Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy

Plinio MONTOYA
Departament de Geologia, Àrea de Paleontologia,
Universitat de València, Doctor Moliner 50, E-46100 Burjassot (Spain)
pmontoya@uv.es

Léonard GINSBURG
Muséum national d'Histoire naturelle, Département Sciences de la Terre,
case postale 38, 8 rue Buffon, F-75231 Paris cedex 05 (France)

María Teresa ALBERDI
Jan VAN DER MADE
Jorge MORALES
María Dolores SORIA
Museo Nacional de Ciencias Naturales (CSIC),
José Gutiérrez Abascal 2, E-28006 Madrid (Spain)
mcnaa3j@mncn.csic.es
mcnjv538@mncn.csic.es
mcnm166@mncn.csic.es

Montoya P., Ginsburg L., Alberdi M. T., Van der Made J., Morales J. & Soria M. D. 2006. — Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28 (1): 137-173.

ABSTRACT
The fossil macromammal locality of Alcoy (province of Alicante, Spain) is known since the middle of the 19th century. Ever since then, its age has been disputed as the latest Miocene or the earliest Pliocene. There are several sites in the area that yielded micromammals: Alcoy-Barranco, Alcoy-N, Alcoy-4B and Alcoy-2, which range in age from MN13 to MN15, that is from the latest Miocene to the early Pliocene. The large mammals, however, all come from Alcoy-Mina, an old lignite mine. We have revised this material kept in various European collections. The faunal list is the following: *Agriotherium insigne* (Gervais, 1859), *Ursus boeckhi* Schlosser, 1899, *Anancus arvernensis* (Croizet

KEY WORDS
Mammalia,
Carnivora,
Artiodactyla,
Proboscidea,
Alcoy,
Spain,
Pliocene,
Ruscinian,
biostratigraphy.

& Jobert, 1828), *Hipparion crassum* Gervais, 1859, *Dihoplus schleiermacheri* (Kaup, 1832), *Sus arvernensis* Croizet & Jobert, 1828, *Alephis boodon* (Gervais, 1853) and *Tragoportax* sp. *Ursus boeckhi* and *Tragoportax* sp. are recognized for the first time in Alcoy. Although in earlier works two species of *Hipparion* were noted, we recognize only one species. Several specific (*Agriotherium insigne*, *Sus arvernensis*) and generic (*Dihoplus schleiermacheri*, *Alephis boodon*) determinations changed. The taxonomical revision of this material allows determination of the biochronological position of the macromammal locality of Alcoy-Mina that is placed in the early Pliocene (Ruscinian, MN14).

MOTS CLÉS
Mammalia,
Carnivora,
Artiodactyla,
Proboscidea,
Alcoy,
Espagne,
Pliocène,
Ruscinien,
biostratigraphie.

RÉSUMÉ
Macromammifères fossiles du gisement pliocène inférieur d'Alcoy (Espagne) et leur importance biostratigraphique.
Le gisement de macromammifères fossiles d'Alcoy (province d'Alicante, Espagne) est connu depuis la moitié du XIXe siècle. Dès lors son âge a été sujet de discussions ; il a été placé soit à la fin du Miocène soit au début du Pliocène. Quelques gisements de cette zone ont fourni des micromammifères : Alcoy-Barranco, Alcoy-N, Alcoy-4B et Alcoy-2, leur âge s'étend de la zone MN13 à la MN15, c'est-à-dire, depuis la fin du Miocène jusqu'au debut du Pliocène. Cependant, les grands mammifères ont tous été trouvés dans Alcoy-Mina, une vieille mine de lignite. Nous avons révisé ce materiel qui est conservé dans différentes collections européennes. La liste faunistique est la suivante : *Agriotherium insigne* (Gervais, 1859), *Ursus boeckhi* Schlosser, 1899, *Anancus arvernensis* (Croizet & Jobert, 1828), *Hipparion crassum* Gervais, 1859, *Dihoplus schleiermacheri* (Kaup, 1832), *Sus arvernensis* Croizet & Jobert, 1828, *Alephis boodon* (Gervais, 1853) et *Tragoportax* sp. *Ursus boeckhi* et *Tragoportax* sp. sont citées pour la première fois à Alcoy. Dans des travaux précédents deux espèces d'*Hipparion* ont éte signalées mais nous n'en reconnaissons qu'une seule. Quelques changements dans la classification ont eu lieu aussi bien au niveau spécifique (*Agriotherium insigne*, *Sus arvernensis*) que générique (*Dihoplus schleiermacheri*, *Alephis boodon*). La révision taxonomique de ce materiel permet de préciser la position stratigraphique du gisement de grands mammifères d'Alcoy-Mina qui est placé dans le Pliocène inférieur (Ruscinien, MN14).

INTRODUCTION: THE FOSSIL MAMMAL SITES FROM ALCOY

The continental Neogene outcrops near Alcoy (province of Alicante, Spain) are part of a wide lacustrine basin belonging to the internal Prebetic sector of the Betic chain, with an age ranging from upper Miocene to Pliocene. Montenat (1973: 1009-1014, fig. 153) presents a revision of a geologic section carried out in the vicinity of Alcoy by Durand Delga *et al.* (1964). Aguirre *et al.* (1975) make some remarks about the neogene-quaternary sequence and, more recently, the basin has been studied in detail by Pierson d'Autrey (1987).

The fossil mammal sites are found in alluvial facies that outcrop in the western edge of the basin (Fig. 1), and that are well visible along the El Gormaget ravine, in the limit between the districts of Alcoy and Cocentaina. The series is basically composed of reddish conglomerates interbedded with grey marls, which contain carbonate beds and lenticular lignite beds. It is in those marly lignitic beds, located in the area of the El Gormaget ravine where some vertebrate sites have been found

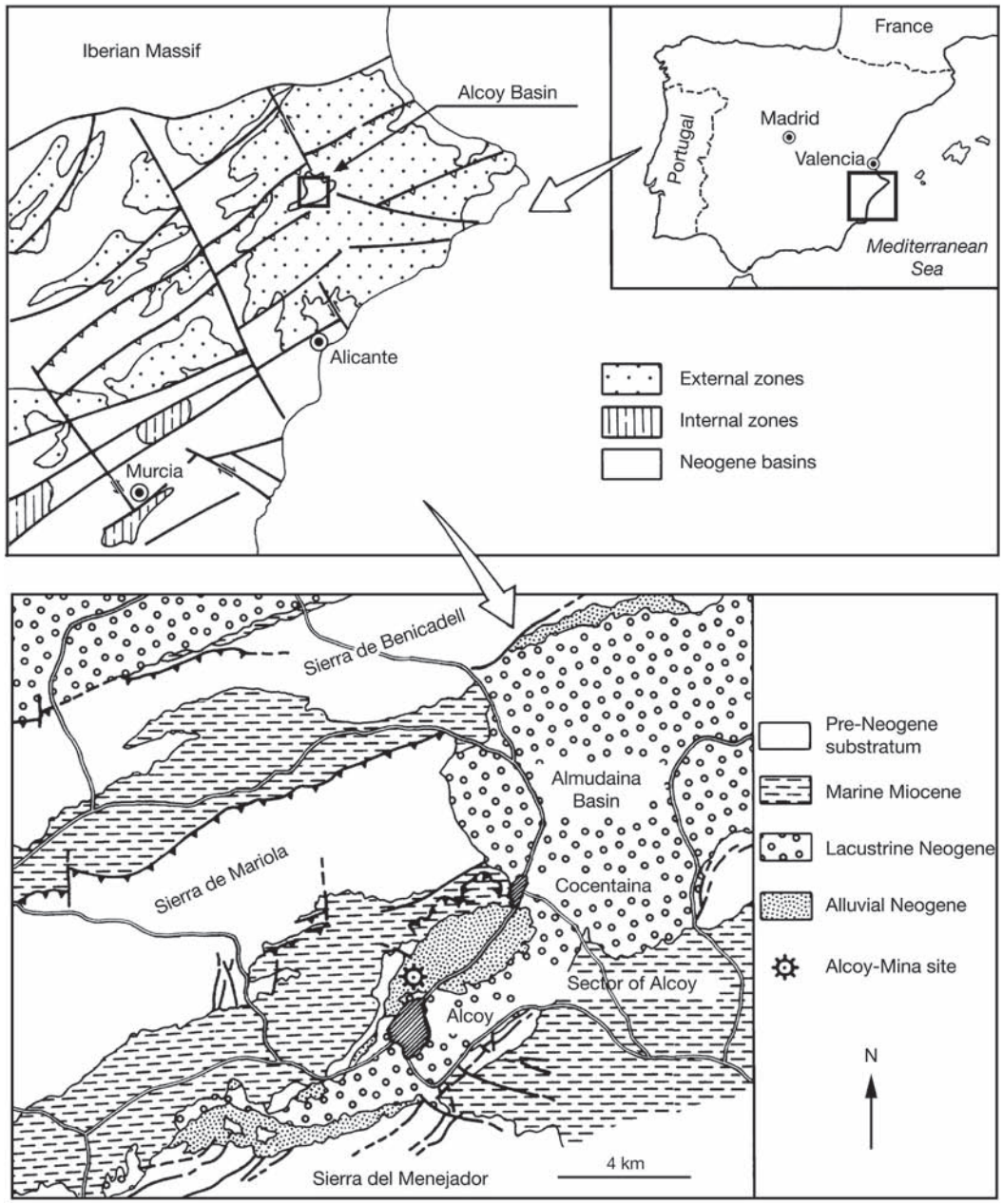

FIG. 1. — Diagram of the eastern sector of the Betic Chain with the location of the Alcoy-Mina site. Figures modified from Rodríguez Estrella (1977), Pierson d'Autrey (1987) and Santisteban *et al.* (1997).

(Santisteban *et al.* 1997). Microammal sites, some of them very rich in fauna and with ages ranging from the upper Miocene (MN13) to the lower Pliocene (MN15), have been cited, but the only site yielding large mammals has been the classical site of the old lignite mine of Alcoy (Alcoy-Mina).

In the present work, the paleontological materials coming from this locality are revised.

The site of Alcoy-Mina

Historically it is an important locality, since it is one of the earliest fossil mammal Spanish sites to be known and it was cited for the first time about the middle of the 19th century. In addition, it is scientifically very interesting since it is the type locality for the species *Alephis boodon* (Gervais, 1853). The macromammal remains were found in the old lignite mine of Alcoy and recovered from the coal beds exploited industrially from 1841 till 1862; later, in 1917, new galleries were open (Vicedo Sanfelipe 1920; Adrover 1969). The fossils obtained during this lapse of time are deposited in the following institutions: Muséum national d'Histoire naturelle (Paris), Museo GeoMinero (Madrid), Museo Nacional de Ciencias Naturales (Madrid), Museo de Ciencias Naturales de Valencia and in the Museu Arqueològic Municipal "Camil Visedo Moltó" (Alcoy). More historical references about this locality can be found in Aguirre *et al.* (1974) and in Montoya & Sánchez (2000).

Numerous authors have studied these fossils and the age of the site (latest Miocene or Pliocene) has been discussed for a long time. The first bibliographic reference corresponds to Ezquerra del Bayo (1850); later Gervais (1853) studied a sample of mammals from this locality, he established the species *Antilope*? *boodon* and cites, furthermore, the taxa *Hyaenarctos* sp., *Mastodon longirostris*, *Hipparion* sp., Ruminant indet. and *Sus palaeochoerus*.

In the first half of the 20th century, the site is mentioned in numerous works. Some of them make different corrections and contributions to the faunal list (see references in Aguirre *et al.* 1974). But it is in the second half of the 20th century when this list became more precise and clear, with the revision of the old materials and the study of new specimens carried out in several papers such as Crusafont & Villalta (1955), Alberdi (1974), Mazo (1977), Gromolard (1980b), Guérin (1980), Morales (1984) and Van der Made & Belinchón (1991).

According to these papers, the macromammal list of the Alcoy-Mina site was established as follows: *Agriotherium* sp., *Anancus arvernensis*, *Hipparion crassum*, *Hipparion gromovae*?, *Lartetotherium schleiermacheri*, *Korynochoerus palaeochoerus*, Cervidae indet., *Parabos boodon*.

The age of the site was considered as Pliocene for a long time because of the similarity of its faunal assemblage with that of the French sites of Montpellier and Perpignan. However, the discovery of the Spanish site of Venta del Moro (province of Valencia), proving the presence at the end of the Miocene (MN13) of genera classically considered as Pliocene, like *Agriotherium* and *Parabos*, which are found both in Venta del Moro and in Alcoy-Mina, and the scarcity of the materials described until that moment, favoured the hypothesis that Alcoy could also belong to the end of the Miocene (Morales 1984).

Since then, the question has been under discussion, and the discovery of micromammals has not clarified the situation because of the coexistence, very near the old mine, of both late Miocene and Pliocene micromammal sites.

Micromammal sites

The micromammal sites found in the area of El Gormaget, near the old lignite mine, are the following: a) latest Miocene: Alcoy-Barranco (Adrover 1969), Alcoy-N (López Martínez 1989) and Alcoy-4B (Freudenthal *et al.* 1998); and b) lower Pliocene: Alcoy-2 (Esteban Aenlle & Lacomba 1988).

Alcoy-Barranco

The Alcoy-Barranco site consists in an outcrop of lignitic beds near the old mine of Alcoy, discovered by Adrover in the mid-60's. The site is located, quoting Adrover (1969), in the "[…] barranco de El Gormaget, […] más arriba de la casa de El Gormaget de Torretes, cerca de uno de los hornos abandonados" (=[…] ravine of El Gormaget, […] above the house of El Gormaget de Torretes, near one of the abandoned furnaces).

The washing of sediments provided the first micromammals from this area, studied at first by Thaler *et al.* (1965) and later by Adrover (1969). In this later work the site is constituted as the type locality for the species *Ruscinomys lasallei* Adrover, 1969.

In both papers a Pliocene age was proposed for the site, but as it happened with the macromam-

mal fauna of Alcoy-Mina, this age was revised and assigned to the end of the Miocene because of the great similarity between the micromammal fauna of Alcoy-Barranco and that from the more recently found site of La Alberca (province of Murcia, Spain), whose age seems clearly to be MN13 (Mein *et al.* 1973; Morales 1984).

The faunal list of the Alcoy-Barranco site, according to the works of Thaler *et al.* (1965), Adrover (1969), Morales (1984) and López Martínez (1989), would be as follows:
– order Insectivora: *Galerix* aff. *exilis*, *Sorex* sp.;
– order Chiroptera: Chiroptera indet.;
– order Lagomorpha: *Prolagus* sp., *Trischizolagus* cf. *maritsae*;
– order Rodentia: *Eliomys* aff. *intermedius*, *Muscardinus* sp., *Parapodemus* sp., *Anthracomys ellenbergeri*, *Stephanomys medius*, *Apodemus* cf. *dominans*, *Ruscinomys lasallei*, *Cricetus kormosi*.

Alcoy-N
The Alcoy-N site is another outcrop of the lignitic beds in the same ravine as the former site, that has also yielded only micromammals. Its age is equally assigned to the end of the Miocene (MN13) and its faunal list, according to López Martínez (1989), is the following:
– order Lagomorpha: *Prolagus michauxi*, *Trischizolagus* cf. *maritsae*;
– order Rodentia: *Eliomys* sp., *Ruscinomys lasallei*, *Cricetus* cf. *kormosi*, Gerbilidae indet., *Occitanomys* sp., *Stephanomys* sp., *Apodemus primaevus*, *Paraethomys miocaenicus*, *P.* cf. *anomalus*.

Alcoy-4B
Freudenthal *et al.* (1998) mention Alcoy-4B and consider it as probably more recent than the classical site (they probably refer to Alcoy-Barranco). In that paper the following rodents are cited: *Apocricetus angustidens*, *A. barrierei*.

Alcoy-2
Close to one of the openings of the old mine and among marly sediments, is exposed a 30 cm thick lignitic bed from which a clearly Pliocene (MN15) fossil mammal assemblage has been obtained. The faunal list of this site, about which only a preliminary note (Esteban Aenlle & Lacomba 1988) has been published so far, is the following:
– order Insectivora: *Galerix* sp., Soricidae indet.;
– order Chiroptera: *Myotis* sp.;
– order Lagomorpha: *Prolagus michauxi*, *Trischizolagus* sp.;
– order Rodentia: *Stephanomys medius*, *Paraethomys jaegeri*, *P. meini*, *Apodemus gorafensis*, *A. dominans*, *Castillomys crusafonti gracilis*, *Trilophomys castroi*, *Ruscinomys* aff. *europaeus*, *Blancomys negletus*.

ABBREVIATIONS

In order to revise the fauna from the old mine of Alcoy (Alicante), the fossil remains from this locality deposited in the following museums have been analyzed:

MAA	Museu Arqueològic Municipal "Camil Visedo Moltó", Alcoy;
MCNV	Museo de Ciencias Naturales de Valencia;
MGM	Museo GeoMinero, Madrid;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris.

To make a comparative study, collections from different sites deposited in the following institutions have also been checked:

AFS	Accademia dei Fisocritici, Siena;
BSPHGM	Bayerische Staatssammlung für Paläontologie und Historische Geologie, München;
DSTUST	Dipartimento di Scienze della Terra, Università degli Studi di Torino;
HLD	Hessisches Landesmuseum, Darmstadt;
HUJ	Hebrew University of Jerusalem;
IPS	Institut Paleontològic M. Crusafont, Sabadell;
IPUW	Institut für Paläontologie der Universität, Wien;
LPUM	Laboratoire de Paléontologie, Université de Montpellier II;
MGUV	Museu de Geologia de la Universitat de València;
NMB	Naturhistorisches Museum Basel;
NMM	Naturhistorisches Museum Mainz;
NMW	Naturhistorisches Museum Wien;
NNML	Nationaal Natuurhistorisch Museum, Leiden;
UCM	Universidad Complutense de Madrid;
UCBL	Université Claude Bernard, Lyon;
ZMA	Zoölogisch Museum, Amsterdam.

Measurements

DAP	antero-posterior diameter;
DT	transverse diameter.

