The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece)

Claude GUÉRIN
UMR CNRS 5276, Laboratoire de Géologie de Lyon, Terre, Planètes, Environnement et Département des Sciences de la Terre, Université Claude Bernard-Lyon I, 27-43 Boulevard du 11 novembre 1918, F-69622 Villeurbanne Cedex (France)
claude.guerin@univ-lyon1.fr

Evangelia TSOUKALA
School of Geology, Aristotle University (AUTH), 54124 Thessaloniki (Greece)
lilits@geo.auth.gr

Guérin C. & Tsoukala E. 2013. — The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas* 35 (2): 447-489. http://dx.doi.org/10.5252/g2013n2a7

ABSTRACT
The fossiliferous site of Milia (Grevena, N. Greece) is best known for the excavation of the longest tusks of *Mammut borsoni* (Hays, 1834) in the world (4.39 m and 5.02 m). In association with this species occur the Tapir *Tapirus arvernensis arvernensis* Croizet & Jobert, 1828, the Rhinocerotidae *Dicerorhinus jeanvireti* Guérin, 1972 and the Suidae *Sus avernensis arvernensis* Croizet & Jobert, 1828. The first species is represented by two fossils corresponding to one adult and one juvenile individual, the second species is represented by 197 identified remains among which 68 are measurable specimens corresponding to eight adult and one juvenile individuals, and the third species by nine specimens. The dimensions are compared with those of European Ruscinian and Villafranchian species from the same families: *Tapirus arvernensis* Croizet & Jobert, 1828 and *T. jeanpiveteaui* Boeuf, 1991 for the tapir, *Dicerorhinus megarhinus* (de Christol, 1834), *D. miguelcrusafonti* Guérin & Santafe, 1978, *D. jeanvireti* Guérin, 1972 and *D. etruscus etruscus* (Falconer, 1859) for the rhinoceros, *Potamochoerus provincialis* (Gervais, 1859), *Sus arvernensis* Croizet & Jobert, 1828 and *S. strozzii* Forsyth Major, 1881 for the boar. The association of *Tapirus arvernensis arvernensis*, *Dicerorhinus jeanvireti* and *Sus arvernensis arvernensis* allows us to date the site to biozone MNQ 16 (Earliest Villafranchian). The degree of evolution of the Milia *D. jeanvireti* population allows us to assign to it an age somewhat younger than that of Vialette. The faunal association is a clear indication of a forested landscape in a warm and relatively wet climate.

KEY WORDS
Mammalia,
anatomy,
biometry,
biochronology,
palaeoenvironment,
Early Villafranchian,
North-Western Greece.

RÉSUMÉ
Les Tapiridae, Rhinocerotidae et Suidae (Mammalia) du gisement villafranchien inférieur de Milia (Grevena, Macédoine, Grèce).
Le gisement de Milia est bien connu pour avoir livré les plus longues défenses connues au monde (4,39 et 5,02 m) ; elles appartiennent à *Mammut borsoni* (Hays, 1834). Parmi la faune associée on y a recueilli entre autres le Tapiridae *Tapirus arvernensis arvernensis* Croizet & Jobert, 1828, le Rhinocerotidae *Dicerorhinus jeanvireti* Guérin, 1972 et le Suidae *Sus arvernensis arvernensis* Croizet & Jobert, 1828. Le premier est représenté par deux fossiles correspondant à deux individus dont un juvénile, le second par 197 restes identifiés dont 68 sont des spécimens étudiables correspondant à au moins huit rhinocéros adultes ou subadultes plus un juvénile, le troisième par neuf restes. Ce matériel est comparé aux diverses espèces connues dans les mêmes familles en Europe au Ruscinien et au Villafranchien : *Tapirus arvernensis* Croizet & Jobert, 1828 et *T. jeanpiveteaui* Boeuf, 1991 pour le tapir, *Dicerorhinus megarhinus* (de Christol, 1834), *D. miguelcrusafonti* Guérin & Santafe, 1978, *D. jeanvireti* Guérin, 1972 et *D. etruscus etruscus* (Falconer, 1859) pour le rhinocéros, *Potamochoerus provincialis* (Gervais, 1859), *Sus arvernensis* Croizet & Jobert, 1828 et *S. strozzii* Forsyth Major, 1881 pour le sanglier. L'association de *Tapirus arvernensis arvernensis*, *Dicerorhinus jeanvireti* et *Sus arvernensis arvernensis* caractérise le Villafranchien inférieur (zone MNQ 16). Le degré d'évolution du *D. jeanvireti* de Milia permet de lui assigner un âge un peu plus récent que celui de Vialette. Cette même association implique un paysage végétal à dominante forestière, sous un climat humide et relativement chaud.

MOTS CLÉS
Mammalia,
anatomie,
biométrie,
biochronologie,
paléoenvironnement,
Villafranchien inférieur,
Nord-Ouest de la Grèce.

INTRODUCTION, LOCATION AND HISTORY OF EXCAVATIONS

Palaeontological research in Grevena district started in 1990, in the "Ambelia" area of Grevena town, 585 m above sea level, in western Macedonia, 190 km west of Thessaloniki, Greece (Fig. 1[GRE]). The excavations of 1992-1995 in the unconsolidated Pleistocene deposits yielded a partial skeleton of the straight-tusked elephant, *Elephas antiquus* Falconer & Cautley, 1847 (MIS – Oxygen Isotope Stage 6; Tsoukala & Lister 1998). In 1996, the same excavating team of Thessaloniki Aristotle University (A.U.TH.) followed up information given by local villagers, and discovered abundant fossilized faunal remains round Milia village, 15 km NNE of Grevena. Milia is situated in a mountainous area (altitude 656 m a.s.l.) close to the Pindos Mountain Chain (40°10'45.45"N; 21°28'36.38"E; WGS84). The locality consists of yellow-brownish loose sands, fluvial deposits of a branch of Aliakmon River, which is the longest in Greece (297 km long). It is widely known by the abundant *Mammut borsoni* (Hays, 1834) material, among which the longest tusks in the world (4.39 m and 5.02 m) (Tsoukala 2000; Agusti & Anton 2002).

There are two main sites with rhino fossils in the area: Milia (MIL) and Agios Georgios Priporos (SGP) (Fig. 1), the former being of major importance with abundant material. The most important rhino fossils are: a complete skull with part of the right hemi-mandible found in 2002 by N. Bacharidis in the MIL3 site, an almost complete skull excavated in 2008 from the MIL8 site, while the most numerous are from the MIL5 site. In 2000, in SGP, a very well preserved mandible and an ulna of a rhino, which were completely intact, were excavated. As the excavations are still in progress, many other rhino and mastodon remains continue to be brought to light from several points, and many fossils are collected by shepherds and local villagers, all deposited and displayed in the collections of the Milia Natural History Museum.

The associated fauna in this area, dominated by two species of mastodons: *M. borsoni* (Hays, 1834) and *Anancus arvernensis* (Croizet & Jobert, 1828), is under study and, in addition to rhinoceroses, suids and tapirs, consists of hipparions, bovids, cervids, carnivores (*Homotherium* sp., ursids, felids), porcupines and turtles.

ABBREVIATIONS

The following abbreviations are used (all dimensions are in mm):

abs.	absolute;
anat.	anatomical;
ant.	anterior;
apo.	apophysis;
arc.	arcus, arch;
art.	articular, articulation;
B	breadth;
cond.	condylus;
constr.	constriction;
D	deciduous premolar;
DAP	antero-posterior diameter;
DDV	dorsoventral diameter;
dia.	diaphysis;
DT	transversal diameter;
Dist.	distance;
dist.	distal;
ext.	exterior;
foram.	foramen;
H	height;
H ant.	anterior height;
int.	interior;
L	length;
maj. occip. cr.	major occipital crest;
max.	maximum;
mid.	middle;
min.	minimum;
masto	mastoideus;
M	molar;
Mc	metacarpal;
Mt	metatarsal;
n	number of specimens;
occip.	occipitalis;
orb.	orbitalis;
P	premolar;
post.	posterior;
proc.	processus;
prox.	proximal;
sup.	superior;
surf.	surface;
sust.	sustentaculum;
tuber	tuberosity;
w	width;
zygom.	zygomatic.

FIG. 1. — Map of Greece with the fossiliferous sites of Grevena area, Milia depicted. Abbreviations: **GRE**, Ambelia straight-tusked elephant site in Grevena town; **MIL**, Milia; **SGP**, Saint George Priporos.

SYSTEMATIC PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family TAPIRIDAE Burnett, 1830
Genus *Tapirus* Brisson, 1762

Tapirus arvernensis arvernensis
Croizet & Jobert, 1828

Two species of tapirs are known in the Pliocene and Pleistocene of Europe (Boeuf 1991; Guérin & Eisenmann 1994): *Tapirus arvernensis* Croizet & Jobert, 1828 and *T. jeanpiveteaui* Boeuf, 1991. The latter is a small species that is currently known only from its type-locality at Barro, near Ruffec in Charente (France); the assigned Pliocene age is not certain. The Tapir of Milia is attributed to *T. arvernensis*.

Tapirus arvernensis is slightly larger and much more common than *T. jeanpiveteaui*. It is defined in Perrier-Les Étouaires (Puy-de-Dôme, France) and anatomically it is close to recent *T. terrestris* (Linnaeus, 1758) from South America. The type-series is composed of a left hemi-mandible with P/3-M/3, a juvenile hemi-mandible with D/1-D/4 and M/1, a right I2/, an atlas and an upper molar

(Croizet & Jobert 1828: pl. II, figs 1, 3, 5 and pl. XII, figs 4-6). Although smaller, *T. arvernensis* presents proportions similar to those of *T. priscus* Kaup, 1833 of the Late Miocene of Europe (Guérin & Eisenmann 1994).

Its size corresponds to the recent *T. pinchacus* Fischer, 1829 of the Andes Mountains. Its total length reached 1.8 to 2 m, its shoulder height ranging from 75 to 80 cm and it weighed over 200 kg.

Tapirus arvernensis minor Michaux, Sigé & Sudre, 1976, is a subspecies defined in the sands of Montpellier (Early Ruscinian, zone MNQ 14), which is smaller and more slender than the nominate subspecies. The authors revived a species name created in 1839 by M. de Serres, but later on abandoned it because it was a recent synonym of *T. arvernensis*. *Tapirus a. arvernensis* is known in the Late Ruscinian (MNQ 15) of Roussillon and the Villafranchian of the Massif Central (Michaux *et al.* 1976).

Guérin & Eisenmann (1994) characterized *T. arvernensis* anatomically as follows: compared to *T. terrestris*, the mandible of *T. arvernensis* shows the same proportions as the Late Miocene European *T. priscus*, including a relative height of the corpus that differs from the extant species. The relative lengths of the upper premolars and molars differ from those of extant species: compared to *T. terrestris* the P1/ and P2/ are longer while the M1/, M2/ and M3/ are shorter. In *T. arvernensis arvernensis* the average lengths of the lower premolars are smaller than those of *T. terrestris* (they are the same as in *T. pinchacus*), except for P/2 and P/4; P/2 and P/3 which are large; the posterior widths of P/3 and P/4 are roughly equivalent to those of *T. priscus*. The average length of M/1 is barely greater than that of the P/4. The relative width of P/3 and P/4 is the only characteristic that seems to distinguish European Miocene and Pliocene tapirs from extant tapirs (with the exception of *T. pinchacus*). The long bones have proportions reminiscent of a small *T. terrestris* with particularly robust diaphyses.

