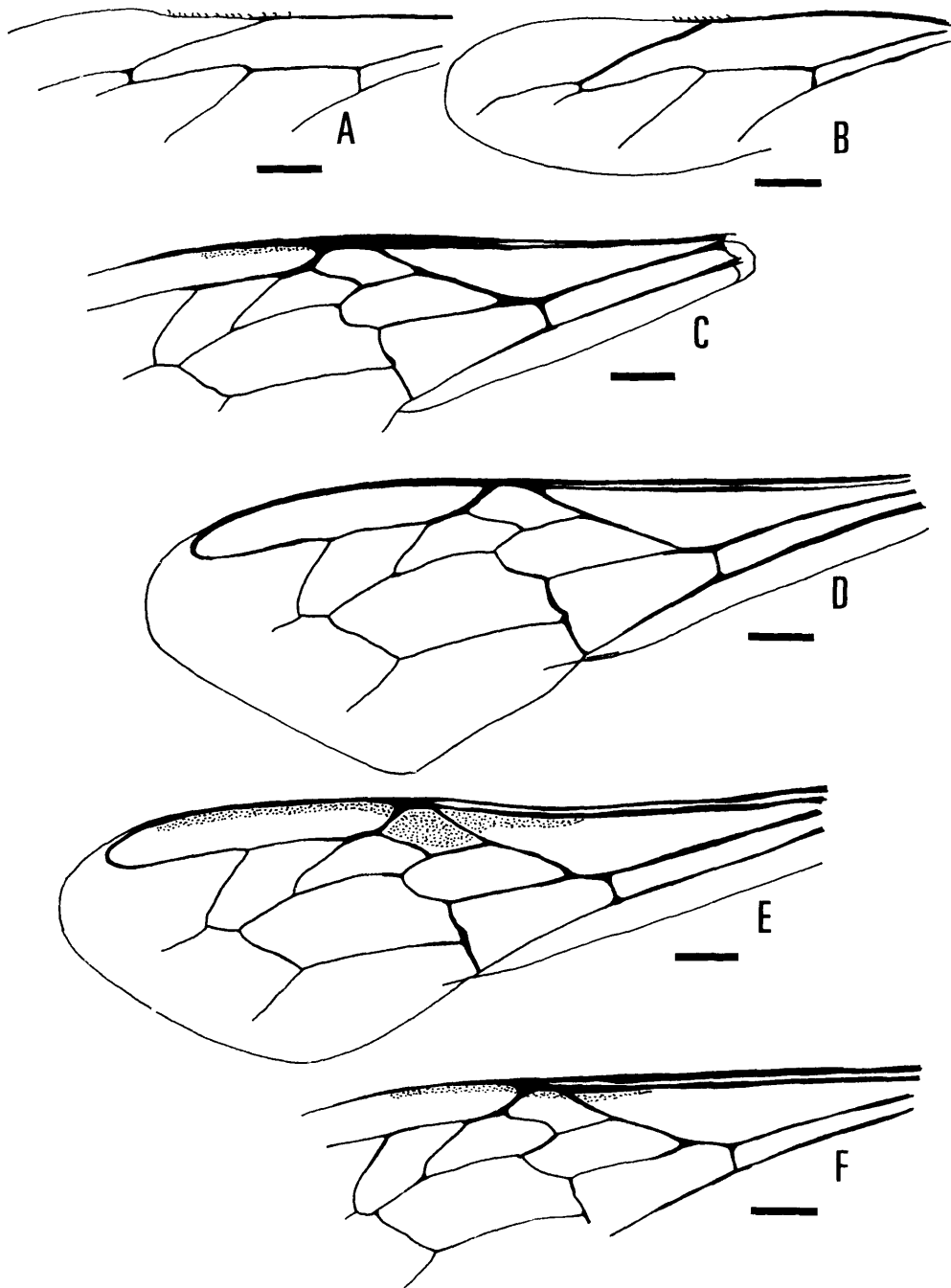
3



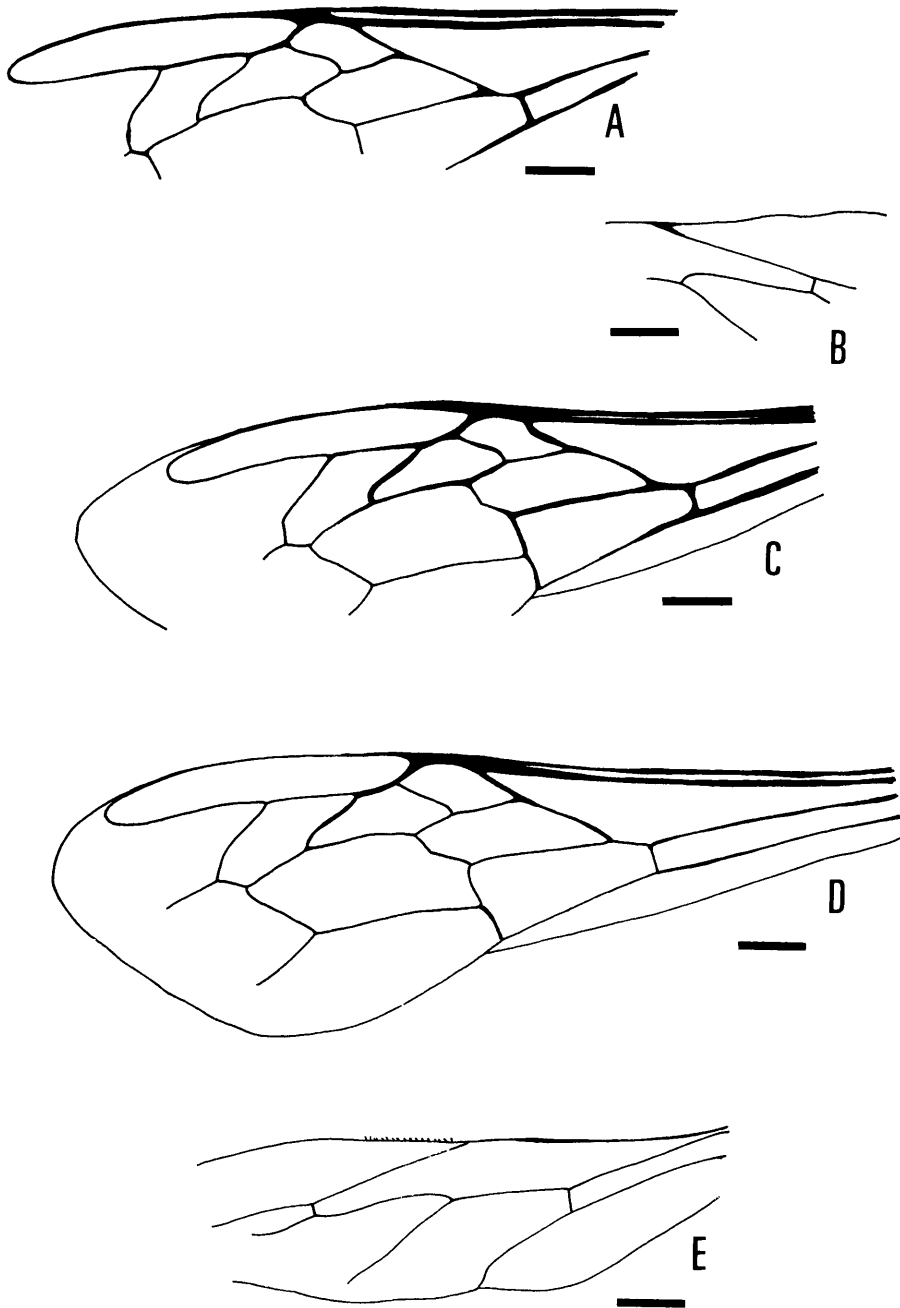
4



5



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 He assigned them to a new species, but in an unpublished thesis of the Ecole Pratique des Hautes Etudes, and it is not possible to examine his specimens as they are held in his private collection.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* Linnaeus, 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*.