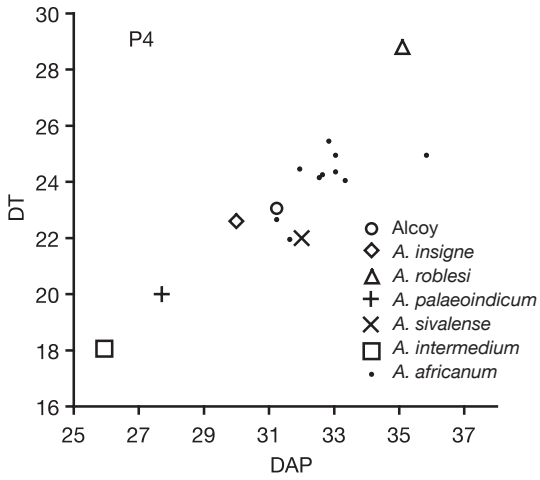

FIG. 2. — Bivariate plot of the P4 of *Agriotherium insigne* (Gervais, 1859) from Alcoy (cast MNHN), *A. insigne* from Montpellier (Gervais 1859b), *A. roblesi* Morales & Aguirre, 1976 from Venta del Moro (MGUV), *A. palaeoindicum* (Lydekker, 1884) and *A. sivalense* (Falconer & Cautley, 1836), *A. intermedium* Qiu & Schmidt-Kittler, 1983 and *A. africanum* Hendey, 1972. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Family URSIDAE Fischer de Waldheim, 1817
Subfamily HEMICYONINAE Frick, 1926
Genus *Agriotherium* Wagner, 1837

Agriotherium insigne (Gervais, 1859)

MATERIAL EXAMINED. — Fragment of a left maxilla with the alveolus of the first three premolars, the complete upper carnassial and an anterior fragment of the M1 (MNHN) (Gervais 1853: pl. IV, fig. 3; 1859a: pl. 81, fig. 2). Unfortunately, the original specimen, as well as other materials from the Alcoy mine, are lost. We could study a cast deposited in the MNHN.

MEASUREMENTS. — See Appendix: Table 1.

DESCRIPTION

The P4 is the only complete tooth preserved in the maxilla. It is a robust tooth, with a very well developed parastyle that shows a single internal edge continued in the lingual cingulum. The protocone is simple and consists of a backwards directed conical cusp, surrounded by a well marked basal cingulum. At the base of the metastyle is a strong lingual cingulum and another weaker one in the labial side.

DISCUSSION

The upper carnassial from Alcoy shows a morphology that can be considered typical of *Agriotherium*, a genus present in Europe from the latest Miocene (MN13) of Venta del Moro (Morales & Aguirre 1976; Morales 1984) until the upper Pliocene (MN16) of Vialette (Helbing 1932). When comparing with *Indarctos atticus* (Weithofer, 1888), it can be noticed that the P4 of this species generally presents a less developed parastyle, even relatively very reduced in some specimens from Concud (Crusafont 1962; Montoya *et al.* 2001). In addition, this parastyle shows two edges (lingual and labial) in *Indarctos atticus*, whereas the specimen from Alcoy only shows a lingual edge, a typical characteristic of *Agriotherium* (Petter & Thomas 1986). Moreover and in contrast to the studied specimen, the protocone in *I. atticus* is nearly always more or less bifurcated (Montoya *et al*. 2001).

The general morphology of the P4 studied in this work is very similar to that of the specimens of *A. palaeindicum* (Lydekker, 1884), *A. sivalense* (Falconer & Cautley, 1836) and *A. insigne* figured by Gervais (1859a: pl. 81), Lydekker (1884: pl. 30) and Frick (1926), and also to most P4 of *A. africanum* Hendey, 1972 (described by Hendey (1972, 1980). Its size falls within the range of the minimal values of *A. africanum*, and is very similar to *A. insigne* and *A. sivalense*. However, it is clearly far from a non-published tooth of *A. roblesi* Morales & Aguirre, 1976 from the latest Miocene (MN13) of Venta del Moro, which is a much larger and more robust tooth with a less individualized protocone. It also differs largely from *A. intermedium* Stach, 1957 from the lower Pliocene of Weze (Stach 1957) and of Xiaoxian (Qiu & Schmidt-Kittler 1983), a relatively small *Agriotherium* (Table 1; Fig. 2).

Although the taxonomical status of some of the species included in the genus has not been revised, the specimen from Alcoy can be assigned to *Agriotherium insigne*, described by Gervais (1859a: 27, 28, pl. 81, figs 3-7) and Viret (1939) from the lower Pliocene of Montpellier (France).

FIG. 3. — *Ursus boeckhi* Schlosser, 1899 from Alcoy: **A**, right M1 (Alc 20); **B**, fragment of left jaw with m1-m2 (Alc 21). Scale bar: 10 mm.

Subfamily URSINAE Fischer de Waldheim, 1817
Genus *Ursus* Linnaeus, 1758

Ursus boeckhi Schlosser, 1899
(Fig. 3)

MATERIAL EXAMINED. — Alc 20, right M1; Alc 21, fragment of left jaw with m1-m2 (MNHN).

MEASUREMENTS. — See Appendix: Table 2.

DESCRIPTION

The M1 is slightly longer than wide, with the paracone somewhat higher than the metacone, and strong metastyle more developed than the parastyle. Protocone not much separate from the metaconule, both forming a crest anteriorly bound to the parastyle and posteriorly to the metastyle. Labial cingulum moderately developed and lingually discontinuous.

The m1 is narrow and slender, having a fairly developed trigonid with low cusps. Low pyramidal paraconid, quite reduced metaconid. The posterior wall of the protoconid-metaconid is strongly excavated by occlusion with the M1. Short talonid bears a protruding hypoconid and a moderately sized entoconid.

The m2 is rather worn, it must have had low cusps. In the trigonid, the presence of a small paraconid is outlined, the protoconid is larger than the metaconid and both are situated face to face. Talonid built similarly to that of the m1.

DISCUSSION

The teeth from Alcoy show the typical morphology of the genus *Ursus*. This can be particularly observed in the m1, with a low trigonid, a pyramidal paraconid, a very reduced metaconid etc. However it presents fairly primitive features like a short talonid with strong predominance of the hypoconid with regard to the entoconid and a m1 longer than the m2. All these characteristics as well as the size, make the bear from Alcoy similar to *Ursus boeckhi* from the Romanian site of Baróth-Köpecz (Schlosser 1899: 87-89, pl. 12, figs 3-8), and clearly different from the more modern Pliocene bears (Depéret 1890; Viret 1954). *Ursus boeckhi* has also been quoted from the Hungarian site, Erdevidek (Maier von Maierfels 1928).

Ursus cf. *boecki* has been found in the Chinese site of Liang-Chia-Ho, province of Shanxi (Zdansky 1927). Although no data are available about the exact age of this locality, according to Flynn *et al.* (1991) the genus *Ursus* appears in Nanzhuanggou-Culiugou levels (Gaozhuang Formation) and in the Mazegou Formation, both belonging to the basin of Yushe, Shanxi province. Both formations have been dated by Flynn *et al.* (1991, 1997) as lower Pliocene.

Morlo & Kundrát (2001) consider *Ursus boeckhi* as a subspecies of *U. minimus* Devèze de Chabriol & Bouillet, 1827. In our opinion, the smaller size and more primitive morphology of *U. boeckhi* supports the maintenance of the species defined by Schlosser.

Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821
Genus *Sus* Linnaeus, 1758

Sus arvernensis Croizet & Jobert, 1828
(Fig. 4)

MATERIAL EXAMINED. — Right M3 (Van der Made & Belinchón 1991: pl. 1, fig. 7); left calcaneum (MAA). MPV 186 ALA-4c, left m3 (Van der Made & Belinchón 1991: pl. 1, fig. 1); MPV not numbered, right m1 (Van der Made & Belinchón 1991: pl. 1, fig. 2); MPV 186 ALA-4a, left I1 (Van der Made & Belinchón 1991: pl. 1, fig. 5); MPV 186 ALA-4b, right M1 (Van der Made & Belinchón 1991: pl. 1, fig. 3); MPV not numbered, fragment of left lower molar (Van der Made & Belinchón 1991: pl. 1, fig. 8); MPV not numbered, right M2 (MCNV).
Left M3 (MNCN) (Van der Made & Belinchón 1991: pl. 1, fig. 6).
Alc 22, upper C; P2; right M1; two left M2; right M2; right M3; left M3; right p4; right m1; two left m2; right m3 (MNHN).

NOMENCLATURE AND MEASUREMENTS. — The nomenclature and measurements follow Van der Made (1996). See Measurements in Appendix: Table 3.

DESCRIPTION

The m3 has a simple third lobe with pentaconid and pentapreconid placed on the axis of the tooth. Such morphologies occur in *Sus arvernensis*, *Propotamochoerus palaeochoerus* (Kaup, 1833), *Propotamochoerus* sp. (*sensu* Fortelius *et al.* 1996) and *Propotamochoerus provincialis* (Gervais, 1859), though in the latter species also a morphotype with a large hexaconid occurs. The specimen is smaller than its homologue in *P. provincialis* and the few specimens known of *Propotamochoerus* sp., but is in the metrical range of *P. palaeochoerus* and *S. arvernensis* (Fig. 5).

The m2 (Fig. 4A, B) and m1 are narrow as is common in the Suinae. They are smaller than the same teeth in *P. provincialis* and *P. palaeochoerus*, but are within the metrical ranges of their homologues in *Propotamochoerus* sp. and *S. arvernensis* (Fig. 5).

The p4 (Fig. 4C-E) has the protoconid placed close to the axis of the tooth. The metaconid is not well developed as an individual cusp and, though worn off, its tip must have been close to that of the protoconid, but placed more to the back. The hypoconid is relatively high, but still much lower than the protoconid. The protoprecristid ends just a little above the anterior cingulum. The morphology of the tooth is very similar to that of several species of *Propotamochoerus* Pilgrim, 1925, including *Propotamochoerus* sp. and *P. provincialis*, but differs from that of *P. palaeochoerus*, which has the metaconid developed as a separate cusp, placed more lingually. In *Sus arvernensis* from Villafranca, the hypoconid and the anterior end of the protoprecristid are higher, and the tooth resembles more the typical *Sus*-type p4. The p4 from Alcoy is smaller than the homologues of *P. palaeochoerus* and *P. provincialis*, but is close in size to *Propotamochoerus* sp. and *S. arvernensis*.

The M3 (Fig. 4I, L) has a third lobe that consists of a lingually placed pentacone and several minor cusplets. This is the common morphology in all the species considered here. The specimens from Alcoy are smaller than the M3 in *Propotamochoerus* sp. and *P. provincialis*, but comparable in size to those of *S. arvernensis* and *P. palaeochoerus* (Fig. 6).

The M2 (Fig. 4J, K) and M1 have the common suid morphology. They are smaller than the homologues in *P. provincialis* and *P. palaeochoerus*, the M2 is also smaller than in *Propotamochoerus* sp., and both specimens are within the ranges of *S. arvernensis*.

The P2 (Fig. 4F-H) is a low and elongate tooth. Behind the paracone, there is a smaller and lower metacone. There is a well developed anterior cingulum. It cannot be seen whether there was a mere postero-lingual cingulum, or a well developed protocone, since this part of the tooth is broken. The large anterior cingulum is more like in *Propotamochoerus* than in *S. arvernensis*. However, the small number of specimens available, may not well represent true variability. The specimen is a little longer than the P2 of *Sus arvernensis* and only slightly shorter than the shortest specimen of *P. palaeochoerus* and clearly shorter than in *P. provincialis* and seven specimens of *Propotamochoerus* sp.

The I1 has a well developed main cusp and a small, but well individualized, distal cusp. Both cusps are well worn and show a dentine islet. At this stage of wear they are still separated by a groove. The crown extends much distally from the distal cusp. At the labial side, the crown is high, higher than in *P. palaeochoerus*, but comparable to the other species.

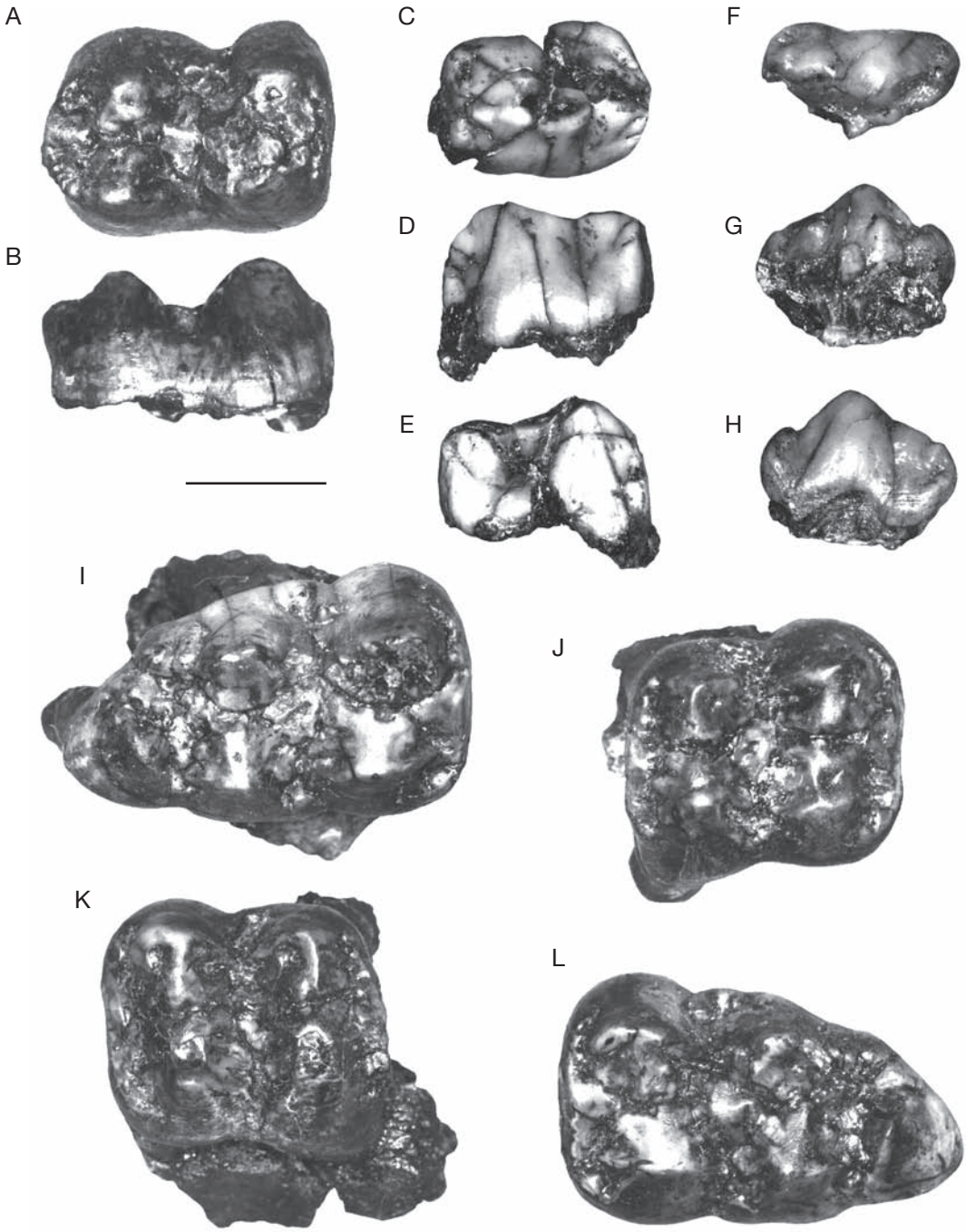

FIG. 4. — *Sus arvernensis* Croizet & Jobert, 1828 from Alcoy: **A**, **B**, left m2 (MNHN); **A**, occlusal view; **B**, lingual view; **C**-**E**, right p4 (MNHN); **C**, occlusal view; **D**, lingual view; **E**, labial view; **F**-**H**, right P2 (MNHN); **F**, occlusal view; **G**, lingual view; **H**, labial view; **I**, right M3 (MNHN), occlusal view; **J**, right M2 (MNHN), occlusal view; **K**, left M2 (MNHN), occlusal view; **L**, left M3 (MNHN), occlusal view. Scale bar: 10 mm.

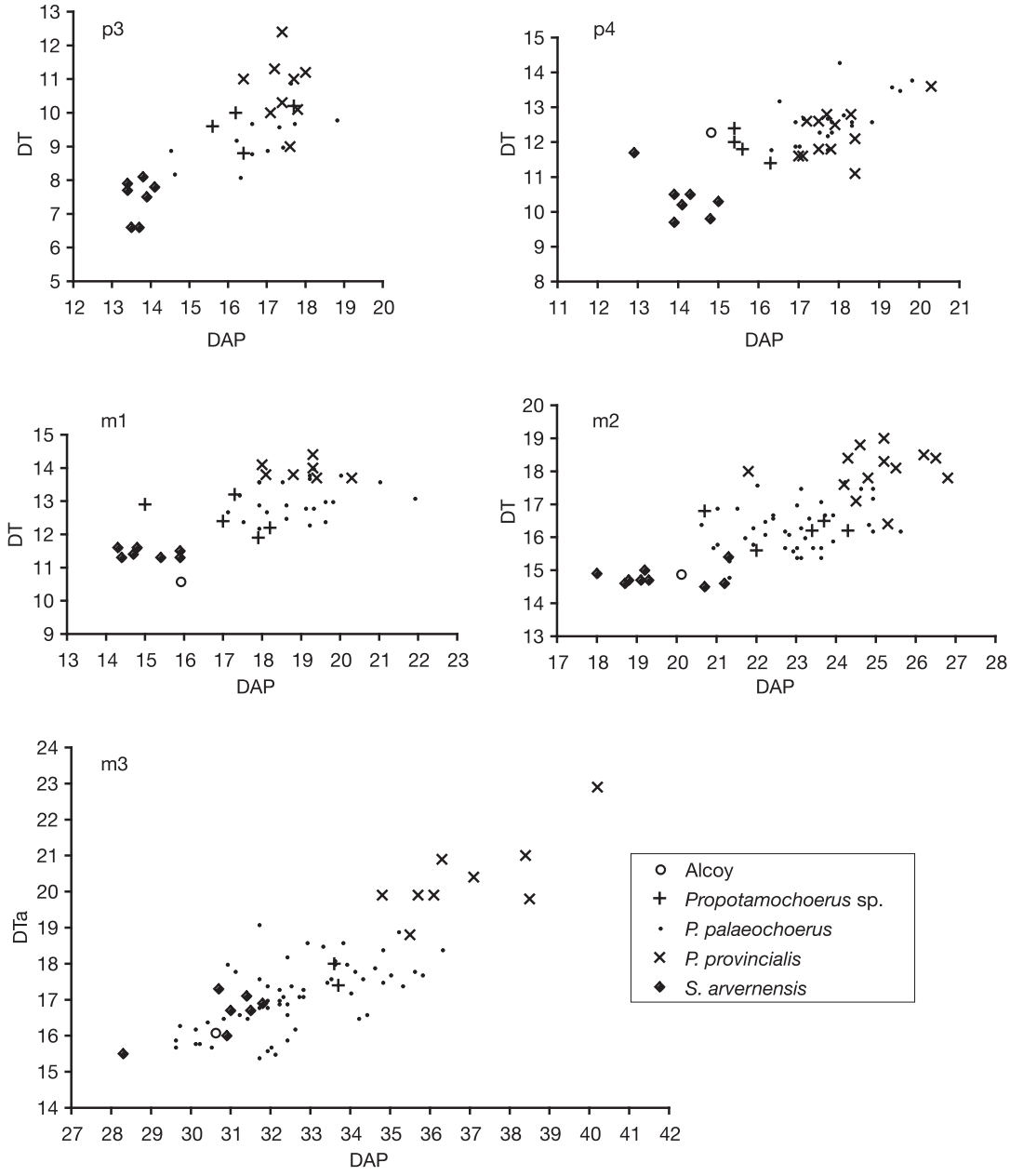

FIG. 5. — Bivariate plots of the lower cheek teeth of *Sus* Linnaeus, 1758 and *Propotamochoerus* Pilgrim, 1925: *S. arvernensis* Croizet & Jobert, 1828 from Alcoy (MCNV, MNHN); *S. arvernensis* from Perpignan (UCBL, NMB) and Villafranca de Asti (NMB); *P. palaeochoerus* (Kaup, 1833) from Eppelsheim (HLD), Wissberg (HLD, NMM), Gau Weinheim (BSPHGM), Esselborn (HLD), Castell de Barberá (IPS), Can Ponsic (IPS), Montréjau (NMB, UCBL), Hennersdorf (NMW), Wienerberg (NMW), Belvedere (NMW), Vösendorf (IPUW, NMW) and Magersdorf (IPUW); isolated specimens from Eppelsheim, Wissberg, Esselborn, Vösendorf and Montréjau are included, but for the rest of localities, only those specimens from tooth rows with premolars are included; *P. provincialis* (Gervais, 1859) from Venta del Moro (MNCN), Arenas del Rey (IPS), Montpellier (UCBL, NMB, LPUM), Roussillon (cast NMB) and Casino (AFS); *Propotamochoerus* sp. of MN11-13 from Maramena (studied in Mainz), Samos (NMW) and Baccinello V3 (NMB). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; **DTa**, transverse diameter of the anterior or first lobe.