Tapirus arvernensis is known in the Ruscinian formations of Montpellier and Perpignan (MNQ 14 and 15 zones) and is remarkably abundant in Vialette and common in Perrier-Les Étouaires, both sites of Early Villafranchian age (zone MNQ 16). It is attested by a tooth fragment in the Late Villafranchian site (zone MNQ 18) of Le Coupet in Haute-Loire (Heintz *et al.* 1974), which is perhaps the youngest occurrence of European tapirs. However, if the remains of *T. arvernensis* of Tegelen (Netherlands) are contemporary with *Sus strozzii* Forsyth Major, 1881 and *Dicerorhinus mercki* (Jäger, 1839) of the same deposits, this species may extend up to the very early Middle Pleistocene (the stratigraphic position of Tegelen large mammals is unclear, see this topic in Guérin 1980: 978, 979). *Tapirus arvernensis* is well represented in the Late Ruscinian and Early Villafranchian of Italy. Thus, it is found in the upper levels of the Casino, Meleto, Barga and Pieve Fosciana (Garfagnana), Sarzanello and Ponzano Magra in Val di Magra, in Gaville and Santa Barbara (both in the Upper Valdarno), and in Monticchiello in Tuscany. It is also known in Monte Biancano and Vignola in Emilia Romagna, in Villafranca d'Asti and Triversa in Piedmont, in Livergnana and Sasso di Glosina near Bologna, in Spoleto in Umbria, in Castel San Pietro (Nera Montoro) in Latio (Kotsakis 1986; Rustioni 1992). According to Rook & Rustioni (1991), it is surely present in the V3 level of Baccinello in Tuscany, probably of Latest Turolian age (MN 13). *Tapirus arvernensis* is also known from the Early Villafranchian of Hajnacka in Slovakia (Fejfar 1964; Janstova 2004). In Romania, Radulescu *et al.* (2003), reported *T. arvernensis* in the Dacian Basin in Malusteni (MNQ 15a), and in the Brasov Depression in Capena (MNQ 15b), Vargha (MNQ 15b), Iaras 1 (MNQ 16), Araci-Fântâna Fagului (MNQ 16a) and in the Ilieni Basin (MNQ 16).

The species had not hitherto been studied in Greece. There is only a short reference by Paraskevaidis (1977) of three upper cheek teeth of *Tapirus* sp. from Servia (W. Macedonia), without description and measurements, but the present location of the specimen is unknown.

Material

– A fragment of right hemi-mandible of a juvenile MIL 649, with the alveoli of D/2 and D/3, with D/4 and M/1; M/2 is unerupted, thus it is not measurable.
– Calcaneum of an adult MIL 1282 dex.

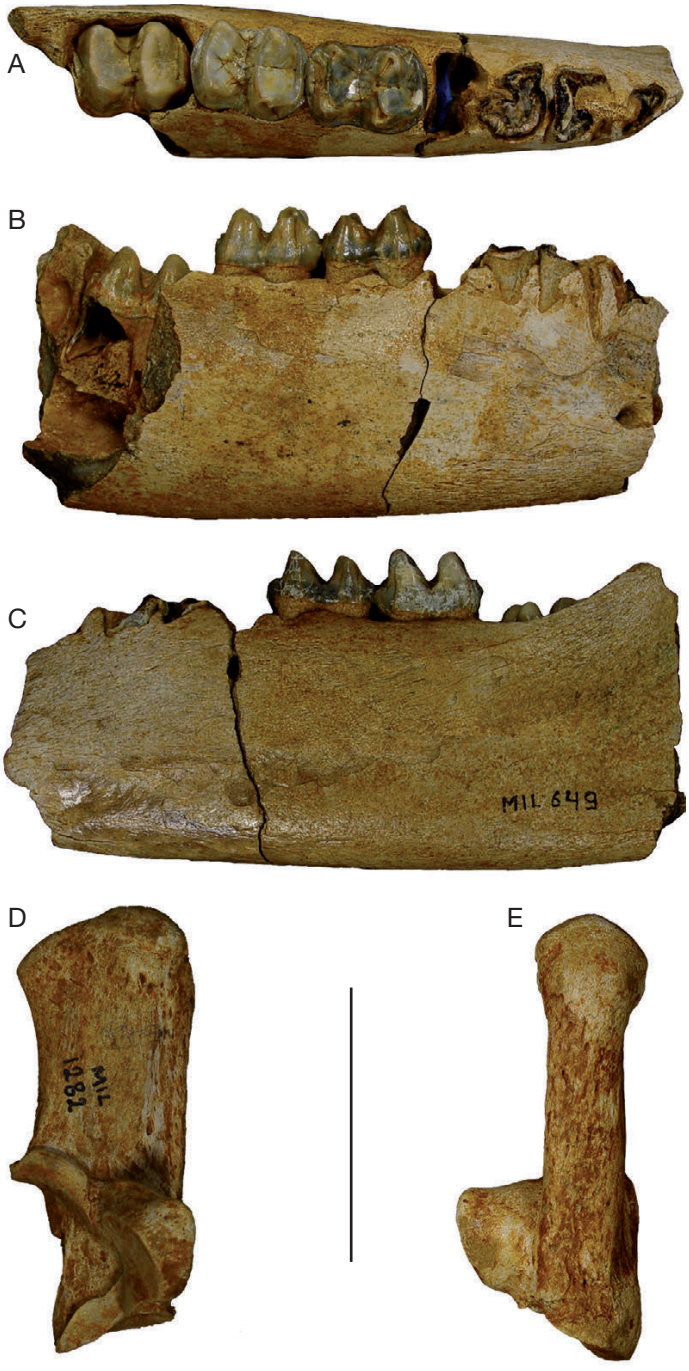

FIG. 2. — The Milia *Tapirus arvernensis arvernensis* Croizet & Jobert, 1828: **A**-**C**, fragment of right juvenile hemi-mandible MIL 649; **A**, occlusal view; **B**, buccal view; **C**, lingual view; **D**, **E**, right calcaneum MIL 1282 of adult; **D**, medial view, **E**, posterior view. Scale bar: 50 mm.

Description

The mandible fragment and teeth

On the mandible fragment (Fig. 2A-C), the height of the corpus between D/4-M/1 reaches 46.5 mm and its transverse diameter at the same level is 27 mm. For nine specimens of *T. arvernensis* the height between P/4 and M/1 averages 46.1 mm (range: 42 to 49.8 mm). The lower cheek teeth have the characteristic appearance of the family with their two transversal ridges and anterior and posterior cingula, particularly well distinguished on the M/1 and M/2 (Fig. 2A-C). The dimensions of the teeth are given in Table 1 (see Appendices), the specimen belongs to juvenile, the D/4 is slightly worn, and the M/1 is not worn at all; the M/2 is not measurable. The Milia M/1 slightly exceeds the average length of 13 specimens of *Tapirus arvernensis arvernensis*, and the two widths are equal to the maximum values measured on a sample of 11 specimens of the same subspecies; thus, in Milia we are dealing with the nominate Villafranchian subspecies, larger than the Ruscinian one.

Janstova (2004) gives some dimensions of undifferentiated M/1 and M/2 which were collected during the new excavations in Hajnacka : length 22 to 23 mm for five specimens, anterior width 14 to 17 mm for 12 specimens.

Calcaneum

This bone looks very rhinocerotoid (Fig. 2D, E) with elevated tuberosity, the beak (= foremost part of the bone) extending at least as far as the tuberosity, and the relatively small sustentaculum tali perpendicular to the vertical axis of the bone.

The dimensions of the calcaneum are in Table 1 (see Appendices).

Compared to a sample of nine to ten specimens of *T. arvernensis* from the Ruscinian of Montpellier (one specimen) and from the Early Villafranchian of Vialette (all others), the Milia calcaneum is particularly large: the observed maximum values of its dimensions exceed all the others

Owing to the largest size of the nominate subspecies this tends to confirm its subspecific identification, but the insufficient size of our comparison sample do not allows us to know precisely the extreme values of the calcaneum dimensions and then prevents us to be certain of it.

Conclusion of the anatomical study of the tapir

Because of their size, the remains of the Milia tapir, which are larger than those of *Tapirus arvernensis minor*, can therefore be attributed to *T. arvernensis arvernensis*.

Biostratigraphic implications

While *Tapirus arvernensis minor* is characteristic of the Early Ruscinian (zone MNQ 14), *T. arvernensis arvernensis* is a subspecies typical of the Late Ruscinian (zone MNQ 15) and the Early Villafranchian (MNQ 16), its presence in more recent levels seems exceptional.

Palaeoecological implications

A consensus has been reached that the fossil tapirs with anatomical characteristics similar to those of extant species, which is the case of *T. arvernensis,* indicate similar ecological requirements : warm climate, dense forest, moist environment and proximity to sufficient amount of water (Eisenmann & Guérin 1994; Guérin & Eisenmann 1994).

Sub-order CERATOMORPHA Wood, 1937
Family Rhinocerotidae Owen, 1845

Genus *Dicerorhinus* Gloger, 1841

Dicerorhinus Gloger, 1841: 125.

Didermocerus Brookes, 1828: 75 (invalidated in 1977, opinion 1080, by the ICZN because it was published in a catalogue).

Atelodus Pomel, 1853: 114, junior synonym.

Ceratorhinus Gray, 1867: 1021, junior synonym.

Stephanorhinus Kretzoï, 1942: 312-314, 341, junior synonym.

Procerorhinus Kretzoï, 1942: 315, junior synonym.

Dicerorhinus jeanvireti Guérin, 1972

Dicerorhinus jeanvireti Guérin, 1972: 133-136, pl. I; 1980: 607, 608. — Hooijer 1981: 472; 1985: 35-37. — Holec 1996: 219-222. — Durisova 2004 : 99.