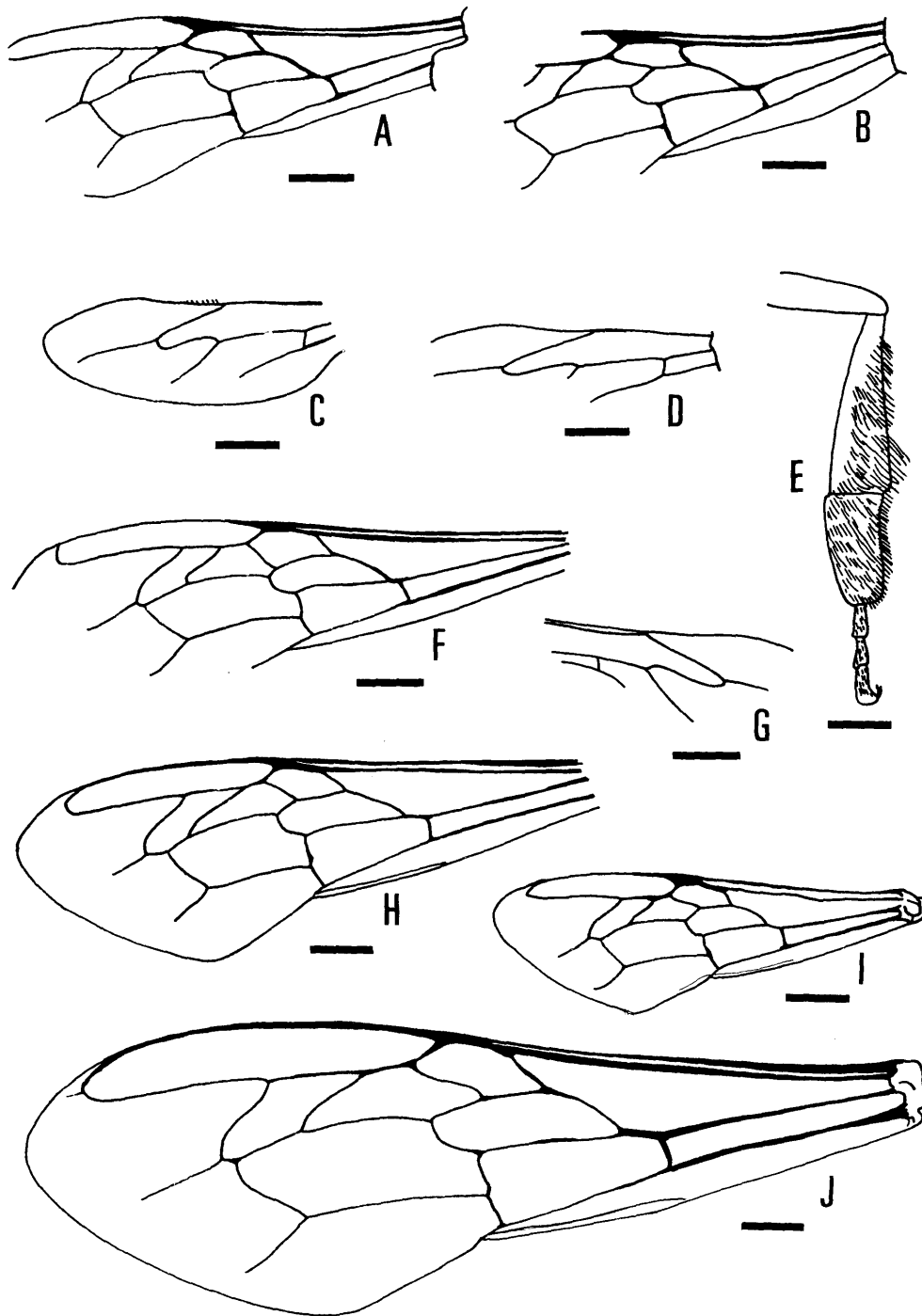
*Apis* sp. J

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 determine 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. Icu-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 (1969b) 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 (1969a, 1969b), 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 Palaeartic. 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 Palaeartic 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 Palaeartic 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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