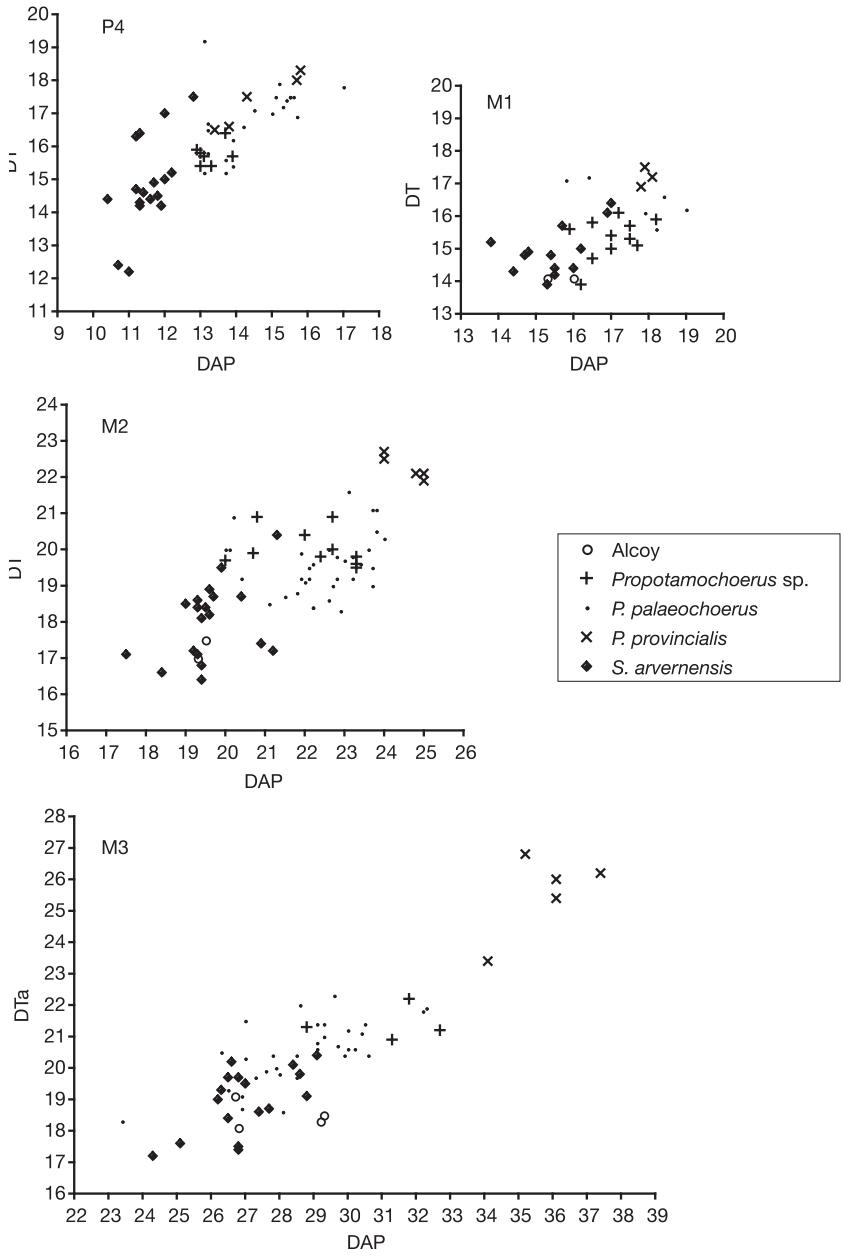

FIG. 6. — Bivariate plots of the upper cheek teeth of *Sus* Linnaeus, 1758 and *Propotamochoerus* Pilgrim, 1925: *S. arvernensis* Croizet & Jobert, 1828 from Alcoy (MCNV, MNHN, MNCN, MAA); *S. arvernensis* from Gorafe IV (IPS), Perpignan (UCBL, NMB, MNCM), Roussillon (casts in NMB), Villafranca de Asti (NMB), Trévoux (UCBL), Bra (DSTUST) and Piedrabuena (studied in MNCN); *P. palaeochoerus* (Kaup, 1833) from Eppelsheim (HLD), Wissberg (HLD, NMM), Gau Weinheim (BSPHGM), Esselborn (HLD), Castell de Barberà (IPS), Drôme (MGL), Münchener Flinz (BSPHGM), Isarbet (cast NMB), Pyrha (cast MNHN), Vösendorf (IPUW) and Wienerberg (NMW); isolated specimens from Eppelsheim, Wissberg, Vösendorf and Montréjau are included, but for the rest of localities only those specimens from tooth rows with premolars or from skull fragments are included; *P. provincialis* (Gervais, 1859) from Venta del Moro (MNCN), Montpellier (UCBL, NMB, Montpellier) and Casino (AFS, IGF); *Propotamochoerus* sp. of MN11-13 from Maramena (studied in Mainz), Samos (NMW), and Baccinello V3 (NMB). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; **DTa**, transverse diameter of the anterior or first lobe.

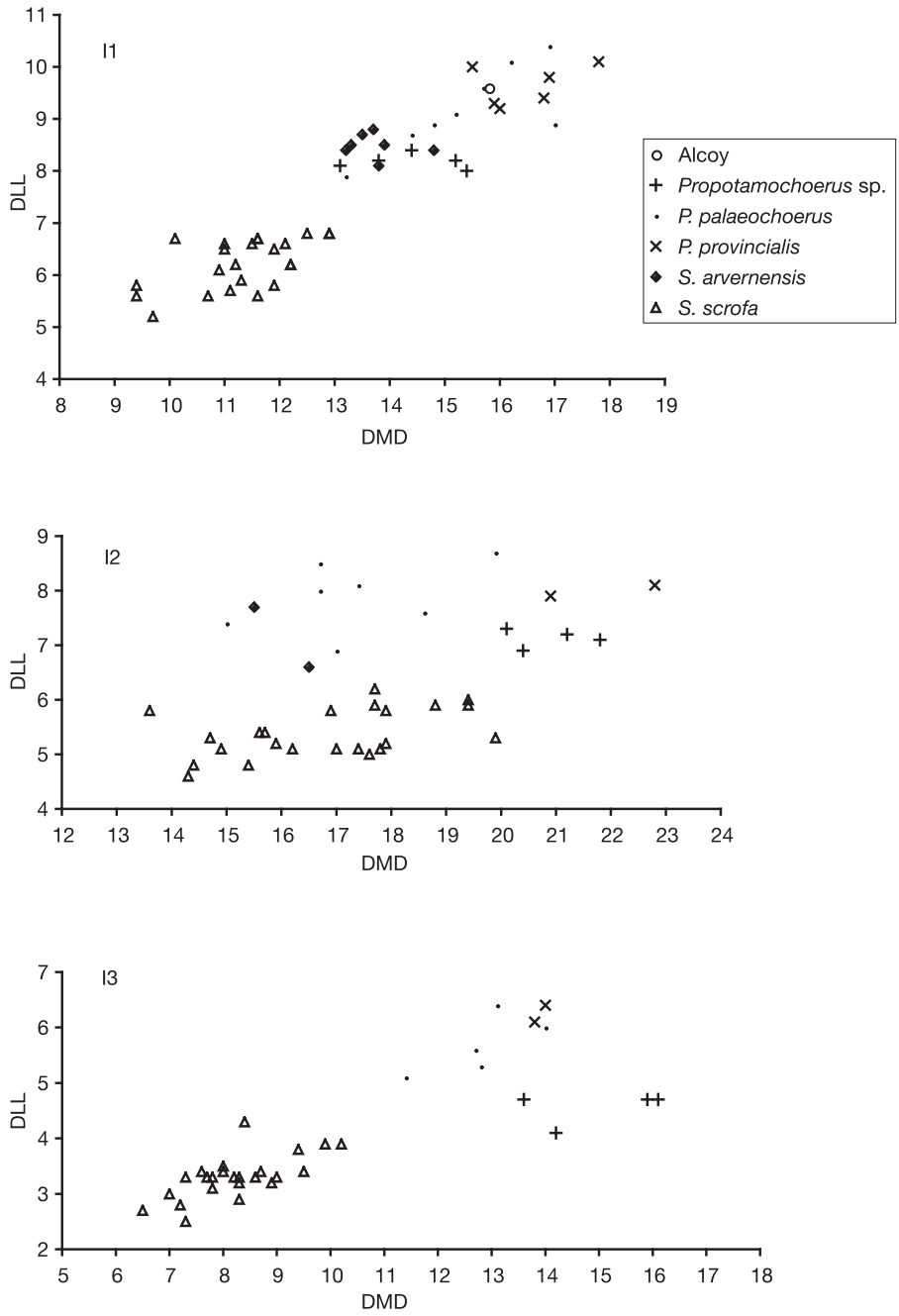

FIG. 7. — Bivariate plots of the upper incisors of *Sus* Linnaeus, 1758 and *Propotamochoerus* Pilgrim, 1925: *S. arvernensis* Croizet & Jobert, 1828 from Alcoy (MCNV), Perpignan (NMB) and Villafranca (NMB); *Propotamochoerus palaeochoerus* (Kaup, 1833) from Wissberg (NMM), Castell de Barberà (IPS), Hostalets (IPS), Montréjau (NMB) and Mariatal (IPUW); *Propotamochoerus provincialis* (Gervais, 1859) from Venta del Moro (MNCN) and Casino (AFS); *Propotamochoerus* sp. of MN11-13 from Maramena (studied in Mainz), Samos (NMW) and Baccinello V3 (NMB); recent *Sus scrofa* Linnaeus, 1758 from Spain (MNCN, UCM), the Netherlands (ZMA, NNML), Germany (ZMA, HUJ) and Israel (HUJ). Abbreviations: **DLL**, labio-lingual diameter; **DMD**, mesio-distal diameter.

There are not many specimens to compare with, but the tooth is slightly larger than the specimens available of *S. arvernensis* and *Propotamochoerus* sp. and within the ranges of *P. palaeochoerus and P. provincialis* (Fig. 7).

The calcanaeum lacks the upper part and the major part of the sustentaculum tali. What remains of the sustentacular facet is concave, as in suids and unlike in ruminants. The size is very close to that of three specimens of *S. arvernensis* from Villafranca, stored in the NMB.

DISCUSSION

The suid fossils from Alcoy have been assigned to *Hyotherium soemmeringi* (von Meyer, 1829), *Sus palaeochoerus* Kaup, 1833, *Hyotherium palaeochoerus* (Kaup, 1833) or *Korynochoerus palaeochoerus* (Kaup, 1833) [= *Propotamochoerus palaeochoerus* (Kaup, 1833) in present usage] and *Sus arvernensis* or its synonym *Sus minor* Depéret, 1890. Gervais (1853) described and figured specimens from Alcoy, which either got completely lost, or else, remnants of that material are the specimens from the MNHN collections described here. Van der Made & Belinchón (1991) described part of the suid material from Alcoy (MCNV, MNCN and MAA collections), noted that the size is closer to that of *Sus arvernensis*, but that I1 morphology was closer to that of *Propotamochoerus* ("*Korynochoerus*") than to a number of species of the genus *Sus*, though they had not studied *S. arvernensis* I1. They could not decide whether the p4 figured by Gervais (1853), was of the dicoryphochoerine type or *Sus* type, and assigned the material to *Korynochoerus palaeochoerus*.

Propotamochoerus palaeochoerus was considered to range from the late middle Miocene to the latest Miocene (Ginsburg 1980; Van der Made 1990a, b; Hellmund 1995). However, Fortelius *et al*. (1996) believed that *P. palaeochoerus* is replaced by a different species, *Propotamochoerus* sp., that is more related to the Chinese *P. hyotherioides*. Bonis & Bouvrain (1996) assigned material from the Greek Turolian to *P. hysudricus*, a species known from Pakistan. It seems to be accepted that a small *Propotamochoerus* occurs in Turolian deposits. It is not *P. palaeochoerus*, though it is not yet clear what species it is.

Given this setting, the Alcoy suid had to be reviewed. The p4 does not help us much in the assignation to either *Sus* or *Propotamochoerus*. Dimensions of the cheek teeth are closer to *S. arvernensis* than to the other species. *Sus arvernensis*, *Propotamochoerus* sp. and *P. provincialis* differ in general size, but have the same proportions. *P. palaeochoerus* has comparatively small M3 and M2 (a primitive character), and small P3 (an advanced trait). The suid from Alcoy follows the pattern of the former three species.

The I1 from Perpignan and Villafranca (both from the NMB) are unlike typical *Sus* incisors in having a well developed endocrista, having a small distal cusp, a less prominent lingual cingulum, in being less hypsodont and in being relatively large. In these characters they resemble *Propotamochoerus* more than other species of the genus *Sus*. *Sus arvernensis* has the I1 and I2 close in size and proportions to *Propotamochoerus palaeochoerus*; it is noteworthy that the I2 is relatively short (DMD, Fig. 7) and wide (DLL, Fig. 7). *Propotamochoerus provincialis* and in particular *Propotamochoerus* sp. have more elongate I2. *Sus scrofa* Linnaeus, 1758 has small I1 and I3 and narrow I2, though the species is larger than *S. arvernensis*. Also other species of *Sus*, including *S. strozzii* Meneghini, 1881 (which lost the I3), have relatively small upper incisors.

Tooth proportions and morphology, in particular of the incisors, suggest that *S. arvernensis* is not only the oldest species of *Sus* known, but that it is also still very close to the presumably ancestral genus *Propotamochoerus*. This closeness is reflected in similarities in many minor details of the dentition and is the reason why during a century and a half the asignation of the scarce material from Alcoy has been controversial. We assign the material here to *Sus arvernensis*.

Family BOVIDAE Gray, 1821
Subfamily BOVINAE Gray, 1821
Tribe BOVINI Gray, 1821
Genus *Alephis* Gromolard, 1980

Alephis boodon (Gervais, 1853)
(Fig. 8A-K)

MATERIAL EXAMINED. — Right P2; right m3; incomplete right m2; distal metacarpal; second phalanx (MAA).

ALA-2, M1, and ALA-3, right m3 (Gromolard 1981: pl. 3, figs 1, 2); incomplete left p4; incomplete left p3 (MCNV).
M-2101, left M3; M-2430, astragalus; M-2434, astragalus; M-2114, astragalus; M-693, second phalanx (MGM).
Alc 1, incomplete left m3; Alc 2, incomplete P4 (Gervais 1853: pl. V, fig. 2); Alc 3, incomplete left M; Alc 4, incomplete left m3; Alc 5, right m3 (Gervais 1853: pl. V, fig. 8); Alc 6, incomplete left m3 (Gervais 1853: pl. V, fig. 7); Alc 23, right m2 (Gervais 1853: pl. V, fig. 6); Alc 9, proximal left metacarpal; Alc 8, right astragalus (MNHN).

MEASUREMENTS. — See Appendix: Tables 4-7.

DESCRIPTION

The dentition of the Bovini from Alcoy is morphologically quite primitive when compared with the typical one of the current representatives of the tribe. Roughly speaking it is similar to that of the large sized Boselaphini although it shows slightly greater hypsodonty. The general characteristics are: moderate hypsodonty, lack of cement, quite flattened cones and conids.

Particularly the upper molars have a labial wall in which the external ribs of the cones are little marked, the lingual wall is bent and converges with the labial one. The fusion between the labial and lingual walls takes place at an advanced wear stage. The central valleys are half-moon-shaped and relatively simple. The ectostyle is poorly developed. Premolars with styles of moderate size, P2 quite long and with a well developed anterior lobe. The lower molars have a wavy lingual wall and conids with weak internal ribs.

Although the material is not very abundant, if we consider the size of the dentition (Table 4), the fossils from Alcoy could belong to only one species *Alephis boodon*, slightly larger than the Bovini from Perpignan, presently classified as *Alephis lyrix* Gromolard, 1980. Morphologically, there is some variability in the lower molars, particularly in the m3. In some individuals the caprine fold is strong whereas in others it is almost imperceptible, the development of the ectostylid is also variable.

Metacarpal: the specimen Alc 9 (Fig. 9C, D) is a 151 mm long proximal fragment of a left metacarpal. As in *Alephis lyrix*, the proximal epiphysis has both the facet for the triangular unciform and that of the magnotrapezoid, with convex dorsal and medial edges; nevertheless, this latter shows as in *Parabos cordieri* (Christol, 1832), a strong concavity (Gromolard 1981). The joint surface has a straight palmar edge and a more semicircular dorsal outline than in the afore-mentioned species, as a whole it shows great similarity to *P. soriae* Morales, 1984 from Venta del Moro.