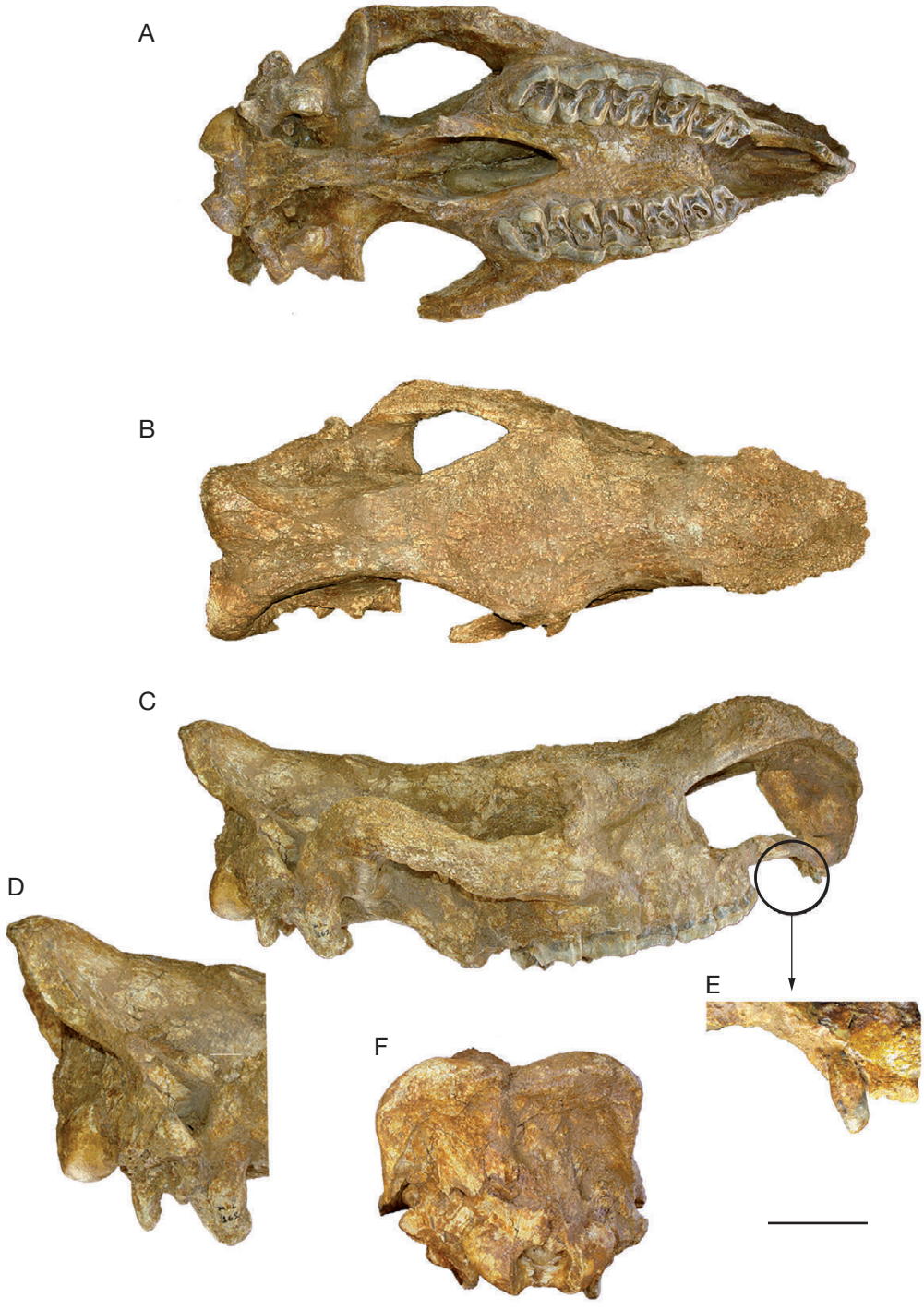

FIG. 3. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 skull MIL 162: **A**, ventral view; **B**, dorsal view; **C**, right side view; **D**, right side view, detail of the tympanico-occipital region; **E**, right side view, enlargement of the premaxillary area with I2/*in situ*; **F**, occipital view. Scale bar: 100 mm.

Rhinoceros elatus Croizet & Jobert, 1828: 144-154. In pursuance of the article 23.12 of the International Code of Zoological Nomenclature, *nomen oblitum* because explicitly rejected by Guérin (1972), i.e. between 6th November 1961 and 1st January 1973, following the article 23b then in force between those dates.

Atelodus aymardi – Pomel 1851-52: 80, *nomen nudum*.

Rhinoceros mesotropus – Aymard *in* Pictet 1853: 298, *nomen nudum*.

Rhinoceros velaunus – Aymard *in* Pictet 1853: 298, *nomen nudum*.

Rhinoceros etruscus – Falconer 1868: 367. — Depéret *et al.* 1923: 37.

Rhinoceros etruscus var. *astensis* – Sacco 1895: 1-31, pls I-IV. Owing to the article 23.12 of the International Code of zoological nomenclature, *nomen oblitum* because explicitly rejected by Guérin (1972), i.e. between 6th November 1961 and 1st January 1973, following the article 23b then in force between those dates.

Rhinocéros de Vialette – Viret 1954: 154, text-fig. 35 and 42.

Dicerorhinus cf. *megarhinus* – Thenius 1955: 10, 11, pl. I, figs 1-4 (non *Rhinoceros megarhinus* de Christol, 1834).

Rhinoceros aff. *megarhinus* – Bout 1960: 188, 189.

Rhinoceros sp. – Bout 1960: 71.

Dicerorhinus megarhinus – Kurtèn 1963: 10, table 1. — Fejfar 1964: 89-101, fig. 47-55.

Rhinoceros megarhinus – Azzaroli 1963: 17.

"À Vialette, forme qui ressemble plutôt au *Rhinoceros megarhinus* de Montpellier qu'au *Rhinoceros etruscus*" – Hürzeler 1967: 635.

Rhinoceros megarhinus astensis – Hürzeler 1967: 636.

Stephanorhinus jeanvireti – Campanino *et al.* 1994: 452, 453. — Mazo 1995: 287. — Gliozzi *et al.* 1997: 171, table 1.l. — Spassov 2005: 203, 204. — Lacombat & Mörs 2008: 160.

Stephanorhinus cf. *elatus* in the sites of Covrigi, Iaras 2 and Ilieni – Radulescu *et al.* 2003: 3, 8.

S. elatus in the sites of Groserea, Cernutesti and Araci-Fântâna Fagului. — Radulescu *et al.* 2003: 3, 4, 8.

Stephanorhinus elatus – Radulescu 2005: 193.

The Ruscinian and Villafranchian European rhinos

Four species of rhinoceros are known in the Ruscinian and Villafranchian of Europe (Guérin 1980), all belonging to the genus *Dicerorhinus* (McKenna & Bell 1997): the Ruscinian *D. megarhinus* (de Christol, 1834), the Late Ruscinian *D. miguelcrusafonti* Guérin & Santafe, 1978, the Early Villafranchian *D. jeanvireti* Guérin, 1972 and the Villafranchian *D. etruscus etruscus* (Falconer, 1859). All remains of the Milia rhinoceros correspond to *D. jeanvireti*.

The genus *Dicerorhinus* Gloger, 1841 is represented today by *D. sumatrensis* (Fischer, 1814): it has many Neogene and Quaternary species in Eurasia and Africa.

Croizet & Jobert (1828: 144-154, pl. I, fig. 7, pl. IV, figs 3-6, pl. V, figs 1-4, pl. VI, figs 1, pl. XI, pl. XII, figs 1, 2, 8) had proposed the name of *Rhinoceros elatus* for the Auvergne rhinoceros whose remains belonged to a mixture of several species, including *D. etruscus* and *D. jeanvireti*, according to the dimensions given in the book of Croizet & Jobert (1828). The exact location of that material is unknown. An important part of it was gathered in Perrier-les Étouaires, where *Dicerorhinus etruscus* and *D. jeanvireti* are sympatric. Another part, namely the mandible, which is the first rhino remain described by Croizet & Jobert (1828: 144-146), is from Malbattu, a much more recent site where *D. etruscus* is the sole rhino (Guérin, 1980). Such a mixture and the lack of diagnostic characteristics are enough to invalidate the specific name *elatus*, also completely forgotten for more than a century, but the fact that the Croizet & Jobert's name is clearly a nomen oblitum is sufficient to discard it.

Dicerorhinus jeanvireti Guérin, 1972 is a very large rhino with slender legs. The massive facial area is very long; the nasals are quite large and reach far forward, bearing an ossified septum in their anterior part. The pseudo-auditory meatus is closed ventrally. The mandible bears a long symphysis and presents a slightly convex lower edge.

The M1/ and the M2/ have an almost flat ectoloph with a very slight paracone fold; there is always a crochet, rarely a crista; the protocone is constricted, there is no internal cingulum. The

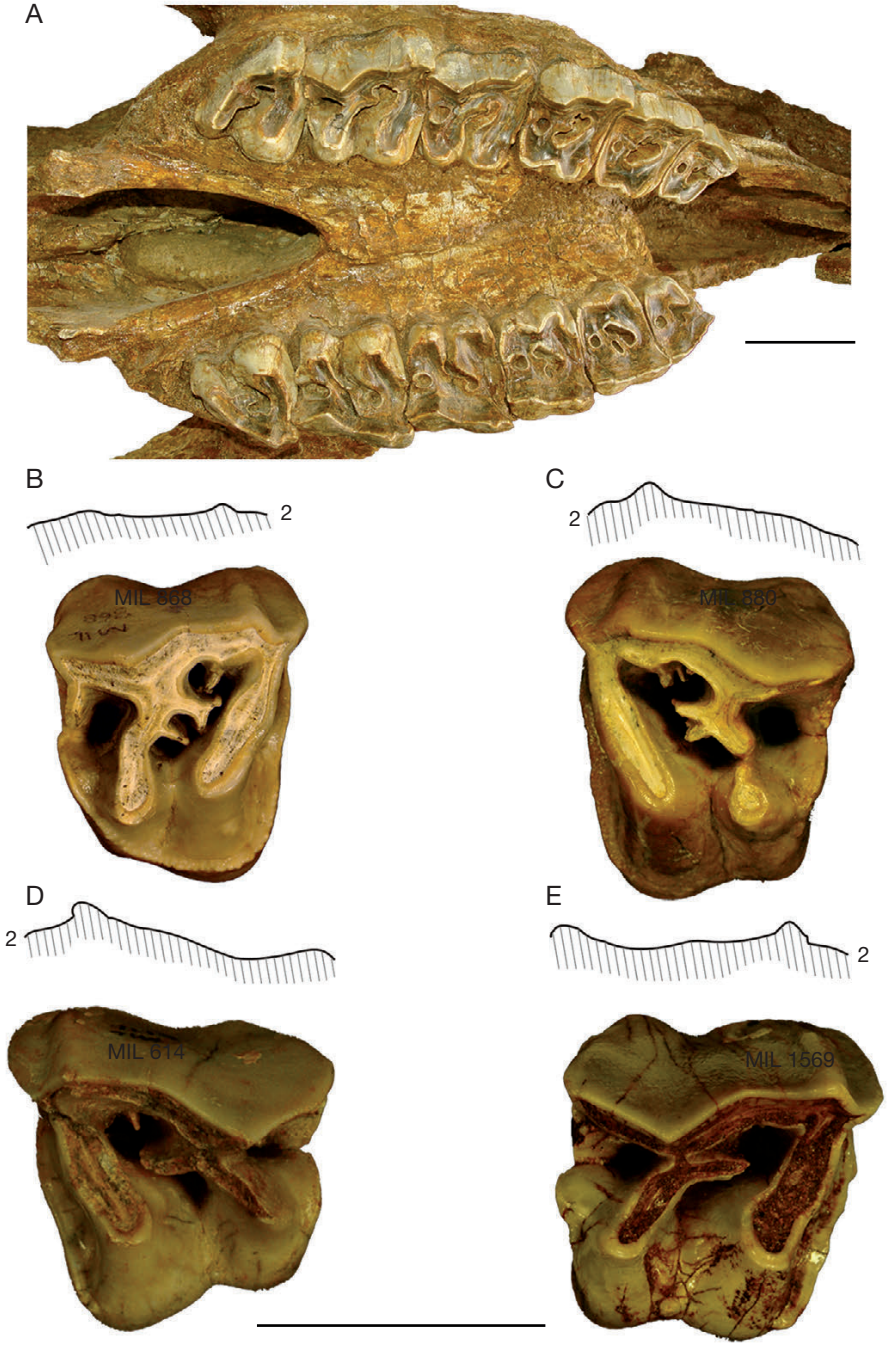

FIG. 4. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 upper cheek teeth: **A**, tooth-rows of the skull MIL162, occlusal view; **B**, isolated P4/right MIL 868 (occlusal view) and ectoloph profile at 2 cm from the collar; **C**, isolated P4/left MIL 880 (occlusal view) and ectoloph profile at 2 cm from the collar; **D**, isolated M1/left MIL 614 (occlusal view) and ectoloph profile at 2 cm from the collar; **E**, M1/isolated right MIL 1569 (occlusal view) and ectoloph profile at 2 cm from the collar. Scale bars: 50 mm.

P3/ and the P/4 with an almost flat ectoloph and a very small paracone fold, always present a crochet, very frequently a crista and often a closed medifossette; the protocone is not constricted and there is always a lingual cingulum. The long bones are very large and slender, the limb segments 2 (radius, tibia) and 3 (metacarpals, metatarsals) are very elongated, and the median metapodials are long and relatively slender.

The species, defined in Vialette, is also known in other French sites, such as Perrier-Les Étouaires and the Desnes-Vincent-Bletterans region near Dôle.