The dorsal and palmar insertion tuberosities are very developed, especially that corresponding to the radial extensor muscle of the wrist; however there is no sign of a groove for the tendon of the lateral digit extensor muscle. The arterial dorsal groove is very thin and superficial. The palmar side of the diaphysis is flat except for the proximal central zone where there is a deep hollow.

The specimen M-698 consists of a distal fragment of metapodial, it is probably a metacarpal (Fig. 8J). The morphology of the distal ends corresponds to the type A of Köhler (1993) and is very similar, even in size, to *Bos gaurus* Smith, 1827, but in the fossil from Alcoy the dorsal grooves are smaller and the external condyles are narrower and with a convex distal edge. In the proximal limb there are more differences partly derived from the greater width of the present specimen. This is more evident in the diaphysis, with a much more compressed section.

The dimensions of both epiphyses (Table 5) coincide with those of *A. lyrix* and *A. tigneresi* Michaux, Aguilar, Calvet, Duvernois & Sudre, 1991 and are much greater than those of *P. cordieri* and to a lesser extent also greater than those of *P. soriae*. The values of the proximal and distal indices DAP/DT are in the average of the species from Roussillon, although they overlap with those of *P. cordieri*. On the contrary, in *P. soriae* these indices are clearly higher, although they are also within the range of variation of *A. lyrix*. In the diaphysis there is apparently a greater difference between *P. cordieri*, with a section more compressed anteroposteriorly, and *A. lyrix*, *P. soriae* and the species from Alcoy, which show greater DAP/DT values (Fig. 9D).

Astragalus (Fig. 8K): there are five astragali with different sizes and degrees of preservation; two of them are stored in the MNHN and three in the MAA. The smallest and most complete is M-2430.

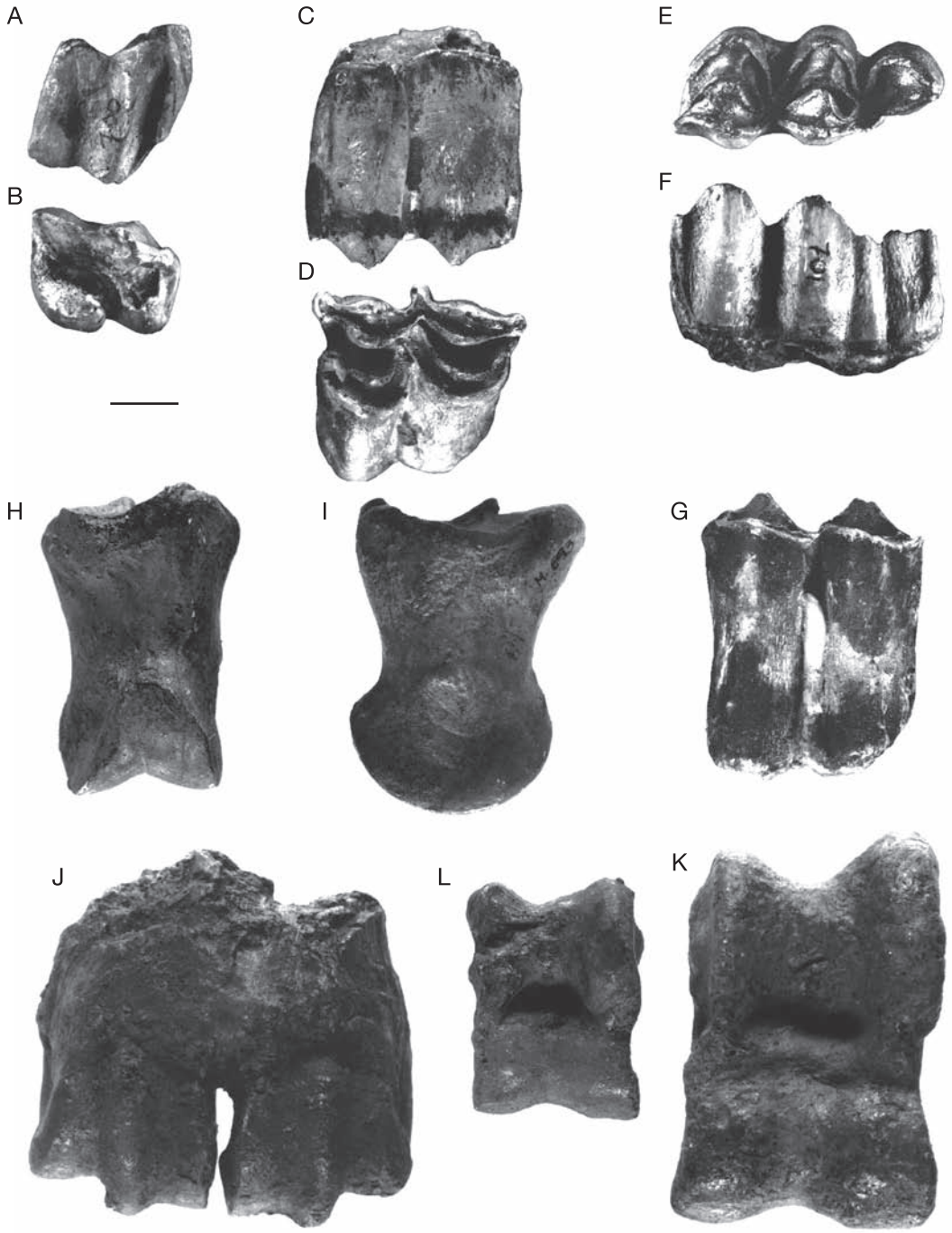

FIG. 8. — Bovidae from Alcoy: **A**-**K**, *Alephis boodon* (Gervais, 1852); **A**, **B**, right P2 (MAA); **A**, labial view; **B**, occlusal view; **C**, **D**, left M3 (M-2101); **C**, labial view; **D**, occlusal view; **E**, **F**, right m3 (MAA); **E**, occlusal view; **F**, lingual view; **G**, right m2 (MAA), labial view; **H**, **I**, second phalanx (M-693); **H**, dorsal view; **I**, lateral view; **J**, distal fragment of metacarpal (M-698), dorsal view; **K**, left astragalus (M-2430), dorsal view; **L**, *Tragoportax* sp., left astragalus (M-2435), dorsal view. Scale bar: 10 mm.

In all of them, the dorsal face has a strong medial process, a stop for the tibia, under which there is a relatively wide insertion surface that spreads transversely between the two trochleas. In the plantar face the stop facets are also very developed, although they are slightly variable, especially the distal lateral one. On the medial face the distal part is quite flat and the distal fossa is very small; the plantar process is little developed in the proximal part and the fossa is almost absent. However, in the lateral face, the projection of the edge of the plantar joint surface produces a very pronounced concavity and a strong proximal process more similar to that of *P. cordieri* than to that of *A. lyrix*. The outline of the proximal trochlea is, on the contrary, as in the latter species (Gromolard 1981). The distal trochlea has diverging medial and lateral processes; the condyles are similar in width and separated by a very broad central groove.

Morphologically they do not show remarkable differences with regard to the astragali of the type Boselaphini from the upper Miocene. Gromolard (1980b, 1981) pointed out the difficulties to morphologically distinguish the astragali of *Parabos cordieri*, *Alephis lyrix* and the species from Alcoy. They are also very similar to those of *P. soriae*, the differences being details like the greater development of the medial fossa or the distal lateral condyle which is more prominent in this species, or differences in the development of lateral face relief: more moderate in the species from Venta del Moro, similar in *Leptobos elatus* (Croizet, 1853) from Villarroya, much more extreme in *Bos* Linnaeus, 1758.

As for the size (Table 6), the variability of the astragali from the Alcoy site is comparable to that existing in *P. cordieri* and *A. lyrix* (measurements in Gromolard 1980b; Gromolard & Guérin 1980), within the range of variation of the latter, although the smallest individuals coincide in their minimal values and therefore overlap with *P. cordieri*. The ratio between the distal width and the lateral length is similar in these three species (Gromolard 1981), in *P. soriae* it is the same as the maximal values of *P. cordieri* and of *A. lyrix* and in *Leptobos elatus* (Villarroya) it is slightly higher (Table 6).

Second phalanx (M-693) (Figs 8H, I; 9A, B): the size and morphological characteristics are very close to those of a posterior phalanx of a female of *Bos gaurus* (MNCN). It has a mixed morphology with the predominance of moderately developed type B characters combined with some type A ones (Köhler 1993). Among type B characters are those related to the interdigital face, the relatively developed extensor dorsal process, the palmar and dorsal expansion of the distal joint surface, the absence of palmar sagittal fossa and the narrowing of the diaphysis in the median zone. Among type A characters are the presence of strong insertion marks for the interdigital ligaments and the superficial flexor of the fingers, and a large postarticular platform.

The outline of the proximal facets is closer to that of *P. cordieri* than to that of *A. lyrix* (Gromolard 1981), although in the fossil from Alcoy the external facet is less prolonged in the posterior part due to the strong reduction of the external tuberosity. This makes the proximal surface outline symmetrical. Something similar happens in *Bos taurus* Linnaeus, 1758. Between the two facets there is a strong edge that ends in a process in the posterior part.

The dimensions of M-693 (Table 7) are within the maximal values of *A. lyrix*, and even exceed them in length and proximal anteroposterior diameter. However the DT/DAP ratio in the epiphyses is close to the average value of these indices in *P. cordieri*, whereas in *A. lyrix*, the width is relatively greater; the opposite happens in *P. soriae* and in *B. gaurus*.

Discussion

Morphologically the dentition of the Bovini from Alcoy is clearly distinguished from that of *Leptobos* Rütimeyer, 1877, which is much more derived in the afore-mentioned characters, and is included in the same group as *Parabos* Arambourg & Piveteau, 1929 and *Alephis*. The differences from the species assigned to these two genera are difficult to evaluate because of the scarcity of the material from Alcoy and because some of the specimens figured by Gervais (1853) have not been found. The metrical differences pointed out by Gromolard (1980a, b) with regard to *A. lyrix* are minimal, and certainly the Bovini from Alcoy is close to the maximal values of *Alephis lyrix*, but only the P2 with a somewhat greater length and the M3 are out of the values

range of the species from Perpignan. According to our opinion the morphological differences pointed out by Gromolard (1980a, b) between Alcoy and Perpignan are not very clearly explained and some of them could simply be due to the larger size of the species from Alcoy. Nevertheless it is probable that the premolars of the species from Alcoy were less reduced.

The size of the preserved postcranial elements of the species from Alcoy is similar to that of their homologues of *A. lyrix*. They are respectively 20% and 15% larger than the average of *P. cordieri* (Gromolard 1981) and *P. soriae*. Although the sample is also poor in this case, there are both morphological and biometrical similarities with *A. lyrix*. Nevertheless some differences are also detected that make the identification of this species uncertain.

In the metacarpal, the shape and the proportions of the proximal facets are close to those of *A. lyrix*, whereas in the second phalanx this species has a less developed anteroposterior diameter in the epiphyses.

It shares with *P. cordieri* the presence in the metacarpal of a concave magnotrapezoid facet and convex distal condyles, but the species from Montpellier has a much more compressed diaphysis, with relatively smaller DAP and greater DT. This happens in a more pronounced way in *Bos*. In the phalanx there is a greater similarity in the shape of the proximal facets and in the proportions between this species and that of Alcoy with greater relative DAP values in the epiphyses. The same happens, more pronouncedly, in *Bos*.

Finally, the astragalus has a proximal trochlea as in *A. lyrix*, but a developed lateral proximal process like in *P. cordieri*. No biometrical differences between the three species were detected with the available data.

The species *Parabos soriae* shows the highest relative DAP values in the metacarpal and the lowest DT values in the second phalanx and in the astragalus.

The A/B morphology of the second phalanx, closer to B due to the lack of a groove for the lateral extensor of the fingers in the proximal metacarpal, suggest a somewhat less humid habitat than that attributed by Köhler (1993) to *P. cordieri* and *P. soriae*.

Gervais (1853) based *Antilope*? *boodon* upon dentition and postcranial remains from the lignite beds of Alcoy (Alcoy-Mina), as a species close to that from Montpellier, *Antilope cordieri*. Depéret (1890) used the specific term to name the large bovid from Perpignan as *Protoryx* (*Mesoryx*) *boodon*. In revising the group, Gromolard (1980a, b) concludes that the forms belong to different species; he names the first one as *Parabos*? *boodon* and creates a new genus and species, *Alephis lyrix*, for the second one.

Evidently there is an old systematic problem about the Alcoy material that particularly affects ruminants with cranial protuberances. The lack of information about the morphology of those protuberances in species whose definition is based upon dentition only creates important identification problems.

The case of the Bovini from Alcoy is paradigmatic. The dentition is only slightly larger than that of *Alephis lyrix*, and could be included within its maximal values, and morphologically is not very different despite the opinion of Gromolard (1980a, b). However we know nothing about the cranial morphology of *Antilope*? *boodon*, and this makes the situation uncertain, since different bovid species based on the morphology of their horns (as it happens in other families of ruminants) can have metrically and morphologically very close dentitions, and with limited samples, they could be practically undistinguishable.

As already mentioned, *Parabos* and *Alephis* show the same dental pattern well differentiated from that of *Leptobos* and the more modern Bovini, but also somewhat different from that of the Boselaphini. They are more derived than the latter in their incipient hypsodonty, in the early fusion of upper molar internal and external lobes, in the development of strong ectostyles, in the tendency to the reduction of premolars, particularly the P2, etc. We do not agree with the separation of these two genera in different tribes, Boselaphini for *Parabos* and Bovini for *Alephis*, as proposed by Gromolard (1980a, b) and by Gromolard & Guérin (1980). Besides the general large size and the same dental pattern, *Parabos* and *Alephis* also share great development of the horns, which, although retaining a subtriangular

transversal section, show a clear thickening trend. The basal position of *Parabos* with regard to the Bovini is well justified (Geraads 1992), but according to our opinion *Alephis* is more probably phylogenetically very close to *Parabos* (Duvernois 1990). Thus, forms like *Alephis tigneresi* (Michaux *et al*. 1991) indicate close relationship between these two genera.

In fact, the species from Alcoy is close to *A. tigneresi* because of the less reduced premolars and also the similarity of the postcranial skeleton, according to the scarce available data. Based on these reasons, we prefer to classify the form of Alcoy as *Alephis boodon*, thus keeping the validity of the other two species of the genus: *Alephis lyrix* and *Alephis tigneresi*.

Tribe BOSELAPHINI Simpson, 1945
Genus *Tragoportax* Pilgrim, 1937

Tragoportax sp.
(Fig. 8L)

MATERIAL EXAMINED. — Left m1 or m2 (MCNV).
M-2435, left astragalus; M-703, left astragalus; M-696, fragment of left calcaneus; M-699, distal fragment of humerus (MGM).
Alc 10, right astragalus; Alc 11, right astragalus; Alc 14, distal fragment of humerus (MNHN).

MEASUREMENTS. — See Appendix: Table 8.

DESCRIPTION
m1 or m2: unworn, quite hypsodont tooth with a small basal pillar, the internal wall is wavy and the stylids are well marked, particularly the metastylid and the anterior conid. There is a caprine fold of normal size. The external selenes are somewhat flattened and well separated.

Astragalus (Fig. 8L): the most complete specimen is M-703 and like the rest of them it is wide and shows the morphological features of the Boselaphini. Some of these features, shared with *Alephis boodon*, have also been mentioned in the description of that species. It is the case of the morphology of the medial and lateral faces: the first one is relatively flat and with little marked relief including the proximal process, and the second one has a strongly concave plantar half with a strong proximal process. The posterior lateral stop facet is very big and deep and the medial one is hardly visible. The distal trochlea has a wide throat centrally located, the edges are less divergent than in *A. boodon* and the lateral condyle is slightly more pronounced than the medial one.

These astragali from Alcoy are generally larger than those of the large representatives of *Tragoportax gaudryi* (Kretzoi, 1941) from Venta del Moro (Moyà 1983; Morales 1984) and Crevillente sites (Montoya 1994; Montoya & Alberdi 1995). This is in agreement with the dimensions of the lower molar (Table 8).

The fragments of calcaneus and humerus do not yield significant data. They are assigned to this species according to their sizes that correspond to that of the astragali.

DISCUSSION
Morphologies of lower molars that combine primitive features (strong stylids, wavy internal wall, separation of the internal and external conids) and relatively strong hypsodonty have been described in the Boselaphini from the upper Miocene of the Teruel basin (Alcalá 1994). This combination of characters has not been found in the other known bovids from the late Miocene and Pliocene of Spain. Therefore, despite the scarcity of the material, we classify this form as *Tragoportax* sp., with a size close to that of the *Tragoportax* from the Teruel basin.

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus *Hipparion* Christol, 1832

Hipparion crassum Gervais, 1859
(Fig. 10)

MATERIAL EXAMINED. — Right P2; two right M1-2; two left M1-2; left p2; two left p3-4; right p3-4; left m1-2; a McIII fragment; 1st and a 2nd phalanges, both of the finger III (MAA).
2433M, right P2; 2108M, left M1-2; 2126M, right M1-2; 2431M, left p3-4 (MGM).
Six lower teeth that could belong to the same indi-

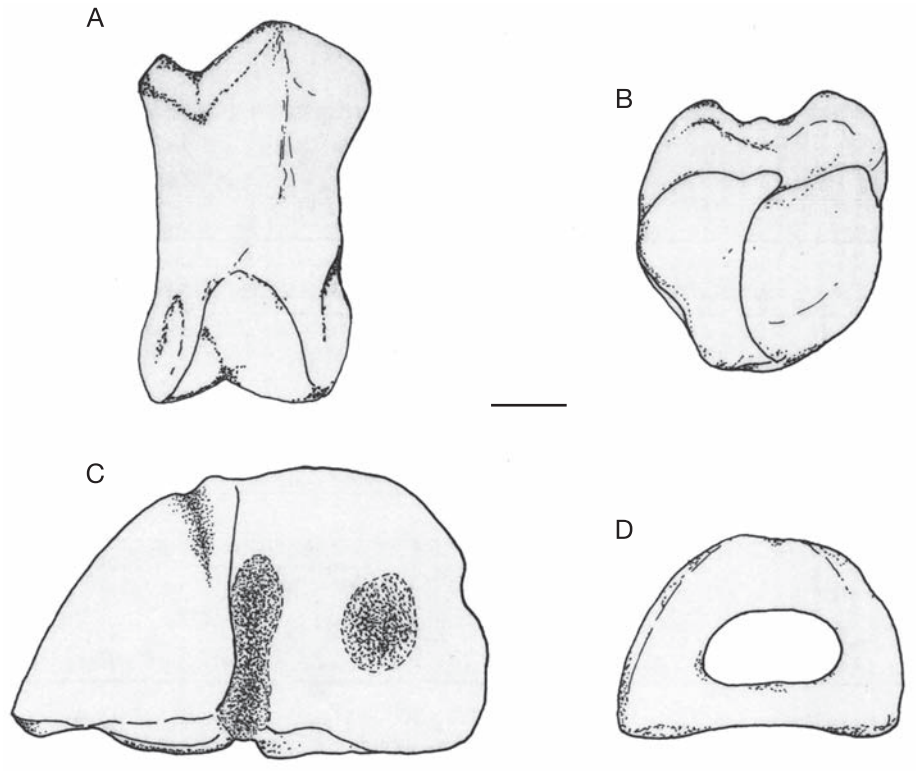

FIG. 9. — *Alephis boodon* (Gervais, 1852) from Alcoy: **A**, **B**, second phalanx (M-693); **A**, dorsal view; **B**, proximal view; **C**, **D**, left metacarpal (Alc 9); **C**, proximal view; **D**, transversal section. Scale bar: 10 mm.

vidual (right m1, m2, and m3 and left p4, m1 and m3) (MNHN).