It is present in the Early Villafranchian of Italy, in Becchi di Castelnuovo Don Bosco (Astigiana), Dusino, Villafranca d'Asti (Piedmont), Capannoli, Montopoli (Lower Valdarno), Pradalbino (Monteveglio, District of Bologna), the Siena region (Guérin 1972, 1980). More recently Campanino *et al.* (1994) described in detail beautiful post-cranial material discovered in Roatto, near Villafranca d'Asti.

Dicerorhinus jeanvireti is probably present in the Netherlands, in the Scheldt Estuary (Hooijer 1981) and in Linden (Hooijer 1985). It is quoted from Germany in the Hambach lignite mine , West of Cologne (Lacombat & Mörs, 2008), a site no farther north than the two preceding ones. It has been recognized in Czechoslovakia, in Hajnacka (Fejfar 1964 ; Durisova 2004) and in Strekov (Schmidt & Halouzka 1970). It was also reported in Bulgaria, in Musselievo (Late MNQ 15 following Spassov 2005), a site which may be the oldest locality of the species.

Finally, in Romania Radulescu *et al.* (2003) reported "*Stephanorhinus elatus*" or "*S.* cf. *elatus*" in the Brasov Iaras – 2 Depression (MNQ 16a), in Araci-Fagului Fantana (MNQ 16a), in Ilieni Basin (MNQ 16) and Cernatu (MNQ 16), and in the Dacian Basin, in Covrigi (MNQ 16a), Groserea (MNQ 16a) and Cernatesti (MNQ 16a), all three in Oltenia.

Lacombat & Mörs (2008) pointed out that the Early Villafranchian rhinos of Kvabebi (Georgia), and of Udunga and Nizhnavodyanoy (Russia) could be *D. jeanvireti*.

Dicerorhinus jeanvireti is characteristic of the Early Villafranchian (zone MNQ 16).

Material

Most of the 1685 fossils from Milia belong to *Mammut borsoni*. 197 pieces are attributed to rhinoceros; 144 are bones and bone fragments, 35 are isolated teeth and tooth fragments, 16 are mandibles and mandible fragments with teeth, a maxilla fragment with upper cheek teeth and two skulls: an almost complete one with complete dentition and a cranial dome. From the postcranial skeleton very few bones are complete, while 68 specimens are measurable and listed as follows:

– two skulls: a skull with complete dentition MIL 162, which is associated with the right hemi-mandible fragment and a facially incomplete skull MIL 1501 without its teeth;

– a fragment of right maxilla MIL 1476, with P2/ damaged and P3/;

– twelve complete or fragmentary mandibles: a mandible with right P/2-P/4 and left P/3-M/1 MIL 658; a mandible with complete tooth rows SGP 1; a right hemi-mandible with M/2-M/3 MIL 244; a left hemi-mandible fragment on the skull associated with M/2-M/3 MIL 162a; a right hemi-mandible with full dentition MIL 281; a right hemi-mandible fragment with M/2-M/3 MIL 245; a right hemi-mandible fragment with M/3 incomplete MIL 1477; a fragment of ramus MIL 267; a right hemi-mandible fragment with D/1 and D/2 MIL 425; a left hemi-mandible fragment with P/2 and P/3 incomplete and P/4 MIL 245; a right hemi-mandible fragment with P/4 and fragments of molars MIL 1324 ; a right hemi-mandible fragment with M/1 MIL 1478;

– an isolated P3/ MIL 806 sin; three isolated P4/: MIL 868 dex, MIL 880 sin and MIL 1287 dex; two isolated M1/ MIL 614 sin and MIL 1569 dex; an isolated M2/ MIL 1197 sin; an isolated M3/ MIL 1119 dex; an isolated M/1 MIL 837 dex; two isolated M/3 MIL 1145 dex and MIL 1343 sin;

– a right scapula fragment MIL 205;

– three distal humerus fragments: MIL 673 dex, MIL 751 dex and MIL 841 sin;

– seven radius fragments: MIL 611 dex (proximal half); MIL 656 sin (distal epiphysis); MIL 657 sin (proximal two-thirds); MIL 987 sin (proximal epiphysis); MIL 1315 sin (two-thirds proximal);

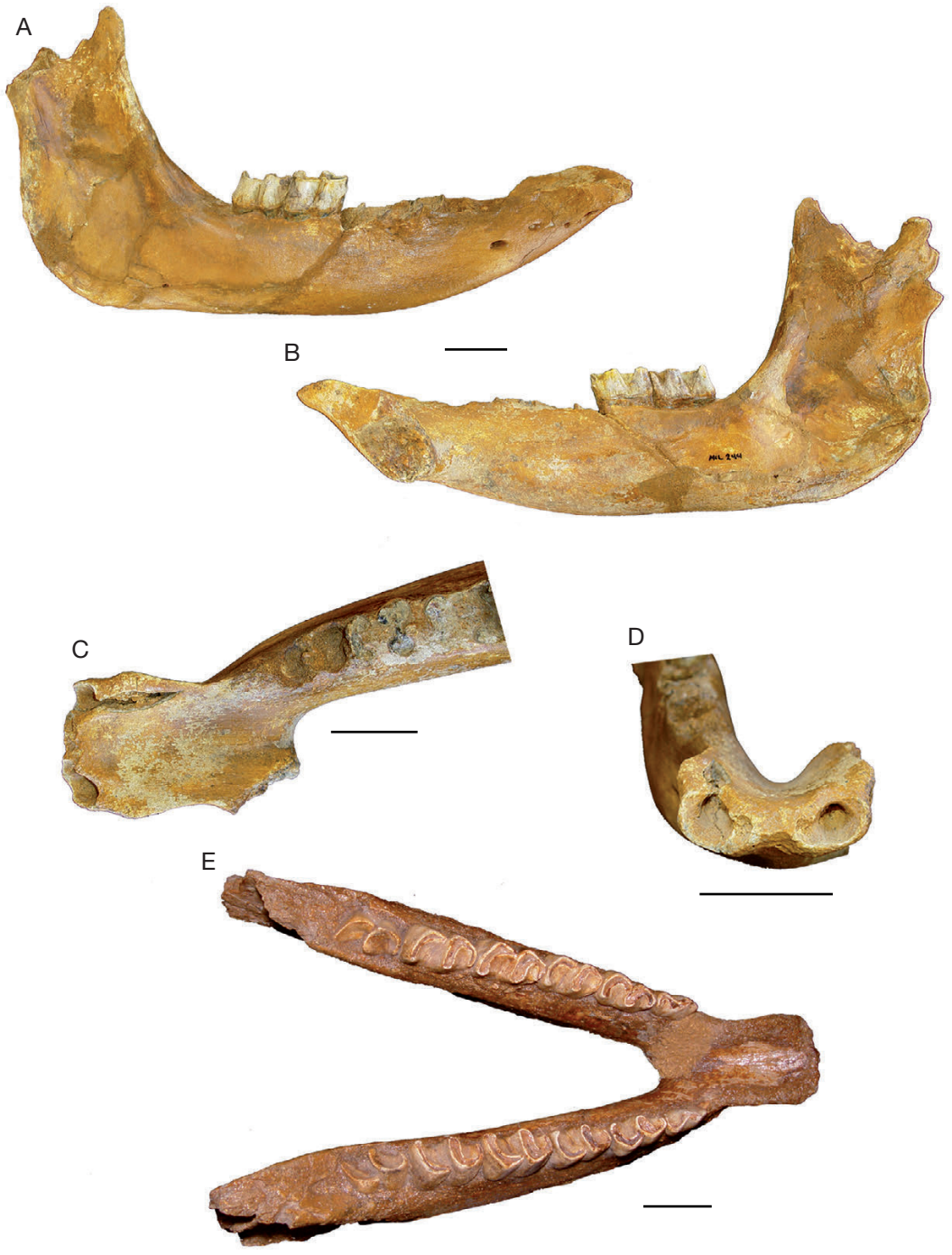

FIG. 5. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 mandibles: **A**-**D**, right mandible with M/2-M/3 MIL 244; **A**, lateral view; **B**, medial view; **C**, dorsal view of symphysis; **D**, anterior view of the symphysis; **E**, mandible with right and left complete tooth rows, GSP1, occlusal view. Scale bar: 50 mm.

MIL 1387 dex (proximal third); MIL 1541 sin (proximal third);
– two ulnae: a complete GSP 2 (sin) and an incomplete MIL 1582 (proximal fragment);
– a magnum MIL 758 dex (incomplete);
– two Mc III: a complete MIL 1587 dex and an incomplete MIL 902 sin (proximal half);
– four femur fragments: MIL 613 (caput), MIL 813 (caput), MIL 651 dex (distal fragment) and MIL 811 (distal fragment);
– two patellae : MIL 340 dex and MIL 1645 sin.
– five complete or fragmentary tibias: MIL 819 dex (complete); MIL 612 dex (distal two-thirds); MIL 1582 sin (distal fragment); MIL 1642 sin (distal fragment); MIL 1645 sin (distal fragment).
– four astragali: MIL 181 dex, MIL 367 sin, MIL 852 sin, MIL 1192 (fragment);
– a complete calcaneum MIL 1703 sin and a calcaneum fragment MIL 723 sin;
– a complete cuboid MIL 1665 dex;
– two Mt III: MIL 368 dex (complete) and MIL 710 sin (proximal fragment);
– two Mt IV: MIL 204 sin (complete) and MIL 767 dex (proximal fragment);
– three distal metapodial fragments, undifferentiated: MIL 741 (axial), MIL 1407 (axial), MIL 1440 (abaxial);
– three phalanges: MIL 206 (Ph I axial, complete), MIL 347 (Ph I abaxial, complete), MIL 1385 (Ph III, fragment).

Sesamoids have not been studied, nor have vertebrae and ribs, or small fragments.

The entire sample is attributed to *Dicerorhinus jeanvireti*.

The most abundant anatomical specimen represented among the Milia rhino material is the mandible, which consists of two sub-complete adult specimens and nine more or less fragmentary hemi-mandibles; seven right (including a juvenile) and two left ones. Radius follows, seven of which are studied: five left (four of which are proximal fragments) and two right (both proximal) ones, whose matching remains are doubtful.

In conclusion, among the Milia material there are at least eight rhino individuals, adults or subadults and a juvenile one.

Description

The reference material used for the Simpson diagrams is the average of 30 to 40 adult individuals of the recent *Diceros bicornis* (Linnaeus, 1758), the African "Black" Rhinoceros (values in Guérin 1980, plus a few new specimens).

Skull

The "wedge-shaped" general form of the Rhinocerotidae skulls is evident in inferior and superior view (Fig. 3A, B). In profile view (Fig. 3C-E), the relative length of the massive facial area is great, which is characteristic of the genus and the species: the ratio of the distances outer occipital bump-ante-orbital process (variable 8 in Table 2 [see Appendices]) / occipito-nasal length (variable 1) reaches 0.57 and 0.56 for the two Milia skulls when the average values are 0.556 for *D. megarhinus* and 0.55 for *D. etruscus etruscus*. The elevation of the massive major occipital crest is well marked; it overhangs the occipital condyles behind. The tip of the nasals extends forwards to the tip of the premaxillae as in the Vialette specimens; the ossified nasal septum extends forwards to the tip of the nasals. On the skull MIL 162 the ossified nasal septum is more than 121 mm in length (it is broken further back), its maximum thickness (back and base of the posterior fracture) reaches 11.5 mm. The skull MIL 1501 shows no trace of ossified nasal septum, but the absence of teeth does not allow the estimation of the age for this individual, which might not be fully adult; note also that Thenius (1955) suggested that there are a few adult specimens of *D. etruscus* in which this wall is not ossified probably representing females. The nasal septum is never ossified in *D. megarhinus*.

The post-glenoid apophysis is very wide from front to rear, more vertically developed than the post-tympanic and paroccipital apophyses and it is tilted forward and down (Fig. 3D). The post-tympanic apophysis is very short. The paroccipital apophysis is quite long, sub-vertical, and bends slightly forwards at the end. In the skull MIL 162, the level of the posterior end of the nasal notch is between P3/-P4/; this position varies from the middle of P3/ to the interval P3/-P4/ in the two specimens of *D. jeanvireti* from Vialette. The infraorbital foramen is above the middle of P4/, it is

FIG. 6. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 radius, ulna and tibia: **A**, **B**, incomplete distal left radius MIL 657; **A**, proximal view; **B**, anterior view; **C**, left ulna SGP 2; **D**-**F**, right tibia MIL 819; **D**, front view; **E**, proximal view; **F**, posterior view. Scale bars: 50 mm.

more anterior in Vialette (interval P3/-P4/ in front of P4/). Finally, the level of the anterior border of the orbit is above between M2/ and M3/, it is above the midst of M2/ on the only Vialette skull where it is observable. Antoine (2002) showed that generally in the family Rhinocerotidae, evolution is reflected by a receding of these relative positions. In superior view (Fig. 3B), the insertion of the posterior horn (frontal) is very broad, and that of the anterior one (nasal) is well marked. The front of the nasal bone is rounded with a small recess in the sagittal plane. The major occipital crest of the skull MIL 1501 is greatly depressed in the middle, while the skull MIL 162 is less concave in its central part. The ante-orbital processes are strong, the supra-orbital ones are slightly prominent and the post-orbital ones are very low.

The occipital (Fig. 3 F) is nearly vertical in its lower and middle parts, and tilted slightly backwards and upwards in its superior part. The depression in the centre of the major occipital crest is clearly visible from this angle. In ventral view (Figs 3A; 4A), the basioccipital muscular tubercule is strong. For the skull MIL 162 the posterior part of the post-palatal notch is posterior to M2/ and it is more advanced (interval M1/-M2/) in the only Vialette skull where such an observation is possible.

The skulls of the Milia rhinos clearly differ from those of *D. megarhinus* : the latter especially possess thicker and wider nasals which are free at their rostral end, whithout any ossified septum, and a longer nasal notch ; the major occipital crest is less depressed medially and with a small central bump ; shape and relative lengths of the postglenoidal, post-tympanical and paroccipital apophysis are different.

The dimensions are given in Table 2 (see Appendices). All measurements exceed those of *D. etruscus* and are slightly lower than those of *D. megarhinus*. Most of them are close to those of the two skulls of Vialette *D. jeanvireti*. The latter, although of similar general proportions, are, however, smaller than those from Milia : in Vialette they are shorter, their nasal notch is shorter, their cranial dome is narrower; the rear of the nasal notch, the infraorbital foramen, the anterior border of the orbit and the rear of the post-palatinal notch are all more reduced in Milia than in Vialette. Due to the small sample available, the only Plio-Villafranchian rhino of Europe in which evolutionary trends have been highlighted in the skull is *Dicerorhinus etruscus etruscus*: they particularly include the increasing distance of the nasal notch-orbit and the enlargement of the cranial dome (Guérin 1980). It is very likely that these trends are similar to *D. jeanvireti*, which belongs to the same subgenus, in which case the Milia specimens are more advanced and therefore somewhat more recent than those of Vialette.

Mandible

The ventral edge of the horizontal branch (corpus) is straight in profile view (Fig. 5A, B). The mandibular foramen is at the alveolar border. The scalloped talon is very prominent backwards, a little beyond the posterior edge of the condyles.

The anterior border of the ramus is subvertical, barely oblique backwards and upwards, in its upper part.

In superior view the symphyseal region (Fig. 5C, E) shows the slightly spatulate space, observed in *D. megarhinus* and *D. jeanvireti* (Guérin 1980). The ventral side of the symphysis bears no median crest. The specimen MIL 244 bears on the front border of the symphysis two small alveoli for I/1, and two large alveoli for I/2, which were well developed into small tusks (Fig. 5D). The spacing between the two tusks is 27 mm and the right alveolus (the only well preserved one) has DT = 19 mm for DDV = 15 mm. The alveoli of the tusks are smaller for MIL 658 (DT = 10 mm, DDV = 9 mm) and less far apart (20.5 mm); these external alveoli, especially for MIL 244, are larger than those typically observed in *D. jeanvireti*. Altough not functional as were the very large I/2 of the Miocene *Dicerorhinus*, which were powerfull weapons, the down-sized I/2 of *D. megarhinus*, button-shaped with a diameter of about 1 cm and a length of about 2 cm, are clearly larger than those of *D. jeanvireti*.

On the mandible GSP 1 the posterior edge of the symphysis is in the middle of P/2, on MIL 658 it is in the middle of P/3 and on MIL 281 it is in the rear of P/3; the position being more distant than in seven specimens of *D. jeanvireti*, where it further forwards (Guérin 1980): it ranged from the mid-P/2 to the extreme front of P/3. Antoine (2002) showed

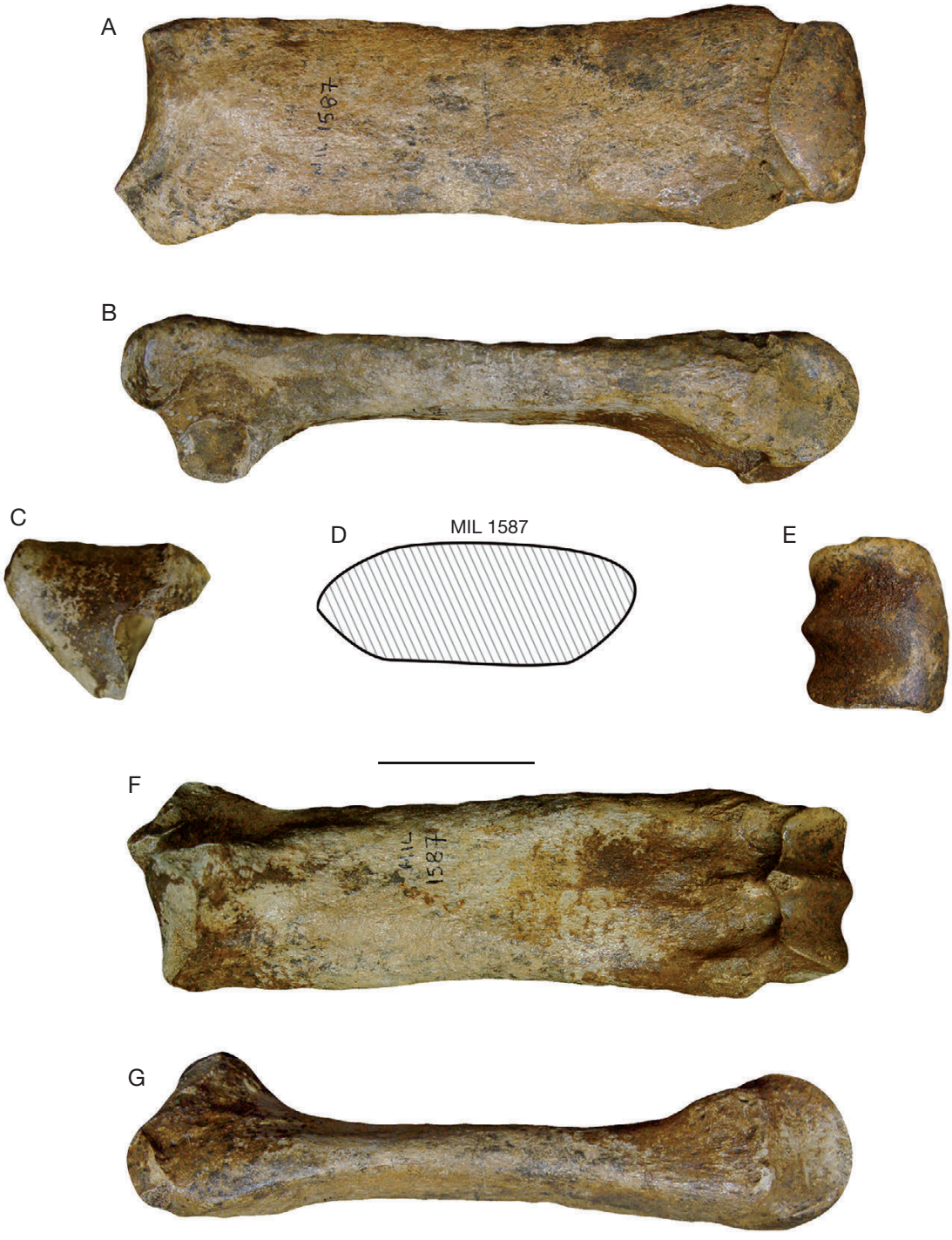

FIG. 7. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 right Mc III MIL 1587: **A**, anterior view; **B**, lateral view; **C**, proximal view; **D**, ross section of diaphysis in the middle; **E**, distal view; **F**, posterior view; **G**, medial view. Scale bar: 50 mm.

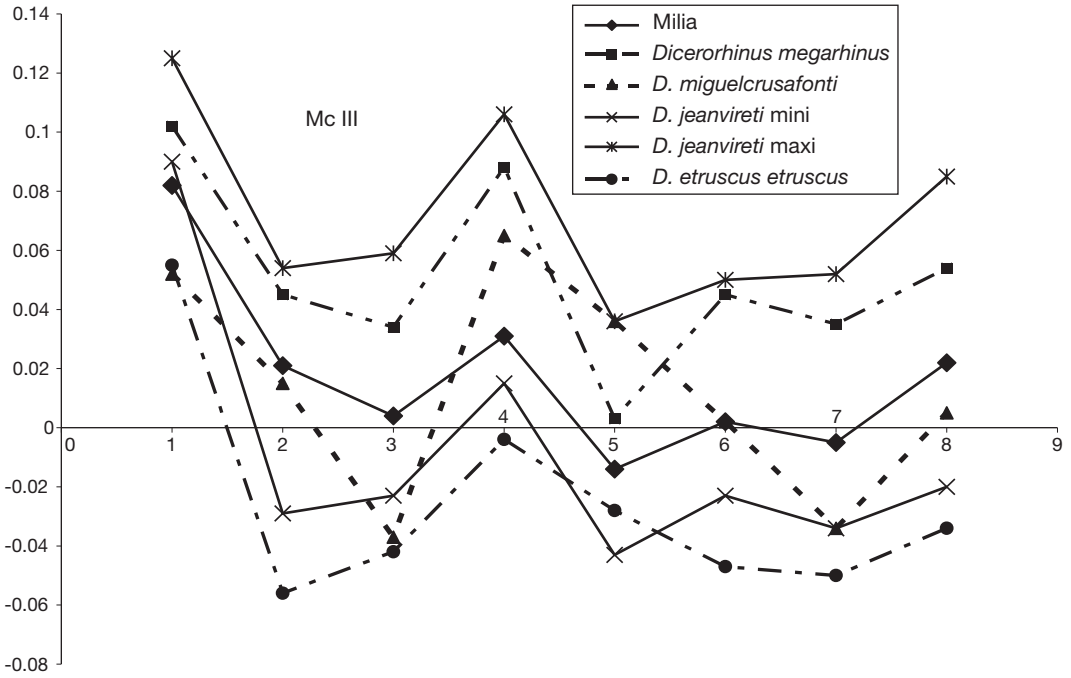

Fig. 8. — Simpson diagram of Mc III: Values of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 specimen, compared to extreme values of *D. jeanvireti* and average values of *D. megarhinus* (de Christol, 1834), *D. miguelcrusafonti* Guérin & Santafe, 1978 and *D. etruscus etruscus* (Falconer, 1859). The variables on the X axis are the same and in the same order as in Table 6 (see Appendices).

that among Rhinocerotidae, the relative position of the posterior border of the symphysis usually tends to recede during the evolution of the family.