MEASUREMENTS. — See Appendix: Tables 9 and 10.

DESCRIPTION

The measurements follow the recommendations of the "Hipparion Conference", New York 1981 (Eisenmann *et al*. 1988) and all are expressed in millimeters.

Tables 9 and 10 show most of the dimensions and some of the characters of the dental remains from the different collections studied. The remains are not very numerous and a clear difference between the size of molars and premolars can be observed. Quite a lot of cement is generally preserved in all of them.

The upper dental remains (Table 9) show some size differences that could reflect age differences of the animals (crown height), since their dimensions at the base of the crown (l/w) are more similar. Most of the teeth correspond to young adults. We could section them and study their characters at comparable wear degrees. The styles, are narrow, thin and well pronounced, both in molars and premolars, and are broader in premolars. Although the parastyle is not wide, it shows a groove-like notch. The protocone is oval, relatively small and sometimes with elongate or angular extremes when the wear is slight. With more advanced wear the protocone is clearly oval. The pli caballin has four or five folds (the only specimen that shows only one caballine fold corresponds to a little worn specimen that could not be sectioned because of its damaged state). The number of fossette folds is variable (Apre 5-6, Dpre 10-12, Apos 6-7 and Dpos 2). The hypocone shows a marked, more or

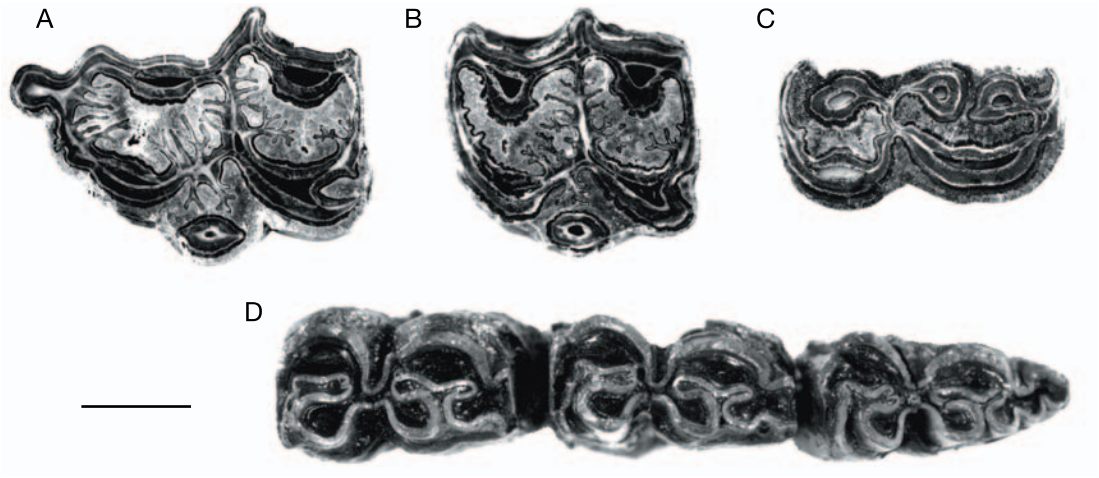

FIG. 10. — *Hipparion crassum* Gervais, 1859 from Alcoy: **A**, right P2 (MAA), reversed section; **B**, right M1-2 (MAA), reversed section; **C**, left p3-4 (MAA); **D**, right m1-m3 (MNHN). Scale bar: 10 mm.

less oval, open distal sinus (SD), that is oriented backwards.

The lower dental remains (Table 10) show size differences between the teeth stored in Paris and those from other collections. The remains from the MNHN, which belong to the same individual, correspond apparently to a smaller *Hipparion*. The length of the right series m1-m3 is 67.1 mm. In the left series are preserved the p3-4, an m1-2 and an m3. The teeth stored in MGM and in the MAA, almost all of them premolars, correspond to a larger animal. Most of them belong to very young individuals, without signs of wear, but already adults. In section they show a typical design with an internal curl particularly in the postflexid, the presence of a protostylid, a median robust size, and an elongate and somewhat angular metaconid-metastylid bow. The linguaflexid is open and shallow in premolars and closer and sharper in molars. The ectoflexid extends inside and nearly reaches the linguaflexid in molars. This does not happen in premolars.

The scarce postcranial skeleton remains, are only those stored in the MAA. A fragment of McIII, attributed by Alberdi (1974: pl. 7, fig. 1) to *Hipparion crassum*, must correspond to *Equus* Linnaeus, 1758, as pointed out by Eisenmann & Sondaar (1989) and Alberdi & Alcalá (1999). The assignation mistake could be due to the comparison with figure 1 of Depéret (1890). The dimensions of the 1FIII are: 1 = 62.2; 2 = 56.3; 3 = 31.7; 4 = 41.7; 5 = 32; 6 impossible to measure; 7 = 36.2; 8 = 22; 9 = 27.5; the dimensions of the 2FIII are: 1 = 44; 2 = 32; 3 = 36.4; 4 = 42.2; 5 = 27; 6 = 40. In addition there are a fragment of calcaneus and another fragment of a metapodial distal end, but they are so damaged that they do not yield any significant data.

DISCUSSION

The wear pattern of the upper teeth shows deep, complex and numerous lateral folds of the fossettes as is characteristic in *Hipparion crassum*. The protocone is oval and small if compared with the tooth; the pli caballin is complex (four or five more or less branched folds); the hypocone is oval, small and open, with a deep distal sinus, less deep as wear advances, and with a less marked lingual sinus that totally disappears with the wear. All this and the size of the teeth relate the material from Alcoy-Mina to a robust medium-sized *Hipparion*. In the same way, the morphology of the lower teeth, with a robust protostylid not always reaching the wear surface (because it is partly masked by the presence of cement), the angular and elongate metaconid-metastylid bow, the internal curl par-

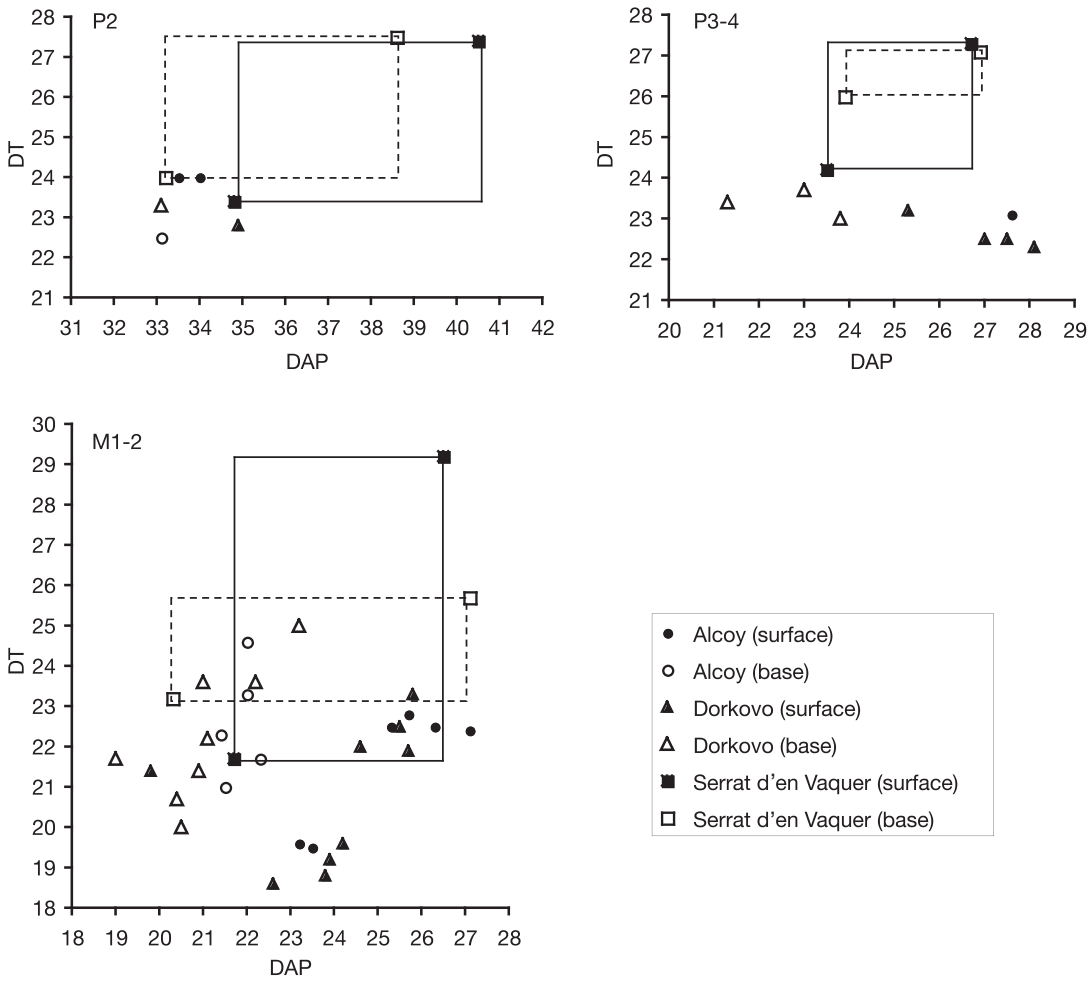

FIG. 11. — Bivariate plots of the upper cheek teeth of *Hipparion crassum* Gervais, 1859 from Alcoy and Serrat d'en Vaquer, and *Hipparion* cf. *crassum* from Dorkovo. Measures taken at the base and at the occlusal surface. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

ticularly in the postflexid, as well as the presence of pli caballin or ptycostilid more pronounced in premolars than in molars, also indicate a robust medium-sized animal.

Most of the studied teeth are homogenous and their dimensions are totally within the distribution of the remains from Serrat d'en Vaquer (Perpignan, Roussillon, France), the type locality of *H. crassum*. In Tables 9 and 10 are also included the dimensions of the remains from Dorkovo (Thomas *et al.* 1986; Alberdi & Alcalá 1999), determined as *Hipparion* cf. *crassum*. The plots based on the dentition dimensions (length and width at the surface) show that the remains from Alcoy and Dorkovo are slightly smaller than those from the French localities of *H. crassum*, but the dimensions are very similar if taken at the base of the tooth. This is clearly observed when the upper molars (M1 and M2), on the one hand, and the lower molars (m1 and m2), on the other hand, are compared (Figs 11; 12).

The comparison of the morphological characters of the dentition from Alcoy with those of other

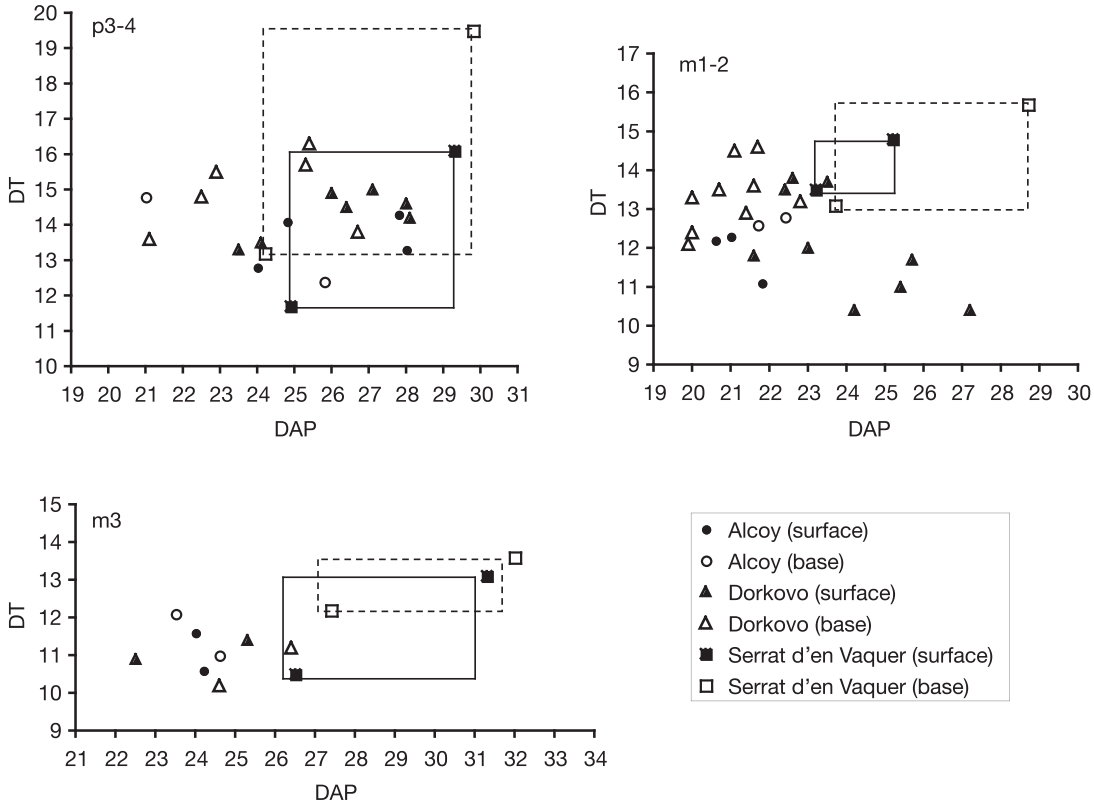

FIG. 12. — Bivariate plots of the lower cheek teeth of *Hipparion crassum* Gervais, 1859 from Alcoy and Serrat d'en Vaquer, and *Hipparion* cf. *crassum* from Dorkovo. Measures taken at the base and at the occlusal surface. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

Pliocene populations of *Hipparion*, indicates that the upper dental remains have narrower and more pronounced styles (parastyle and mesostyle) than the rest of Spanish Pliocene forms studied by Alberdi & Alcalá (1999). This can be seen both in the parastyle and in the mesostyle, although the first one is generally wider than the second one, and both are wider in premolars than in molars. Also the protocone of the remains from Alcoy is comparatively smaller than that of other Spanish Pliocene forms in which it is elongate and larger, relative to tooth size. As for the lower teeth, in the Pliocene dolichopodial populations of *Hipparion* (and depending on the wear degree of the teeth), the ectoflexid crosses the isthmus and approaches the linguaflexid both in premolars and in molars, whereas in the remains from Alcoy this can only be observed in molars.

The lower teeth stored in the MNHN are apparently smaller and more slender than the specimens from Alcoy stored in the other institutions. But, as already mentioned, it can be observed in the plots (Figs 11; 12) that the differences between the compared populations of *Hipparion* disappear when the utilized dimensions have been taken at the base of the teeth. The result is that these differences depend on the age of the animal and are not due to real size differences in the studied sample.

There are only two remains of the postcranial skeleton (1FIII and 2FIII). Both are robust and are within the range of variation of the phalanges of *H. crassum* from Perpignan and Le Soler (Lit de la

Têt) (Alberdi & Aymar 1995). On the other hand, they are identical, both in size and robustness to those of *H.* cf. *crassum* from Dorkovo (Bulgaria).

All the mentioned characters indicate that these remains correspond to a robust medium-sized *Hipparion* with primitive (abundant and deep folds) and relatively brachydont cheek teeth. In addition, the only remains of the appendicular skeleton indicate a strong structure similar to that of *Hipparion crassum*, which characterizes the morphotype 4 of Alberdi (1989), who considered it as representative of the lower Ruscinian (Alberdi 1986, 1989). This species was described by Depéret (1890: 76, 77) from Perpignan (Roussillon, France) placed by Mein (1990) and De Bruijn *et al*. (1992) in the upper Ruscinian (MN15). The structure and morphological characters of this *Hipparion* indicate a more covered environment and with a softer substratum than those of the Pliocene dolichopodial forms of the Iberian Peninsula (Alberdi & Alcalá 1999). Besides this, the presence of a mastodont, *Anancus* Aymard, 1855, an animal that feeds on branches and leaves and is generally associated with more wooded environments, could indicate a relatively covered environment on soft ground in the surroundings of the Alcoy site.

Family RHINOCEROTIDAE Owen, 1845
Subfamily RHINOCEROTINAE Owen, 1845
Genus *Dihoplus* Brandt, 1878

Dihoplus schleiermacheri (Kaup, 1832)
(Fig. 13)

MATERIAL EXAMINED. — Right P3; left m2 (MAA).
2118M, left lower molar (MGM).
Alc 24, right p3; Alc 25, left p4; Alc 26, right m1; Alc 27, left m1 (Gervais 1853: pl. IV, fig. 9); Alc 28, right m3; Alc 29, fragment of left m3 (MNHN).

MEASUREMENTS. — See Appendix: Table 11.

DESCRIPTION
The only upper tooth found is a P3 that lacks its labial part. The protoloph is thin and oriented obliquely backwards. It is joined to the metaloph and closes lingually the anterior valley. The metaloph is thin and curiously semilunar, the back point being joined to the posterior wall. This arrangement is very unusual in the Rhinocerotidae. Apparently it is only known in *Dicerorhinus* Gloger, 1841 and *Dihoplus*. This can be seen in *Dicerorhinus etruscus* (Falconer, 1868) from Sénèze figured by Guérin (1980: pl. 15, fig. C1), the P3 of *Dicerorhinus miguelcrusafonti* Guérin & Santafé, 1978 from Layna (Guérin & Santafé 1978: pl. 1, fig. G) and *D. schleiermacheri* from La Roma (Cerdeño 1989: fig. 30).

The p3 lacks the posterior part of the second lophid. The metalophid consists of three elements perpendicular to each other; the anterior element is clearly transversal; the larger median one, forms its labial wall. This labial wall is flat and nearly longitudinally oriented. The anterior valley is important. The hypolophid is more curved. The median labial groove is, at the base only, a wide depression that narrows towards the apex to form a real groove.

The p4 differs from the p3 in its metalophid, with the median part more obliquely oriented and the larger posterior part more obliquely (but backwards) oriented. In the posterior part, the hypolophid consists of three elements: two labial elements that form a very neat angle of 120°, and a third distal one, short and transversely oriented.

The three lower molars are of the same kind. The metalophid is not very different from that of the p4. On the contrary, the hypolophid consists of only two elements. The anterior one is short and longitudinally oriented. The posterior one is twice as long and obliquely oriented. These two elements form an angle of more or less 120°.

REMARKS
All these teeth could belong to the same individual. However the right m3, which is complete, shows insignificant wear of the hypolophid, whereas the fragment of left m3, which is the postero-lingual extremity of the hypolophid, is severely worn. It must be admitted that the left m3 had a growth advance of roughly 9 mm over the right m3.

DISCUSSION
The teeth of the Rhinocerotidae from Alcoy belong to the species *D. schleiermacheri*, whose type is a complete skull from Eppelsheim (MN9) in rhenish

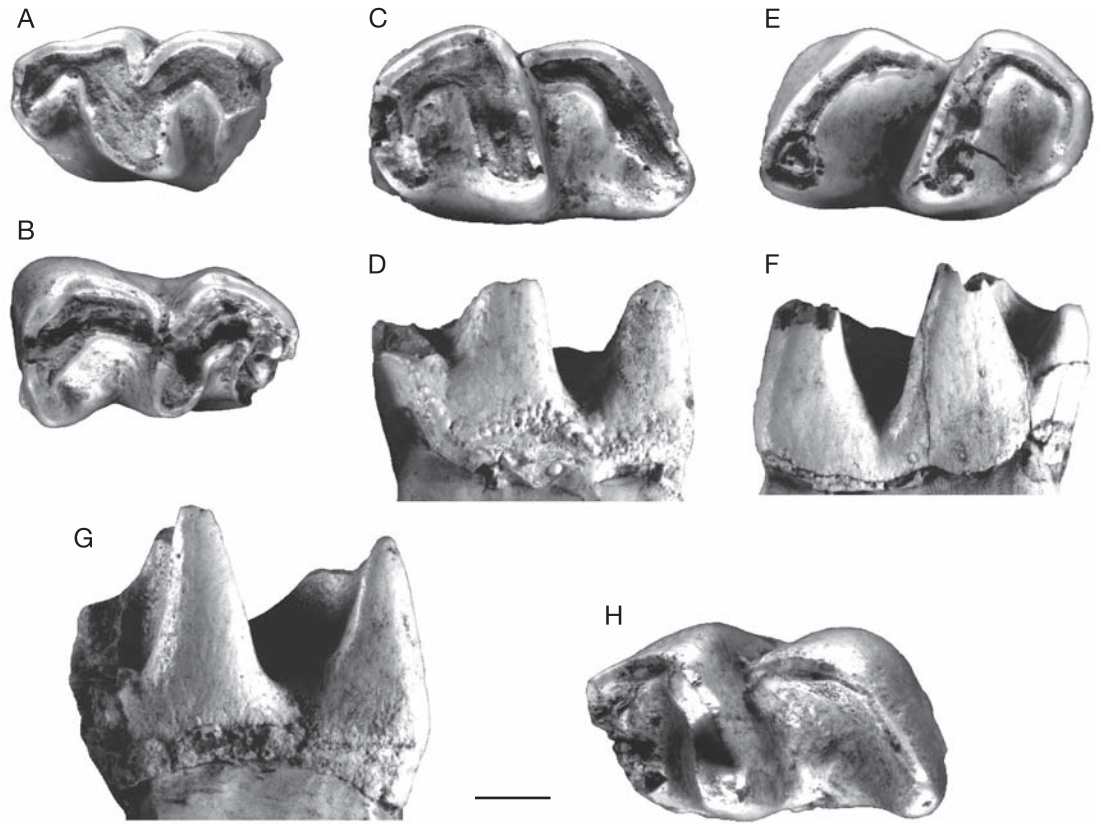

FIG. 13. — *Dihoplus schleiermacheri* (Kaup, 1832) from Alcoy: **A**, right p3 (Alc 24), occlusal view; **B**, left p4 (Alc 25), occlusal view; **C**, **D**, right m1 (Alc 26); **C**, occlusal view; **D**, lingual view; **E**, **F**, left m1 (Alc 27); **E**, occlusal view; **F**, lingual view; **G**, **H**, right m3 (Alc 28); **G**, lingual view; **H**, occlusal view. Scale bar: 10 mm.

Hesse, described and figured by Kaup in 1832 and 1834. The teeth found, including the peculiar P3, are morphologically identical and the dimensions are within the variation limits of the species as given by Guérin (1980).

The species was at first attributed to the genus *Rhinoceros* Linnaeus, 1758. Brandt (1878) established the genus *Dihoplus* on the base of this species. Zittel (1893) admitted *Dihoplus* as a subgenus of *Rhinoceros*, and the name *Dihoplus* was abandoned. Viret (1955) and Guérin (1980) included the species in the genus *Dicerorhinus.* Heissig (1999) again used the generic term *Dihoplus* for the species from Eppelsheim. We will follow this determination since the skull of the current *Dicerorhinus sumatrensis* (Fischer, 1814) is clearly different from that of *Dihoplus schleiermacheri.* This latter is lower, more elongate and with a lower occipital part. The zygomatic apophysis is less elevated in the posterior part and the nasal recess is less open in lateral view. In addition, the mandible is also different with a concave and not convex lower edge. Therefore, they are two different genera.

As for what concerns the stratigraphic distribution, *Dihoplus schleiermacheri* has been found so far in 25 localities (rhenish Germany, Switzerland, France and Spain), all of them considered as Vallesian or Turolian (Guérin 1980; Cerdeño 1989). The specimen from Venta del Moro (Morales 1984: fig. 12) is the most similar to that of Alcoy. They have in common the slightly oblique orientation of the median part of the metalophid, which is generally

FIG. 14. — *Anancus arvernensis* (Croizet & Jobert, 1828) from Alcoy, left m3 (332M), occlusal view. Scale bar: 10 mm.

longitudinally oriented. It is interesting to remark that Venta del Moro is placed between the Turolian and the Ruscinian.

Order PROBOSCIDEA Illiger, 1811
Suborder ELEPHANTOIDEA Osborn, 1921
Family GOMPHOTHERIIDAE Cabrera, 1929
Subfamily ANANCINAE Hay, 1922
Genus *Anancus* Aymard, 1855

Anancus arvernensis (Croizet & Jobert, 1828)
(Fig. 14)

MATERIAL EXAMINED. — Different fragments of molars and a tusk fragment (MAA).
332M, left m3 (MGM).

MEASUREMENTS. — See Appendix: Table 12.

DESCRIPTION

Left m3 (332M) probably had five lophs and a talonid with four tubercles. The first loph is broken. The tooth shows intermediate wear. The entoconids show a binary division, the ectoconids are trefoiled and the central conules are strong and always between the ectoconids. The talonid presents a clear angular arrangement that can be neatly observed along the tooth. The wear is more pronounced in the labial edge, and diminishes backwards from the first lophid, in the fourth loph the wear has started but without giving rise to the typical trefoiled figures. In the internal edge the wear reaches the first three lophs. The dimensions of this specimen are shown in Table 12.

Among the material stored in the MAA there are seven dental fragments that correspond to different teeth and show different wear degrees, although some of them could belong to the same individual. Three of them correspond to the talon of the tooth and do not fit the rest of the fragments. All are bunodont and display a clear anancoidy (angle formed by the arrangement between entocones and ectocones). The very robust talon forms a sort of tubercle platform, and the last loph is clearly anancoid with a maximal width of 70 mm and a height between 45 and 50 mm. This talon is 58.7 mm wide and 40 mm high. The largest fragment consists of two and a half lophs, anancoid, little worn, without showing wear, and with clearly bunodont cones. Another of the studied fragments consists in part of a cone, where the enamel characteristics of these teeth are clearly observed: very thick and fibrous or laminated, but not rugose.

The fragment of tusk actually corresponds to small fragments assembled as the apical part of the tusk, where remains of the enamel band can be observed.

DISCUSSION

Despite the scarcity of the dental material, the features both of the molar 332M and of the fragments in the MAA and the kind of enamel are

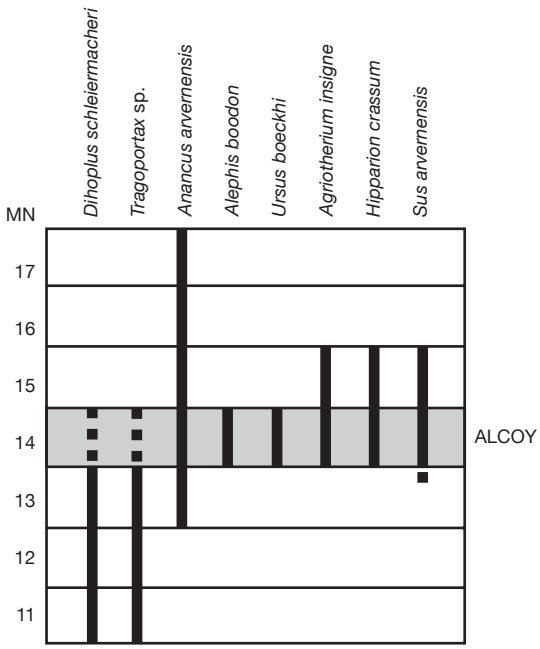

FIG. 15. — Biochronological distribution of taxa represented in the Alcoy fauna.

very characteristic, and can belong only to *Anancus arvernensis*, described and figured by Croizet & Jobert (1828: 133-138, pl. I, figs 1-4, pl. II, fig. 7) from the upper Pliocene (MN16) of Perrier (Auvergne, France). This form is found in the Iberian Peninsula from the Turolian and reaches the lower Villafranchian in the site of Las Higueruelas (Ciudad Real). In France and Italy it lived until the middle Villafranchian-earlier late Villafranchian, thus coexisting probably with *Mammuthus meridionalis* (Nesti, 1825).

BIOSTRATIGRAPHY AND COMMENTS ABOUT THE FAUNA

Based on the study of the materials of large mammals from the site of Alcoy-Mina stored in different institutions, the faunal list is as follows:
– *Agriotherium insigne* (Gervais, 1859);
– *Ursus boeckhi* Schlosser, 1899;
– *Sus arvernensis* Croizet & Jobert, 1828;
– *Alephis boodon* (Gervais, 1852);
– *Tragoportax* sp.;
– *Hipparion crassum* Gervais, 1859;
– *Dihoplus schleiermacheri* (Kaup, 1832);
– *Anancus arvernensis* (Croizet & Jobert, 1828).

Ursus boeckhi and *Tragoportax* sp. are recognized for the first time in the site of Alcoy-Mina; the rest of species have already been cited previously, either with a different specific name, like *Agriotherium insigne* (instead of *Agriotherium* sp.) and *Sus arvernensis* (instead of *Korynochoerus palaeochoerus*), or with different generic names, like *Alephis boodon* or *Dihoplus schleiermacheri*. The presence of *Ursus boeckhi* should be especially remarked, since it could be the oldest citation of this genus; the species is clearly more primitive than those represented in the upper Ruscinian sites (Perpignan and Layna).

In the continental upper Miocene of the Iberian Peninsula the youngest site with a good large mammal representation is Venta del Moro (Morales 1984). The occurrence of *Paraethomys* correlates it with zone M3 from Van Dam (1997), and its absolute age has been estimated in about 5.8 my (Opdyke *et al.* 1997). Above it, next to the Mio-Pliocene limit, several localities like Almenara M (Agustí 1990; Köhler *et al.* 2000), Purcal (Martín Suárez *et al.* 1998) and Zorreras (Martín Suárez *et al.* 2000) have provided especially micromammals. In this interval the entrance of Gerbilidae has been detected in the Iberian Peninsula (Agustí & Llenas 1996). Alcoy-Mina shares with Venta del Moro the presence of the species *Dihoplus schleiermacheri* and *Anancus arvernensis* (Cerdeño 1989; Mazo 1996). However, *Agriotherium insigne*, *Ursus boeckhi* and *Hipparion crassum* have only been mentioned so far in the early Pliocene. The genus *Agriotherium* is well recorded in Venta del Moro, but with a different species (Morales & Aguirre 1976; Morales 1984). On the other hand, *Sus arvernensis* is a typical Pliocene species although there are some indications of its appearance at the end of the Miocene. According to the present knowledge about the biochronology of the upper Miocene-lower Pliocene, together with the fact that in the surroundings of one of the old mine openings there is a clearly Pliocene bed (Alcoy-2), it seems logical to assign Alcoy-Mina to the early Pliocene, and it can be regarded as the

youngest site containing *Dihoplus schleiermacheri* and *Tragoportax* sp.

Nevertheless, both the afore-mentioned appearance in Alcoy-Mina of taxa already present in the upper Miocene, and the Gerbilidae occurrence in Alcoy-N (López Martínez 1989) do not allow us to rule out the possibility that the Alcoy-Mina large mammal assemblage is actually representative of the Mio-Pliocene transition. As it has been already discussed, no site with a good large mammal representation has still been found in the Iberian Peninsula for this interval. Therefore, at the present time, this last hypothesis cannot be tested.

As previously discussed, an early Pliocene age (lower Ruscinian, MN14) is the most appropriate for this fauna, considering the biochronological record of the represented species (Fig. 15). The fauna from Alcoy-Mina has numerous characteristics in common with the faunas close to the Mio-Pliocene boundary of Western Europe (Venta del Moro, Brisighella, Montpellier) and forms a group clearly distinct from the other Spanish Ruscinian faunas, represented in the Teruel basin, by the localities of La Gloria 4, La Calera and Orrios (Alcalá 1994) and, in the Tajo basin, by the site of Layna (Aguirre *et al*. 1981; Pérez & Soria 1990). It is remarkable that in these early Pliocene faunas, ruminants are represented by hypsodont forms like *Gazella* Blainville, 1816 or *Protoryx* Forsyth Major, 1891. Possibly the Alcoy fauna represents a wetter environment than the rest of the afore-mentioned sites.

Acknowledgements

Dr Maria Dolores Soria passed away during the making of this work, the coauthors wish to dedicate this paper to her memory. The present study has been carried out in the framework of the DGICYT projects PB94-0071, PB 96-1026-C03-02, PB 98-0691-C03-01 and BTE2003-0301. We are grateful to the people that have allowed us access to fossil collections: J. Agustí, F. Alférez, P. Van Bree, F. Campanino, G. Daxner-Höck, B. Engesser, C. Guérin, K. Heissig, H. Lutz, H. Mayr, A. Mazo, G. Rabeder, K. Rauscher, F. Schrenk, C. Smeenk, J. Sudre, E. Tchernov, and specially to A. Arribas (MGM), J. M. Segura (MAA) and M. Belinchón (MCNV). Thanks are also due to Jordi Guillem for text translation and to Elvira Martín Suárez for comments about the micromammal faunas from Alcoy and to the MAA staff who gave every facility to section the teeth of *Hipparion crassum*. The valuable suggestions of the reviewers, Larry J. Flynn and Claude Guérin, have improved the manuscript.

REFERENCES

ADROVER R. 1969. — Los micromamíferos del Plioceno inferior de los lignitos de Alcoy. I. *Ruscinomys*. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)* 67: 245-272.

AGUIRRE E., HOYOS M. & MORALES J. 1975. — Alcoy: observaciones preliminares sobre la secuencia Neógeno-Cuaternaria del Serpis. *Acta Geológica Hispánica* 10 (2): 75-77.

AGUIRRE E., ALBERDI M. T., CUENCA A., MORALES J., PASCUAL V. & SEGURA J. M. 1974. — Depresiones Bético-Levantinas, *in* AGUIRRE E. & MORALES J. (eds), *Libro-Guía, Coloquio Internacional sobre Biostratigrafía Continental del Neógeno Superior y Cuaternario Inferior, Montpellier-Madrid.* CSIC, Madrid: 135-151.

AGUIRRE E., SORIA D. & MORALES J. 1981. — Accumulated bones in a Pliocene cave in Cerro Pelado, Spain. *National Geographic Society Research Reports* 13: 69-81.

AGUSTÍ J. 1990. — The Miocene Rodent succession in Eastern Spain: a zoogeographical apraisal, *in* LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 375-404.

AGUSTÍ J. & LLENAS M. 1996. — The late Turolian muroid rodent succession in Eastern Spain. *Acta zoologica cracoviensia* 39 (1): 47-56.

ALBERDI M. T. 1974. — El género *Hipparion* en España. Nuevas formas de Castilla y Andalucía, revisión e historia evolutiva. *Trabajos sobre Neógeno-Cuaternario* 1: 1-146.

ALBERDI M. T. 1986. — The Pliocene species of *Hipparion* and their biostratigraphical meanings. *Geobios* 19: 517-522.

ALBERDI M. T. 1989. — A review of old world Hipparionine horses, *in* PROTHERO D. R. & SCHOCH R. M. (eds), *The Evolution of Perissodactyls*. Oxford University Press, New York: 234-261.

ALBERDI M. T. & AYMAR J. 1995. — Étude et comparaison des restes d'*Hipparion crassum* Gervais (Perissodactyla, Mammalia) provenant de la nouvelle localité « Le Soler (Lit de la Têt) », Pyrénées-Orientales, France. *Estudios Geológicos* 51: 75-82.

ALBERDI M. T. & ALCALÁ L. 1999. — A study of the new samples of the Pliocene *Hipparion* (Equidae, Mammalia) from Spain and Bulgaria. *Transactions of the Royal Society of Edinburgh (Earth Sciences)* 89: 167-186.

ALCALÁ L. 1994. — *Macromamíferos neógenos de la fosa de Alfambra-Teruel*. Instituto de Estudios Turolenses, Museo Nacional de Ciencias Naturales, Teruel, 554 p.

BONIS L. DE & BOUVRAIN G. 1996. — Suidae du Miocène supérieur de Grèce. *Bulletin du Muséum national d'Histoire naturelle* Paris, 4e sér., sect. C, 18 (1): 107-132.

BRANDT J. F. 1878. — Tentemen synopseos Rhinocerotidum viventium et fossilum. *Mémoire de l'Académie impériale des Sciences de Saint Petersbourg* XXVI (5): 1-66.