The dimensions of the mandibles are given in Table 3 (see Appendices). They are all in the range of variation of 2 to 14 specimens of *D. jeanvireti*, while those of 2 to 42 specimens of *D. etruscus etruscus* are smaller and those of 1 to 42 specimens of *D. megarhinu*s are a little larger.

Although of more or less similar dimensions the mandibles of the Milia rhinos clearly differ from those of *D. megarhinus*: the latter especially possess a more elongated symphysis, a longer, thicker and lower corpus, a talon more proeminent backwards and an anterior border of the ramus oblique backwards and upwards.

Upper teeth

An anterior upper tooth is preserved on the right side of the skull MIL 162 (Fig. 3E). This is the first time that an upper front tooth is seen in Pliocene and Pleistocene rhinoceroses of Europe. Conical, high, it goes just beyond the base of the premaxilla and is located at the base of this bone, 76.5 mm in front of P2/ in the same side, and 54 mm from the rostral end of the intermaxillary; it is probably a dI/2 or I/2, the inability to assess the thickness of the enamel prevents its determination as a deciduous or permanent tooth. Its transversal diameter is 9 mm, the antero-posterior diameter is 10 mm and its height reaches 22.5 mm. This incisor does not show any obvious trace of wear and lacks occlusion, thus it was not functional.

The cheek teeth of the skull MIL 162 (Fig. 4A) are all present but worn.

The protoloph of P2/ is notched in the middle, while the only internal fold is a crista and there is a continuous lingual cingulum.

On the P3/ ectoloph there is a strong parastyle, also there is a small paracone fold and a very small metacone fold. Crista and crochet are present and on the left tooth, the two folds merge distally to

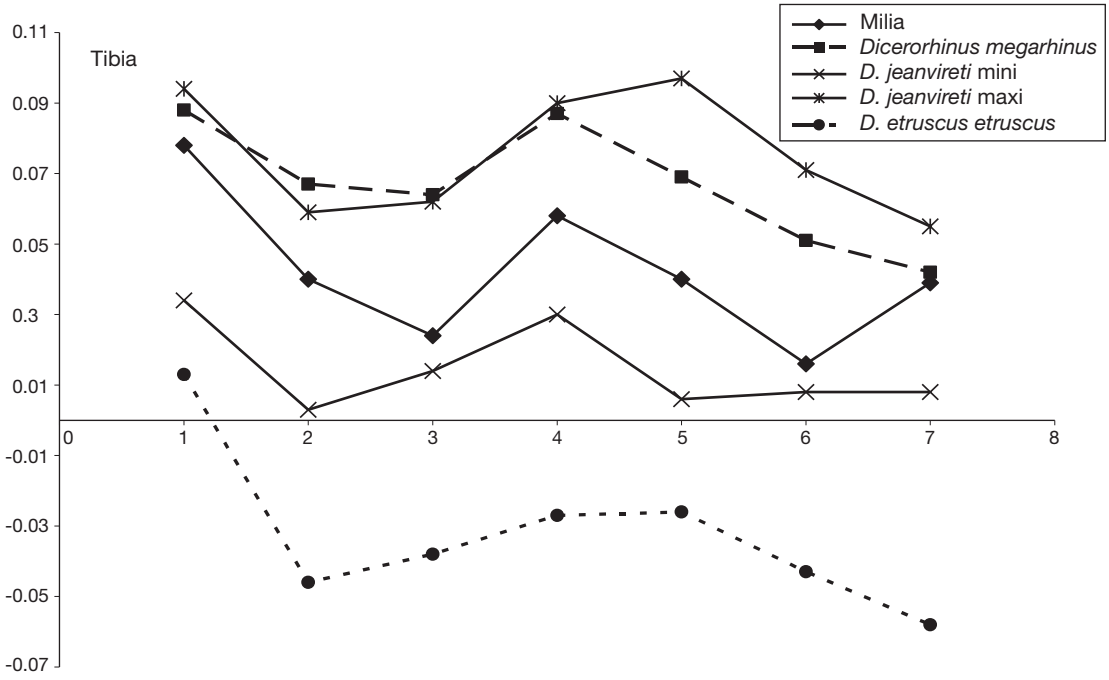

FIG. 9. — Simpson diagram of tibia: values of complete the Milia *Dicerorhinus jeanvireti* Guérin, 1972 specimen, compared to extreme values of *D. jeanvireti* and average values of *D. megarhinus* (de Christol, 1834) and *D. etruscus etruscus* (Falconer, 1859). The variables on the X axis are the same and in the same order as in Table 7 (see Appendices).

form a closed middle fossette. The lingual cingulum is discontinuous. On maxilla fragment MIL 1476, the P3/ has no crista. The unworn isolated P3/ MIL 806 has a multiple crochet and a small crista, no constriction of protocone or lingual cingulum and there is a small mesostyle. The height of the crown is 43.5 mm and has a hypsodonty index of 101.2.

The P4/ is constructed along the same lines as the P3/, but the crochet is multiple, the lingual cingulum is discontinuous and the protocone is slightly constricted. A very small mesostyle is noted in the middle of the ectoloph. The isolated P4/ MIL 868 (Fig. 4B) is characterized by its multiple crochet, its lack of constriction of protocone and its continuous lingual cingulum; the isolated P4/ MIL 880, also bears a multiple crochet but not lingual cingulum, and the hypocone is isolated at its end (Fig. 4C); finally the P4/ MIL 1287 shows a continuous lingual cingulum.

The M1/ has an ectoloph, whose posterior part is directed outwards and a shows a strong paracone fold A crochet is the only internal fold and there is no lingual cingulum; the constriction of the protocone is intense. The M1/ MIL 614 (Fig. 4D) is characterized by a discontinuous lingual cingulum, a slight crista in addition to its crochet, and a small mesostyle. Another isolated M1/ MIL 1569 shows a moderately developed constriction affecting the hypocone as well as the protocone, and a lingual cingulum reduced to two buttons (Fig. 4E).

The M2/ has the same ectoloph profile as in M1/. There is a crista and a crochet. Constriction of the protocone is strong. There is no lingual cingulum. The isolated M2/ MIL 1187 is very similar but lacks the crista.

The M3/ has no crochet and a discontinuous lingual cingulum. Constriction of protocone is well marked. The isolated M3/ MIL 1119 is very similar.

The morphology of the Milia upper cheek teeth corresponds to that of *D. jeanvireti,* although in the molars the paracone fold is more marked and the ectolph less flat than for the molars of Vialette.

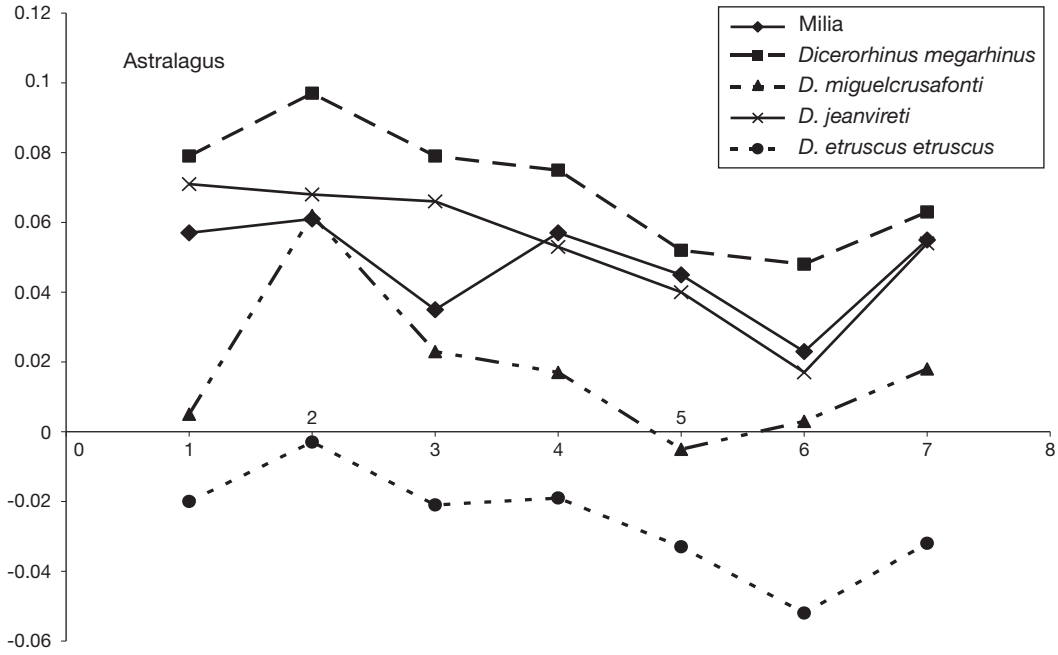

FIG. 10. — Simpson diagram of astragalus: mean values of the Milia *Dicerorhinus jeanvireti* Guérin, 1972, compared with average values of the *D. jeanvireti, D. miguelcrusafonti* Guérin & Santafe, 1978*, D. megarhinus* (de Christol, 1834) and *D. etruscus etruscus* (Falconer, 1859). The variables on the X axis are the same and in the same order as in Table 8 (see Appendices).

The dimensions of the upper cheek are given in Table 4 (see Appendices). In the Milia specimens the dimensions are slightly higher than those of the comparative sample of *D. jeanvireti*.

The four Plio-Villafranchian European rhino species pertaining to the same genus, there are no important differences in the morphology of their upper cheek-teeth; the ectoloph profiles are only slightly different, e.g., a thicker paracone fold for the *D. megarhinus* P3/-4/.

Lower teeth

The type of construction of the lower cheek teeth of Pliocene and Pleistocene rhinoceroses is very monotonous in general, and there are no anatomical characteristics that distinguish the diverse species of *Dicerorhinus*. The lower cheek teeth of the Milia rhinoceros (Fig. 5E) can only be specifically identified from their dimensions.

The M/2 of the mandible MIL 162 bears two V-shaped lingual valleys, which between them present a small difference in level something that happens in most cases of the M/2 of D. jeanvireti, however some of them have an anterior U-shaped valley.

The M/3 of the mandible MIL 162 with its anterior V-shaped valley, its posterior U-shaped valley and the high difference of the level between the two valleys, also represents the general case, the variability focuses essentially on the difference in level between the two valleys. It is confirmed in the Milia specimens, that the two isolated M/3s MIL 1145 and MIL 1343 have their two valleys V-shaped, with a difference in level which is reduced in the former but stronger in the latter.

In *D. jeanvireti* the P/2 does not show any particular character, the P/3 and P/4 lack of lingual or buccal cingula and have V-shaped valleys with a difference in levels between them from low to medium. These observations apply to the lower premolars from Milia.

The dimensions are given in Table 5 (see Appendices). The Milia lower cheek teeth fall within the range of variation of *D. jeanvireti*, some being marginally larger than the maximum values of the comparative sample.

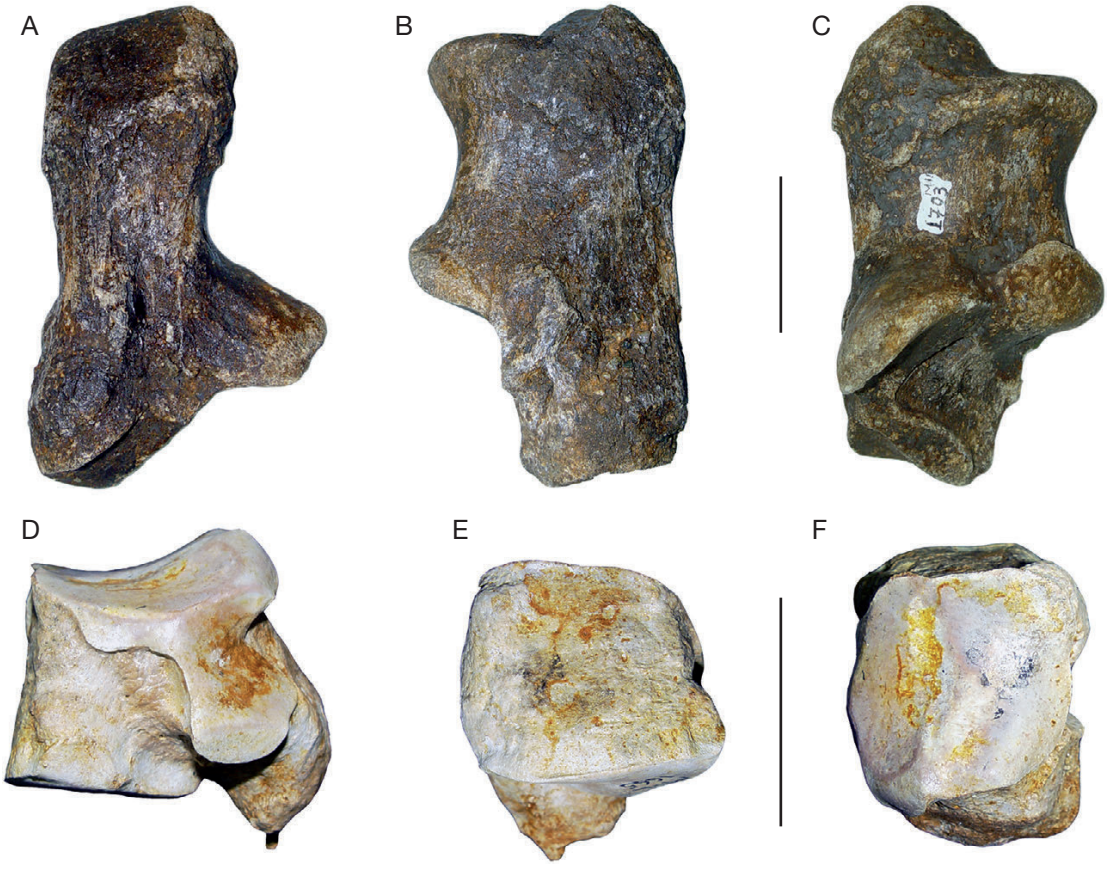

FIG. 11. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 tarsals: **A**-**C**, left calcaneum MIL 1703; **A**, posterior view; **B**, lateral view; **C**, medial view; **D**-**F**, right cuboid MIL 1665; **D**, medial view; **E**, front view; **F**, upper view. Scale bars: 50 mm.

Radius and Ulna

There are six specimens of proximal radius, of which specimen MIL 657 is the best preserved (Fig. 6A, B). The anatomical characteristics are those of *D. jeanvireti*, particularly the proximal articulation distinctly undulating on its anterior border, with a strong medial re-entrant, to the posterior edge forming an obtuse angle, and on the lateral facet slightly extending outwards, whose front edge is recessed from the front edge of the medial facet (Fig. 6A). In anterior view, notable are the strong lateral tuberosity of the proximal epiphysis, which is well developed below the articulation, and the convex medial border of the same epiphysis, and the strong insertion of the biceps brachii shifted slightly medially (Fig. 6B).

The proximal DT varies from 97.5 to 102 mm (average for four specimens: 99.6 mm), the DAP proximal 64 to 75 mm (average for four specimens: 70.8 mm), the DT of diaphysis 57 to 60 mm (average for two specimens: 58.5 mm), the DAP diaphysis 37.5 to 39 mm (average for two specimens: 38.3 mm). These dimensions fall within the range of variation of a sample of 10 to 12 radii of *D. jeanvireti*, whose respective average values are 101.6 mm, 69.9 mm, 56.5 mm and 39.1 mm (Guérin 1980: 479, table 92).

The single almost complete ulna (Fig. 6C) measures 560 mm long, which is much more than the maximum value measured on a sample of five ulnae of *D. jeanvireti* (maximum 529 mm, with an average of 519.4 mm), but less than 580 mm in the Roatto ulna (Campanino *et al.* 1994).

Mc III

There is a complete third metacarpal (Fig. 7) and a half one. The anatomical characteristics are those of *D. jeanvireti*: a long and relatively slender bone (Fig. 7A, F); a proximal articulation with a clearly convex anterior border (Fig. 7C); an anterior proximo-lateral articular surface much larger than the posterior, with a distal part as high as the proximal part; a proximo-lateral posterior facet a little higher than wider (Fig. 7B), which is noted to be of trapezoidal shape instead of triangular as in Vialette; a diaphysis of elliptical midsection and slightly depressed in the posterior border (Fig. 7D).

The dimensions are given in Table 6 (see Appendices). Except for the length, which is somewhat smaller than the minimum value of the sample of comparison, the Milia specimens fall within the range of variation of 8 to 11 specimens of *D. jeanvireti* Mc III. The Simpson diagram in Figure 8 shows that the extreme values of *D. jeanvireti* surround those of Milia rhinoceros, except for the length. The peculiar design of the graph corresponding to *D. miguelcrusafonti* was noted incidentally.

In 1980, Guérin was not able to identify the evolutionary trends on the *D. jeanvireti* Mc III.

Tibia

The single complete Milia specimen MIL 819 (Fig. 6D-F) shows the anatomical features of *D. jeanvireti*, which were established by Guérin in 1972 and 1980: proximal epiphysis with strong tibial tuberosity untrammelled and projecting upwards; brims of the tibial spine shifted backwards (the lateral being more posterior), but not really shifted vertically, the popliteal notch strongly carved; distal epiphysis with the medial malleolus very clear and rather square in outline and relatively low fibular notch.

The distal articulation has DT = 85 mm for DAP = 64 mm; the DT distal articulation of a Desnes tibia reaches 86 mm. The two diameters of articulation are stronger in the Roatto specimen: 92.5 and 75 mm (Campanino *et al.* 1994).

The other dimensions are given in Table 7 (see Appendices). The dimensions of Milia tibiae are within the range of variation of 8 to 13 specimens of *D. jeanvireti*, and are close to the average of this sample. The Roatto tibia is significantly longer (Campanino *et al.* 1994).

The Simpson diagram in Figure 9 shows that the complete Milia tibia is perfectly framed by the extreme values of *D. jeanvireti*. It is also noted that the proportions of *D. megarhinus* are rather different compared to the maximum values of *D. jeanvireti*; the average length is a little lower, but the proximal epiphysis is larger, the diaphysis is less deep and the distal epiphysis is smaller.

In 1980, Guérin showed that from Vialette (the dawn of zone MNQ 16) to Montopoli (near the end of the zone), the tibia of *D. jeanvireti* seems to have tendencies of elongating and reducing the width of the proximal epiphysis.

Astragalus

The trochlea of the astragalus in *D. jeanvireti* is wider, shallower and more asymmetrical than in *D. megarhinus*; this is also observed in Milia but the trochlea is carved and more symmetrical on MIL 367 and MIL 181 specimens.

In medial view, the distal tubercle is shifted backwards and near the distal edge of the bone.

In distal view, the articular surface for the navicular has its anterior border depressed; in relation to this anterior border, the articular surface for the cuboid is slightly shifted forwards.

All these characteristics are those of *D. jeanvireti*. The dimensions are given in Table 8 (see Appendices). The dimensions of the three Milia astragali are within the range of variation of 8 to 15 astragali of *D. jeanvireti*. The Roatto astragalus is significantly larger (Campanino *et al.* 1994).

Figure 10 confirms the proximity of the average size of Milia with the average of *D. jeanvireti*; compared to *D. megarhinus* the width is similar but the DAP and particularly the height are lower. Note incidentally an analogy between the graphs corresponding to *D. miguelcrusafonti* and *D. etruscus etruscus*, which reveals a certain similarity between the proportions despite the much greater size of the former.

The unique evolutionary trend found for the astragalus between the beginning and the end of the zone MNQ 16, is the significant reduction of the transversal diameter (Guérin 1980).

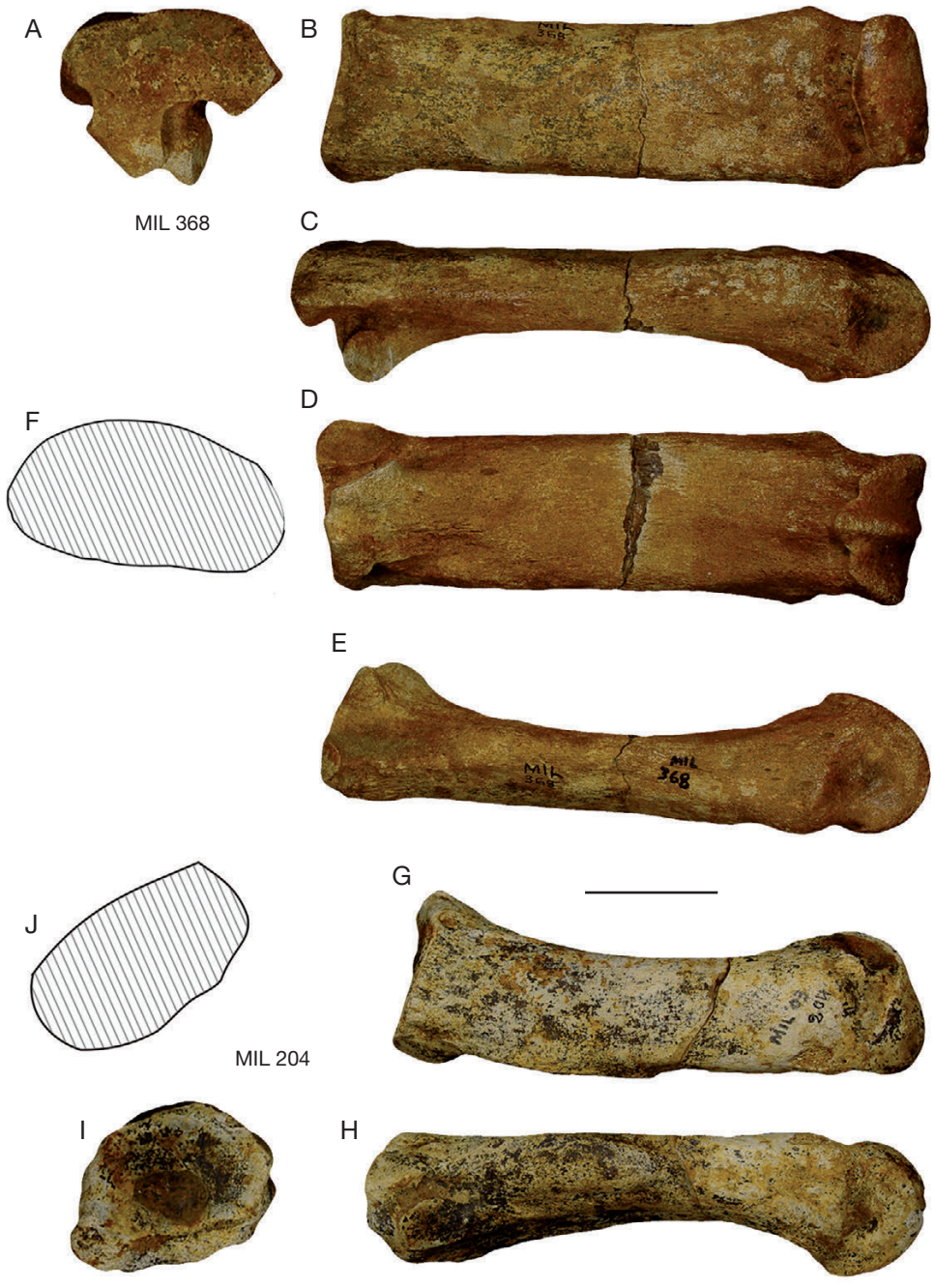

Fig. 12. — The Milia *Dicerorhinus jeanvireti* Guérin, 1972 metatarsals: **A**-**F**, Right Mt III MIL 368; **A**, proximal view; **B**, anterior view; **C**, lateral view; **D**, posterior view; **E**, medial view; **F**, cross section in the middle of the diaphysis, **G**-**J**, left Mt IV MIL 204; **G**, anterior view; **H**, medial view; **I**, proximal view; **J**, cross section in the middle of the diaphysis. Scale bar: 50 mm.