BRUIJN H. DE, DAAMS R., DAXNER-HÖCK G., FAHLBUSCH V., GINSBURG L., MEIN P. & MORALES J. 1992. — Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsletter Stratigraphy* 26 (2/3): 65-118.

CERDEÑO E. 1989. — *Revisión de la sistemática de los rinocerontes del Neógeno de España.* Editorial de la Universidad Complutense, Madrid, 429 p., 64 tab., 51 pls.

CROIZET J. B. & JOBERT A. 1828. — *Recherches sur les ossemens fossiles du département du Puy-de-Dôme*. Adolphe Delahays, Paris, 226 p.

CRUSAFONT M. 1962. — *Indarctos atticus*, un nuevo carnívoro del Pikermiense español. *Teruel* 27: 177-184, 1 pl.

CRUSAFONT M. & VILLALTA J. F. 1955. — Sur l'âge des mammifères d'Alcoy (Espagne). *Comptes Rendus sommaires des Séances de la Société géologique de France* 12: 148.

DEPÉRET C. 1890. — Les animaux pliocènes du Roussillon. 1ère partie. *Mémoires de la Société géologique de France* 3: 1-139, 18 pls.

DURAND DELGA M., GARCÍA RODRIGO B., MAGNE J. & POLVECHE J. 1964. — À propos du Miocène de la région d'Alcoy (province d'Alicante, Espagne). *Cursillos y Conferencias* 9: 213-217.

DUVERNOIS M.-P. 1990. — Les *Leptobos* (Mammalia, Artiodactyla) du Villafranchien d'Europe occidentale. Systématique, évolution, biostratigraphie, paléoécologie. *Documents des Laboratoires de Géologie de Lyon* 113: 1-213.

EISENMANN V. & SONDAAR P. 1989. — Hipparions and the Mio-Pliocene boundary. *Bollettino della Società Paleontologica Italiana* 28 (2-3): 217-226.

EISENMANN V., ALBERDI M. T., DE GIULI C. & STAESCHE U. 1988. — Collected papers after the "New York International *Hipparion* Conference, 1981", *in* WOODBURNE M. & SONDAAR P. Y. (eds), *Studying Fossil Horses*. E. J. Brill, Leiden, 71 p.

ESTEBAN AENLLE J. & LACOMBA J. I. 1988. — El yacimiento de Alcoy-2. Nuevo nivel con micromamíferos del Plioceno inferior (MN15) en el área de Alcoy. *Com. Colloqui Homenatge a R. Adrover "Bioeventos y sucesiones faunísticas en el Terciario continental ibérico"*, Sabadell: 17.

EZQUERRA DEL BAYO J. 1850. — Ensayo de una descripción general de la estructura geológica del terreno de España en la península: sección 3ª. *Memorias de la Academia de Ciencias de Madrid* 1: 161-184.

FLYNN L. J., TEDFORD R. H. & QIU Z. 1991. — Enrichment and stability in the Pliocene mammalian fauna of North China. *Paleobiology* 17 (3): 246-265.

FLYNN L. J., WU W. & DOWNS W. R. 1997. — Dating vertebrate microfaunas in the late Neogene record of Northern China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133: 227-242.

FORTELIUS M., VAN DER MADE J. & BERNOR R. L. 1996. — Middle and Late Miocene Suoidea of Central Europe and the Eastern Mediterranean: Evolution, biogeography, and paleoecology, *in* BERNOR R., FAHLBUSCH V. & MITTMANN W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 348-377.

FREUDENTHAL M., MEIN P. & MARTÍN SUÁREZ E. 1998. — Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona* 7: 11-93.

FRICK C. 1926. — The Hemicyoninae and an American Tertiary bear. *Bulletin of the American Museum of Natural History* 56: 1-119.

GERAADS D. 1992. — Phylogenetic analysis of the tribe Bovini (Mammalia, Artiodactyla). *Zoological Journal of the Linnean Society* 104: 193-207.

GERVAIS P. 1853. — Description des ossements fossiles de mammifères rapportés d'Espagne par MM. de Verneuil, Collomb et de Lorière. *Bulletin de la Société géologique de France* 2e sér., 10: 147-168, pls 3-6.

GERVAIS P. 1859a. — *Zoologie et paléontologie françaises.* 2e éd. Arthus Bertrand, Paris, 544 p., 84 pls.

GERVAIS P. 1859b. — Sur une nouvelle espèce d'*Hipparion* découverte auprès de Perpignan. *Comptes Rendus de l'Académie des Sciences de Paris* 48: 1117-1118.

GINSBURG L. 1980. — *Xenohyus venitor*, suidé nouveau (Mammalia, Artiodactyla) du Miocène inférieur de France. *Geobios* 13: 861-877.

GROMOLARD C. 1980a. — Une nouvelle interprétation des grands Bovidae (Artiodactyla, Mammalia) du Pliocène d'Europe occidentale classés jusqu'à présent dans le genre *Parabos*: *Parabos cordieri* (De Christol) emend., ?*Parabos boodon* (Gervais) et *Alephis lyrix* n. gen. n. sp. *Geobios* 13: 767-775.

GROMOLARD C. 1980b. — Révision du type de l'espèce *Parabos* ? *boodon* (Gervais) (Mammalia, Artiodactyla, Bovidae) du gisement Néogène d'Alcoy (Espagne). *Bulletin de la Societé linnéenne de Lyon* 9: 525-533.

GROMOLARD C. 1981. — *Les grands Bovidae (Mammalia, Artiodactyla) du Pliocène d'Europe occidentale. Biostratigraphie, paléoneurologie, systématique, évolution, paléoécologie*. Thèse, Université Claude Bernard,

Lyon, France.
GROMOLARD C. & GUÉRIN C. 1980. — Mise au point sur *Parabos cordieri* (De Christol), un bovidé (Mammalia, Artiodactyla) du Pliocène d'Europe occidentale. *Geobios* 13: 741-755.
GUÉRIN C. 1980. — Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* 79: 1-1182.
GUÉRIN C. & SANTAFÉ J. V. 1978. — *Dicerorhinus miguelcrusafonti* nov. sp., une nouvelle espèce de rhinocéros (Mammalia, Perissodadyla) du gisement pliocène supérieur de Layna (Soria, Espagne) et de la formation pliocène de Perpignan. *Geobios* 11 (4): 457-491.
HEISSIG K. 1969. — Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim bei Ingolstadt in Bayern und ihre phylogenetische Stellung. *Bayerische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse Abhandlungen* NF, 138: 1-133.
HEISSIG K. 1999. — Family Rhinocerotidae, *in* RÖSSNER G. E. & HEISSIG K. (eds), *The Miocene Land Mammals of Europe*. Dr Friedrich Pfeil, München: 175-188.
HELBING H. 1932. — Über einen *Indarctos*-Schädel aus dem Pontien der Insel Samos. Nebst einen Anhang: *Hyaenarctos* spec. aus dem Pliocaen von Vialette (Haute-Loire). *Mémoires de la Société paléontologique de Suisse* 52: 1-18, 1 pl.
HELLMUND M. 1995. — The Vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 13. Suidae (Artiodactyla, Mammalia). *Münchener Geowissenschaftliche Abhandlungen* A, 28: 143-156.
HENDEY Q. B. 1972. — A Pliocene ursid from South Africa. *Annals of the South African Museum* 59 (6): 115-132, 2 pls.
HENDEY Q. B. 1980. — *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Annals of the South African Museum* 81 (1): 1-109.
KAUP J.-J. 1832. — *Description d'ossements fossiles de mammifères inconnus jusqu'à présent qui se trouvent dans le muséum grand-ducal de Darmstadt*. Heyer, Darmstadt: cahiers I-III.
KAUP J.-J. 1834. — *Description d'ossements fossiles de mammifères inconnus jusqu'à présent, qui se trouvent au Muséum grand-ducal de Darmstadt.* III. *Pachydermes.* Rhinoceros schleiermacheri. Heyer, Darmstadt: 33-45.
KÖHLER M. 1993. — Skeleton and habitat of recent and fossil Ruminants. *Münchener Geowissenschaftliche Abhandlungen* A, 25: 1-88.
KÖHLER M., MOYÀ-SOLÀ S. & ALBA D. M. 2000. — *Macaca* (Primates, Cercopithecidae) from the Late Miocene of Spain. *Journal of Human Evolution* 38: 447-452.
LYDEKKER R. 1884. — Siwalik and Narbada Carnivora. *Memoirs of the Geological Survey of India, Palaeontologia Indica* ser. X, vol. II, part 6: 178-363, pls 26-45.
LÓPEZ MARTÍNEZ N. 1989. — Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 3 (3): 1-350.
MAIER VON MAIERFELS S. 1928. — Az *Ursus böckhi* Schlosser ösmedve maradványai az Erdélyi levantei korú lignitiböl. *Földtani Szemle Budapest* 1 (5): 273-286, 1 pl.
MARTÍN SUÁREZ E., OMS O., FREUDENTHAL M., AGUSTÍ J. & PARÉS J. M. 1998. — Continental Mio-Pliocene transition in the Granada Basin. *Lethaia* 31: 161-166.
MARTÍN SUÁREZ E., FREUDENTHAL M., KRIJGSMAN W. & RUTGER FORTUIN A. 2000. — On the age of the continental deposits of the Zorreras Member (Sorbas basin, SE Spain). *Geobios* 33 (4): 505-512.
MAZO A. V. 1977. — *Revisión de los mastodontes de España*. Tesis Doctoral, Universidad Complutense, Madrid, 440 p., 14 pls.
MAZO A. V. 1996. — Gomphotheres and mammutids from the Iberian Peninsula, *in* SHOSHANI J. & TASSY P. (eds), *The Proboscidea, Evolution and Palaeoecology of Elephants and their Relatives*. Oxford University Press, Oxford; New York; Tokyo: 136-142.
MEIN P. 1990. — Updating of MN zones, *in* LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 73-90.
MEIN P., BIZON G., BIZON J.-J. & MONTENAT C. 1973. — Le gisement de mammifères de La Alberca (Murcia, Espagne méridionale). Corrélations avec les formations marines du Miocène terminal. *Comptes Rendus de l'Académie des Sciences, Paris* 276: 3077-3080.
MICHAUX J., AGUILAR J.-P., CALVET M., DUVERNOIS M.-P. & SUDRE J. 1991. — *Alephis tigneresi* nov. sp., un bovidé nouveau du Pliocène du Roussillon (France). *Geobios* 24: 735-745.
MONTENAT C. 1973. — *Les Formations néogènes et Quaternaires du Levant espagnol (Provinces d'Alicante et de Murcia).* Thèse Sciences, Université Orsay-Paris-Sud, France, 1170 p.
MONTOYA P. 1994. — *Los macromamíferos del Mioceno superior del área de Crevillente (Alicante)*. Tesis Doctoral, Universitat de València, Spain, 421 p.
MONTOYA P. & ALBERDI M. T. 1995. — Crevillente 15 y Crevillente16, dos nuevos yacimientos con macromamíferos en el Mioceno superior de Alicante (España). *Estudios Geológicos* 51 (3-4): 159-182.
MONTOYA P. & SÁNCHEZ E. J. 2000. — La colección paleontológica "Camil Visedo Moltó", *in* AURA J. E. & SEGURA J. M. (eds), *Catálogo. Museo Arqueológico Municipal Camil Visedo Moltó. Alcoi*. Ajuntament d'Alcoi, Caja de Ahorros del Mediterráneo, Alcoy:

245-261.

MONTOYA P., ALCALÁ L. & MORALES J. 2001. — *Indarctos* (Ursidae, Mammalia) from the Spanish Turolian (Upper Miocene). *Scripta Geologica* 122: 123-151.

MORALES J. 1984. — *Venta del Moro: su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo*. Editorial de la Universidad Complutense, Madrid, 340 p.

MORALES J. & AGUIRRE E. 1976. — Carnívoros de Venta del Moro. *Trabajos sobre Neógeno-Cuaternario* 5: 31-82.

MORLO M. & KUNDRÁT M. 2001. — The first carnivoran fauna from the Ruscinium (Early Pliocene, MN15) of Germany. *Paläontologische Zeitschrift* 75 (2): 163-187.

MOYÀ SOLÀ S. 1983. — Los Boselaphini (Bovidae, Mammalia) del Neógeno de la Península Ibérica. *Publicaciones de Geología de la Universidad Autónoma de Barcelona* 18: 1-237, 17 pls.

OPDYKE N., MEIN P., LINDSAY E., PÉREZ GONZÁLEZ A., MOISSENET E. & NORTON V. L. 1997. — Continental deposits, magnetostratigraphy and vertebrate paleontology, late Neogene of Eastern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133: 129-148.

PÉREZ B. & SORIA D. 1990. — Análisis de las comunidades de mamíferos del Plioceno de Layna (Soria) y La Calera (Teruel). *Paleontologia i Evolució* 23: 231-238.

PETTER G. & THOMAS H. 1986. — Les Agriotheriinae (Mammalia, Carnivora) néogènes de l'Ancien Monde. Présence du genre *Indarctos* dans la faune de Menacer (ex-Marceau), Algérie. *Geobios* 19 (5): 573-586.

PIERSON D'AUTREY L. 1987. — *Sédimentation et structuration synsédimentaire dans le bassin néogène d'Alcoy (Cordillères Bétiques externes Orientales Espagne).* Thèse, Université de Paris, France, 315 p.

QIU Z. & SCHMIDT-KITTLER N. 1983. — *Agriotherium intermedium* (Stach 1957) from a Pliocene fissure filling of Xiaoxiang county (Anhuei Province, China) and the phylogenetic position of the genus. *Palaeovertebrata* 13 (3): 65-81, 1 pl.

RODRÍGUEZ ESTRELLA T. 1977. — Síntesis geológica del Prebético de la provincia de Alicante. II) Tectónica. *Boletín Geológico y Minero* 88 (4): 273-299.

SANTISTEBAN C. DE, MONTOYA P., USERA J. & ROBLES F. 1997. — El Terciario marino y continental de Alicante, *in* ALCALÁ L. & ALONSO A. M. (eds), *Itinerarios Geológicos en el Terciario de Centro y Este de la Península Ibérica*. Universidad Complutense de Madrid, Consejo Superior de Investigaciones Científicas, Madrid: 73-107.

SCHLOSSER M. 1899. — *Parailurus anglicus* und *Ursus böckhi* aus den Ligniten von Baróth-Köpecz, Comitat Háromszék in Ungarn. *Mittheilungen aus dem Jahrbuche der Königlich Ungarischen Geologischen Anstalt* 13: 65-95, 3 pls.

STACH J. 1957. — *Agriotherium intermedium* n. sp. from the Pliocene bone breccia of Weze. *Acta Palaeontologica Polonica* 2 (1): 1-17, 2 pls.

THALER L., CRUSAFONT M. & ADROVER R. 1965. — Les premiers micromammifères du Pliocène d'Espagne; précisions chronologiques et biogéographiques sur la faune d'Alcoy. *Comptes Rendus de l'Académie des Sciences de Paris* 260: 4024-4027.

THOMAS H., SPASSOV N., KODJUMDGIEVA E., POIDEVIN J.-L., POPOV V., SEN S., TASSY P. & VISSET D. 1986. — Preliminary results of the first Bulgarian-French paleontological research project at Dorkovo (Pazardjik district, Bulgaria). *Comptes Rendus de l'Académie des Sciences de Paris* 302 (2) 16: 1037-1942.

VAN DAM J. A. 1997. — The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): paleobiology and paleoclimatic reconstructions. *Geologica Ultraiectina* 156: 1-204.

VAN DER MADE J. 1990a. — Iberian Suoidea. *Paleontologia i Evolució* 23: 83-97.

VAN DER MADE J. 1990b. — A range chart for European Suidae and Tayassuidae. *Paleontologia i Evolució* 23: 99-104.

VAN DER MADE J. 1996. — Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology* 33 (1-4): 3-254 + 14 tables on 1 microfiche.

VAN DER MADE J. & BELINCHÓN M. 1991. — *Korynochoerus palaeochoerus* from the Upermost Miocene of Alcoy. *Revista Española de Paleontología* no. extr.: 173-180.

VICEDO SANFELIPE R. 1920. — *Historia de Alcoy y su región.* Tomo I: *Prehistoria*. Imprenta El Serpis, Alcoi, 342 p.

VIRET J. 1939. — Monographie paléontologique de la faune de vertébrés des Sables de Montpellier. III. Carnivora Fissipedia. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 37 (2): 7-26, 2 pls.

VIRET J. 1954. — Le Loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* 4: 3-200.

VIRET J. 1955. — Perissodactyla, *in* PIVETEAU J. (ed.), *Traité de Paléontologie*, 6 (2). Masson, Paris: 368-475.

ZDANSKY O. 1927. — Weitere Bemerkungen über fossile Carnivoren aus China. *Palaeontologia Sinica* ser. C, 4 (4): 1-30, 2 pls.

ZITTEL K. A. VON 1893. — *Handbuch der Palaeontologie.* I. *Palaeozoologie.* Bd. IV. *Vertebrata (Mammalia)*. Oldenburg, München, 799 p.

Submitted on 11 August 2004;
accepted on 25 July 2005.

APPENDIX

TABLE 1. — Measurements (in mm) of the upper carnassial (P4) of *Agriotherium* from Alcoy (cast MNHN), compared with the homologous element of *A. insigne* (Gervais, 1869) from Montpellier (Gervais 1859a), *A. roblesi* Morales & Aguirre, 1976 from Venta del Moro (MGUV), *A. palaeoindicum* (Lydekker, 1884) and *A. sivalense* (Falconer & Cautley, 1836) (Lydekker 1884), *A. intermedium* Qiu & Schmidt-Kittler, 1983 (Qiu & Schmidt-Kittler 1983) and *A. africanum* Hendey, 1972 (Hendey 1980). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

	DAP	DT
A. insigne (Alcoy)	31.2	23.1
A. insigne (Montpellier)	30.0	22.6
A. roblesi (Venta del Moro)	35.1	28.8
A. palaeoindicum (Siwalik)	27.7	20.0
A. sivalense (Siwalik)	32.0	22.0
A. intermedium (Xiaoxian)	25.9	18.1
A. africanum (Langebaanweg)	32.8	25.5
	32.6	24.3
	31.9	24.5
	31.6	22.0
	31.2	22.7
	32.5	24.2
	33.0	24.4
	33.0	25.0
	33.3	24.1
	35.8	25.0

TABLE 2. — Measurements (in mm) of the *Ursus boeckhi* Schlosser, 1899 material from Alcoy. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

	Alcoy	Baróth-Köpecz (Schlosser 1899)	China (Zdansky 1927)
M1			
DAP	19.6		
DT	16.6		
m1			
DAP	22.0	20.5	20.7
DT	10.5	10.0	9.8
m2			
DAP	17.5	18.0	
DT	12.6	11.0	
m3			
DAP		14.0	
DT		10.8	

TABLE 3. — Measurements (in mm) of the *Sus arvernensis* Croizet & Jobert, 1828 material from Alcoy. Abbreviations: **DAP**, antero-posterior diameter; **DAPmax**, maximum DAP of the calcaneus; **DAPsf**, DAP of the calcaneus at the level of the sustentaculum facet; **DLL**, labio-lingual diameter in incisors; **DMD**, mesio-distal diameter in incisors; **DMDo**, mesio-distal occlusal diameter in incisors; **DTa**, transverse diameter of the anterior or first lobe of the tooth; **DTp**, transverse diameter of the second lobe of the tooth; **DTpp**, transverse diameter of the third lobe of the third molar; **Ldist**, length of the lower part of the calcaneus.

Collection	Element	right/left	DAP DMD	DTa DLL	DTp DMDo	DTpp
MNCN	M3	l	29.3	18.5	17.0	12.9
MAA	M3	r	26.8	18.1	16.0	10.2
MCNV	m3	l	30.6	16.1	14.5	11.1
MCNV	m	l	-	15.0	-	-
MCNV	m1	r	15.9	>10.1	10.6	
MCNV	M2	r	17.7	-	17.1	
MCNV	M1	r	15.3	14.1	14.6	
MCNV	I1	l	15.8	9.6	21.8	
MNHN	M2	l	19.5	17.5	17.6	
MNHN	M1	r	16.0	14.1	14.8	
MNHN	M2	r	19.3	17.0	16.7	
MNHN	M3	r	29.2	18.3	16.7	10.4
MNHN	M2	l	>19.2	17.3	≥16.5	
MNHN	M3	l	26.7	19.1	16.5	9.7
MNHN	m3	r	32.2	-	-	-
MNHN	m2	l	-	-	16.5	
MNHN	m2	l	20.1	14.6	14.9	
MNHN	m1	r	-	12.7	-	
MNHN	p4	r	14.8	10.7	12.3	
MNHN	P2		13.6	6.2	-	
			DAPsf	**DAPmax**	**Ldist**	
MAA	calcaneus	l	21.1	27.1	26.8	

TABLE 4. — Measurements (in mm) of the teeth of *Alephis boodon* (Gervais, 1852) from Alcoy. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

	MAA P2	ALA-2 M1	M-2101 M3	Alc 23 m2	MAA m3	ALA-3 m3	Alc 5 m3
DAP	22.0	27.0	34.0	32.0	41.4	42.2	43.0
DT	18.0	27.0	31.5	18.0	19.3	18.1	17.5

TABLE 5. — Measurements (in mm) of metacarpals of *Alephis boodon* (Gervais, 1852) from Alcoy. The diaphysis has been measured at 120 mm from the proximal end. Dimensions of *Alephis lyrix* Gromolard, 1980 and *Parabos cordieri* (Christol, 1832) from Gromolard (1981); those of *A. tigneresi* Michaux, Aguilar, Calvet, Duvernois & Sudre, 1991 from Michaux *et al.* (1991). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; **dist**, distal; **diaph**, diaphysis; **prox**, proximal.

	Coll.		DAP prox	DT prox	DAP diaph	DT diaph	DAP dist	DT dist	DAP/ DT prox	DAP/ DT diaph	DAP/ DT dist
Alephis boodon	Alc 9		39.2	60.4	30.2	34.2			65	88	
	M-698						36.9	60.6			61
Alephis lyrix		min.	32.0	50.4	26.2	32.6	34.4	55.9	61	80	56
		mean	36.4	55.6	27.9	33.9	37.1	59.4	66	82	62
		max.	44.4	64.7	30.0	35.8	38.9	67.3	71	88	68
Alephis tigneresi	BAH 2		38.7	61.8	31.7	37.8	37.5	62.7	63	84	60
Parabos soriae	VV1889		35.0	50.2	25.6	29.0	34.1	51.3	70	88	66
Parabos cordieri		min.	25.2	42.1	20.8	26.9	28.0	44.3	57	69	66
		mean	28.5	46.7	22.7	29.5	30.2	48.8	61	73	80
		max.	31.7	50.2	24.1	31.5	31.0	53.4	66	63	81
Bos taurus	MNCN		39.6	63.8	27.2	39.6	36.0	61.0	62	68	59

TABLE 6. — Measurements (in mm) of astragali of *Alephis boodon* (Gervais, 1852) from Alcoy. Dimensions of *Alephis lyrix* Gromolard, 1980 from Gromolard (1980b); those of *Parabos cordieri* (Christol, 1832) from Gromolard & Guérin (1980). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; **L**, length; **dist**, distal; **lat**, lateral; **med**, medial; **prox**, proximal.

	Coll.		L lat	L med	DAP lat	DAP med	DT prox	DT dist
Alephis boodon	AAL 7		72.2		40.5			46.4
	Alc 8			65.7		*c*. 39.0		
	M-2430		64.6	61.0	36.2	37.5	37.4	41.6
	M-2434		75.6		40.4			46.4
Alephis lyrix		min.	65.1			35.0		41.2
		mean	71.9			38.0		45.1
		max.	77.4			40.5		51.9
Parabos soriae	VM 511		65.9	60.0	36.1	34.4	36.2	38.3
	VM 314		69.0		36.5	36.7		46.2
	VM 1619		67.0	63.8	39.0	39.2	39.6	44.5
Parabos cordieri		min.	59.4					34.7
		mean	64.3					40.1
		max.	69.7					45.3
Leptobos elatus	Villarroya (MNCN)		77.8	72.7	41.7	43.5	45.0	*c*. 53.6
Bos gaurus	MNCN		77.6	69.6	46.0	44.0	47.0	51.6

TABLE 7. — Measurements (in mm) of the phalanx II of *Alephis boodon* (Gervais, 1852) from Alcoy. The dimensions of *Alephis lyrix* Gromolard, 1980 and *Parabos cordieri* (Christol, 1832) have been taken from Gromolard (1981). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; **L**, length; **diaph**, diaphysis; **ant**, anterior; **dist**, distal; **post**, posterior; **prox**, proximal.

	Coll.		L	DAP prox	DT prox	DAP diaph	DT diaph	DAP dist	DT dist
Alephis boodon	M-693		50.4	34.9	31.1	23.6	23.1	32.0	25.8
Alephis lyrix		min.	44.9	26.0	23.5	21.1	19.9	25.0	20.7
		mean	47.0	30.6	27.8	22.9	21.4	28.3	24.9
		max.	49.6	32.4	32.5	24.5	23.6	31.6	31.0
Parabos soriae	ZV256		43.2	31.2	24.6	20.1	17.7	30.7	21.2
	VV2584		47.5	32.2	25.2	21.2	19.9	27.7	21.3
Parabos cordieri		min.	34.2	21.7	20.6	17.2	15.1	19.2	15.6
		mean	40.8	27.0	23.6	20.0	18.2	24.9	19.8
		max.	46.0	30.1	25.2	22.5	20.2	28.1	23.4
Bos gaurus	MNCN	ant	54.0	41.6	32.5	29.8	25.7	39.0	28.7
		post	54.2	38.2	31.5	26.5	23.3	32.5	25.0

TABLE 8. — Measurements (in mm) of the m1 or m2, and the astragali of *Tragoportax* sp. from Alcoy. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; **L**, length; **dist**, distal; **lat**, lateral; **med**, medial.

m1 or m2	DAP	DT			
MCNV w/n	21.0	12.5			
Astragalus	**L lat**	**L med**	**DT dist**	**DAP lat**	**DAP med**
Alc 10	40.1	36.9	25.0		22.0
Alc 11			26.0		
M-2435	>40.4	38.0	27.0	22.3	

TABLE 9. — Measurements (in mm) and principal morphological traits of the upper cheek teeth of *Hipparion crassum* Gervais, 1859 from Alcoy, and *Hipparion* cf. *crassum* from Dorkovo. Abbreviations: **Ls**, length in occlusal surface; **ls**, breadth in occlusal surface; **Lb**, length at the base; **lb**, breadth at the base; **H**, parastyle height; **Pr**, protocone mesio-distal length; **shape Pr**, shape of the protocone; **Plc**, pli caballin or ptycostilid; **Apref**, anterior zone of the prefossette; **Ppref**, posterior zone of the prefossette; **Apostf**, anterior zone of the postfossette; **Ppostf**, posterior zone of the postfossette; **Hy**, hypocone; **hyp gr**, hypoconal groove; **w/n**, without number; **elong**, elongate; **round**, rounded.

Number	Alcoy-Mina	Ls	ls	Lb	lb	H	Pr	shape Pr	no. Plc	Apref/ no. plis	Ppref/ no. plis	Apostf/ no. plis	Ppostf/ no. plis	Hy	Other characters
2433M	P2 right	-	>23.1	-	-	39.2	7.3	-	4	6	12	-	-	broken	only 1/2 tooth
MAA w/n	P2 right	34.0	24.0	33.1	22.5	47.5	-	unworn							
C.Villalta w/n	P2 right	33.5	24.0	-	-	>48.0	unworn								
C.Villalta w/n	P3-4 right	27.6	23.1	-	-	>50.0	unworn	elong	1	1	3 open	1	open	unworn	unworn
MAA w/n	M1-2 left (M1)	25.7	22.8	22.0	23.3	50.0	6.6	oval	5	6	11	7	2	hyp gr big, hy constrict	strong styles
MAA w/n	M1-2 left (M2)	23.5	19.6	21.5	21.0	55.0	unworn								
MAA w/n	M1-2 right (M1)	25.3	22.5	22.0	24.6	48.7	6.25	oval	4	5	10	6	2	hyp gr big, hy constrict	strong styles
MAA w/n	M1-2 right (M2)	23.2	19.6	21.4	22.3	55.5	unworn								
2126M	M1-2 right	26.34	22.51	21.9	-	>55.0	8.3	unworn							little worn
2108M	M1-2 left	27.15	22.4	22.25	21.75	62.0	8.15	unworn	1	2	4	1	open	unworn, hyp gr marked	little worn
	Dorkovo														
DKV-16	P2 left	34.9	22.8	33.1	23.3	46.5	8	unworn							little worn, cement
DKV-16	P3 left	27.5	22.5	25.9	-	50.0	unworn								little worn, cement
DKV-16	M1 left	25.5	22.5	21.1	22.2	45.0	5.9	round	2	5	11	8	2	open, elongate	thin styles
DKV-16	M2 left	23.9	19.2	20.9	21.4	50.5	8.1	unworn							thin styles
DKV-12	P3-4 left	28.1	28.1	21.3	23.4	52.0	5.0	oval	2	1 unworn	9	4	unworn	unworn	little worn
DKV-63	P3-4 left	27.0	22.5	23.8	23.0	46.0	7.8	oval	4	9	9	9	2	angulate	cement
DKV-11	P3-4 right	25.3	23.2	23.0	23.7	42.5	5.5	round	3	8	11+ plis	10	11	open, angular	cement
DKV-104	P3-4 right	26.7	-	24.4	-	50.0	5.1	round small	3	4	8	8	5	angular	hyp gr big, lingual mark
DKV-10	M1-2 right	25.7	21.9	21.0	23.6	54.5	6.1	oval	2	6	11	5	1	unworn	thin styles
DKV-9	M1-2 right	23.8	18.8	20.4	20.7	48.3	7.5	oval		2	5	7	2	open, angular	unworn
DKV-61	M1-2 left	22.6	18.6	20.5	20.0	52.0	7.5	oval	3	6	8	5	1	open, angular	cement
DKV-101	M1-2 left	25.8	23.3	23.2	25.0	>57.0	7.0	unworn							little worn
DKV-105	M1-2 left	24.6	22.0	22.6	23.6	50.3	6.8	oval	2	4	8	6	2	strangulate, elongate	styles narrow and thin
DKV-121	M1-2 left	19.8	21.4	19.0	21.7	32.7	5.5	round small	2	3	10	8	3	hyp gr big, hy small constrict	small, cement
DKV-13	M3 left	20.2	16.2	23.0	18.5	48.0	unworn								little worn
DKV-59	M3 left	21.1	16.1	21.2	19.4	52.4	unworn								little worn
DKV-62	M3 left	19.3	15.7	20.5	18.7	37.8	6.8	oval		3	7	5	3	strangulate, small	small styles, cement
DKV-113	M3 right	21.1	18.0	24.1	20.7	48.8	worn								unworn
DKV-140	upper row P2	36.4	24.0	41.0	-	45.0									unworn
DKV-140	upper row DP3/P3														unworn
DKV-140	upper row DP4/P4														unworn
DKV-140	upper row M1	25.5	22.5			>53.0	7	oval, small	2	5	9	6	3	unworn	styles narrow and thin
DKV-140	upper row M2	24.2	19.6			>54.0	little worn								
DKV-140	upper row M3	little worn													unworn
DKV-140	upper row L M1-M3	*c.* 73.4													

TABLE 10. — Measurements (in mm) and principal morphological traits of the lower cheek teeth of *Hipparion crassum* Gervais, 1859 from Alcoy, and *Hipparion* cf. *crassum* from Dorkovo. Abbreviations: **L**, length; **Ls**, length in occlusal surface; **ls**, breadth in occlusal surface; **Lb**, length at the base; **lb**, breadth at the base; **H**, height in the mesial part; **plc**, pli caballin; **w/n**, without number.

Number	Alcoy-Mina	Ls	ls	Lb	lb	H	L post-flexid	L double knot	Other characters
MAA w/n	p2 left	30.0	13.0	-	-	>43.0	unworn	unworn	
MAA w/n	p3-4 left	28.0	13.3	25.8	12.4	>46.0	little worn	little worn	
MAA w/n	p3-4 right	27.8	14.3	-	-	*c.* 40.0	little worn	little worn	cement
MAA w/n	p3-4 left	24.8	14.1	-	-	*c.* 50.0	11.0	13.4	broken
2431M	p3-4 left	-	>12.6	-	-	40.0	11.8	broken	inside enamel plications
MNHN w/n	p3-4 left	24.0	12.8	21.0	14.8	46.6	10.8	14.5	
MNHN w/n	m1-2 right (m1)	20.6	12.2	22.4	12.8	38.2	7.4	13.0	
MNHN w/n	m1-2 right (m2)	21.8	11.1	21.7	12.6	43.5	7.2	12.4	
MNHN w/n	m3 right	24.0	11.6	23.5	12.1	*c.* 45.0	7.0	11.5	
MNHN w/n	m1-2 left	21.0	12.2	21.0	12.2	38.8	7.7	12.5	
MNHN w/n	m3 left	24.2	10.6	24.6	11.0	42.0	6.7	11.2	
MNHN	L m1-m3 right	67.1							
	Dorkovo								
DKV-47	p2 right	28.6	13.1	27.2	13.4	30.5	13.4	8.0	plications-cement
DKV-43	p2 right	28.0	13.7	28.2	15.1	17.0	9.6	6.7	cement, plc small groove
DKV-40	p2 right	29.5	15.1	29.9	15.8	19.0	13.0	7.2	inside enamel plications, plc small groove
DKV-106	p2 left	32.3	14.5	-	-	17.0	13.2	13.5	very worn, plc small groove
DKV-123	p2 left	32.0	15.0	30.0	13.7	>31.0	14.1	13.3	cement, plc marked
DKV-53	p3-4 right	28.1	14.2	26.7	13.8	>53.0	unworn	-	robust, cement
DKV-36	p3-4 left	27.1	15.0	25.3	15.7	48.5	12.5	7.4	robust, cement, unworn, plc inside plication
DKV-42	p3-4 left	26.0	14.9	25.4	16.3	22.2	12.3	6.7	robust, cement, plc inside plication
DKV-58	p3-4 left	26.4	14.5	22.9	15.5	54.5	12.0	6.5	little worn
DKV-17	p3 right	24.1	13.5	22.5	14.8	45.5	11.9	7.1	inside enamel plications, double knot acute
DKV-17	p4 right	23.5	13.3	21.1	13.6	50.0	11.6	6.5	inside enamel plications, double knot acute
DKV-114	p3-4 left	28.0	14.6	-	-	14.0	10.9	16.7	very worn, plc small groove, protostylid
DKV-38	m1-2 right	23.5	13.7	21.1	14.5	35.0	11.1	5.5	double knot acute, plc marked
DKV-50	m1-2 left	22.4	13.5	21.6	13.6	35.0	11.0	5.0	double knot acute, cement, no plc
DKV-44	m1-2 left	22.6	13.8	21.7	14.7	30.3	9.4	5.6	double knot acute, cement, no plc
DKV-48	m1-2 left	24.2	10.4	19.9	12.1	46.0	unworn	unworn	cement
DKV-39	m1-2 left	23.0	12.0	22.8	13.2	30.2	10.2	5.2	double knot rounded, cement, plc small groove
DKV-100	m1-2 left	27.2	10.4	20.0	13.3	55.0	unworn	-	protostylid
DKV-119	m1-2 left	25.4	11.0	20.7	13.5	54.0	11.7	11.0	little worn, protostylid
DKV-116	m1-2 right	25.7	11.7	21.4	12.9	50.0	10.3	14.3	typical morphology, protostylid
DKV-129	m1-2 right	21.6	11.8	20.0	12.4	32.0	10.4	12.1	typical morphology, small in size, no protostylid
DKV-41	m3 right	25.3	11.4	26.4	11.7	47.2	-	4.5	little worn, cement
DKV-46	m3 right	22.5	10.9	24.6	10.2	45.0	8.8	3.2	inside enamel plications, double knot acute, plc small groove

TABLE 11. — Measurements (in mm) of the teeth of *Dihoplus schleiermacheri* (Kaup, 1832) from Alcoy. First number (in bold), after Heissig (1969); second number, after Guérin (1980). Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter.

	Alc 24 **p3**	**Alc 25** **p4**	**Alc 26** **m1**	**Alc 27** **m1**	**MAA** **m2**	**Alc 28** **m3**
DAP	(**40**) 34	**40** 37	**45** 39	**45** 39	**48** 40	**52** 43
DT	22	21	29	28	31	29.5

TABLE 12. — Measurements (in mm) of the left m3 of *Anancus arvernensis* (Croizet & Jobert, 1828) (332 M) from Alcoy.

	Total	**1st loph**	**2nd loph**	**3rd loph**	**4th loph**	**5th loph**	**talonid**
Length	*c*. 190						
Width		-	80.1	78.5	71.0	60.1	39.5
Height		-	42.3	41.7	49.2	32.5	37.4