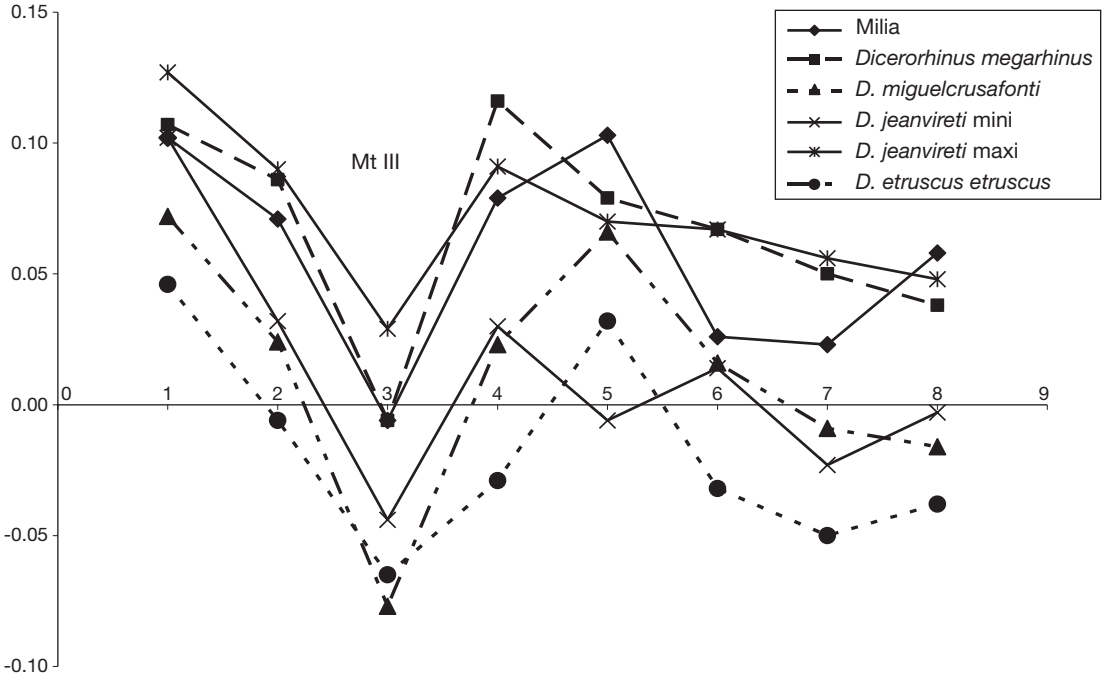

FIG. 13. — Simpson diagram of Mt III: Values of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 specimen, compared to extreme values of *D. jeanvireti* and average values of *D. megarhinus* (de Christol, 1834), *D. miguelcrusafonti* Guérin & Santafe, 1978 and *D. etruscus etruscus* (Falconer, 1859). The variables on the X axis are the same and in the same order as in Table 11 (see Appendices).

Calcaneum

In posterior view (Fig. 11A), the sustenculum tali axis is slightly inclined towards the bottom and it makes a slightly obtuse angle with the axis of the body of the bone. In lateral and medial views (Fig. 11B, C), the front of the tuberosity is situated slightly behind the beak (= foremost part of the bone), the anterior edge between these two points is concave. The posterior edge of the lateral face is rectilinear for the lower three quarters of its height.

The dimensions of the Milia calcaneum are situated well within the range of variation of 10 and 14 of *D. jeanvireti* calcanea (Appendices, Table 9).

Cuboid

The medial face (Fig. 11D) is typical of *D. jeanvireti*. The anterior face (Fig. 11E) is trapezoidal and not taller than broader, with a medial edge longer than that of the medial face. On the proximal articulation (Fig. 11F) the lateral facet is shorter but once again broader than the medial one.

The dimensions (Appendices, Table 10) of the Milia cuboid are situated within the range of variation of two to nine cuboids of *D. jeanvireti*, somewhat below the mean except for the height of the bone.

Mt III

The complete Mt III (Fig. 12A-F) presents all the anatomical characteristics of *D. jeanvireti*: an elongated and relatively slender bone (Fig. 12B, D), the proximal articulation is not very broad but deep and the anterior border is regular and weakly convex (Fig. 12A); the proximo-lateral articulation consists of two facets with similar length and height, the former being well above the posterior (Fig. 12C). The proximo-medial articulation has two distinct facets in which the posterior one, situated below, is significantly larger than the anterior one (Fig. 12E). The cross section of the diaphysis is trapezoidal with a rounded posterior border, which is slightly depressed (Fig. 12F).

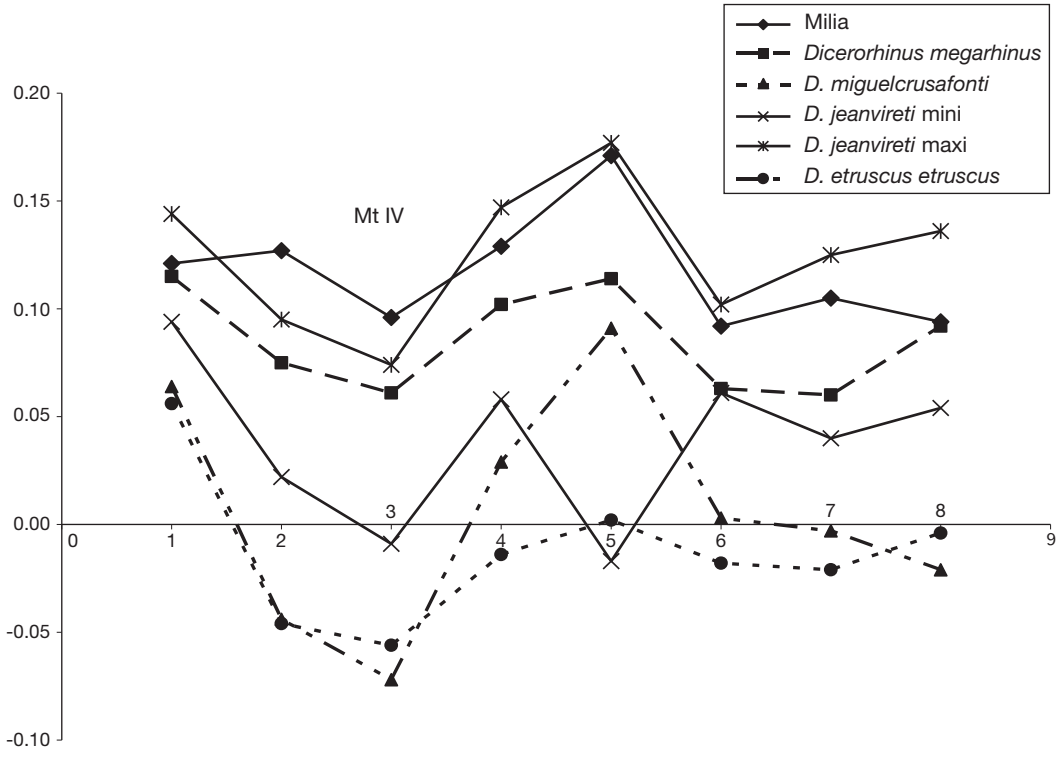

FIG. 14. — Simpson diagram of Mt IV: values of the Milia *Dicerorhinus jeanvireti* specimen, compared to extreme values of *D. jeanvireti* and average values of *D. megarhinus* (de Christol, 1834), *D. miguelcrusafonti* Guérin & Santafe, 1978 and *D. etruscus etruscus* (Falconer, 1859). The variables on the X axis are the same and in the same order as in Table 12 (see Appendices).

The dimensions are given in Table 11 (see Appendices). The Milia specimens fall in the range of variation of 6 to 11 specimens of Mt III of *D. jeanvireti*, two of them (the DT of diaphysis and the distal articulation) are, however, marginally higher than the maximum values of the sample for comparison. The Roatto Mt III is significantly larger (Campanino *et al.* 1994).

The Simpson diagram in Figure 13 shows that the extreme values of *D. jeanvireti* frame more often those of the Milia rhinoceros, where however, the DAP of diaphysis and the distal epiphysis exceed the maximum values observed. Note here again a certain parallelism in the graphs corresponding to *D. miguelcrusafonti* and *D. etruscus etruscus*.

From the beginning to the end of the zone MNQ 16, the proximal epiphysis tends to shrink; the diaphysis becomes shallower and narrower at its base (Guérin 1980).

Mt IV

The complete specimen represented in Figure 12G, J, also presents the anatomical and biometric characteristics of *Dicerorhinus jeanvireti*. The bone is slender and elongated (Fig. 12G, H). The proximal articulation, a little wider than longer, is pentagonal, with an anterior border having a very open angle and a posterior margin barely emarginated (Fig. 12I). The proximo-medial articulation bears two facets, the anterior one, which is smaller and more or less trapezoidal in shape and is located much higher than the posterior one, which is larger and elliptical (Fig. 12H). The cross section of the diaphysis (Fig. 12J) is a rounded parallelogram, with the medial border shorter than the lateral one.

The dimensions are given in Table 12 (see Appendices). The Milia specimen is within the range

of variation of a sample of five to ten specimens of *D. jeanvireti*, but its proximal epiphysis has two diameters slightly greater than the maximum values of our sample. Durisova (2004) gives the dimensions of two Mt IV which were collected during new excavations in Hajnacka. These dimensions, reported in Table 12 (see Appendices), correspond perfectly to those of *D. jeanvireti*.

Figure 14 shows that the proportions of the Milia Mt IV are those of *D. jeanvireti*, with dimensions close to the maximum values of the comparative sample, and confirms the high volume of the Milia proximal epiphysis. The evolutionary trends (Guérin 1980) are: an increase in length, a narrowing of the diaphysis at mid-shaft and a broadening to its base.

Conclusion of the anatomical study of the rhinoceros

The Milia rhinoceros presents all the anatomical and biometric characteristics of *D. jeanvireti*. In Figure 15, there is a comparative Simpson diagram of the lengths of the limbs for these four types of European rhinoceros considered in this article. It shows a certain similarity which reflects attribution to the same genus *Dicerorhinus* (the lengthening of metapodials, especially of abaxial ones, compared to *Diceros bicornis*, which serves as the reference material, is remarkable), and also shows that *D. jeanvireti* was more cursorial than *D. megarhinus* with its metapodials relatively longer, but shorter humerus, femur and tibia.

Biostratigraphic implications

D. jeanvireti is known from the zone MNQ 16, which corresponds to the Early Villafranchian. Considering the evolutionary trends highlighted in the European *Dicerorhinus* by Guérin (1980), and for Rhinocerotidae in general by Antoine (2002), it may be presumed that the Milia *D. jeanvireti* is a bit more advanced than that of Vialette; thus Milia could be a little more recent than Vialette, which lies at the base of the zone MNQ 16, but not younger than the Perrier-les Étouaires rhino, which is located near the top of the same zone. The age of Vialette is around 3 Ma and that of Perrier-les Étouaires is 2.5 + 0.1 Ma (Guérin 2007).

Palaeoecological implications

The preferential habitat of *Dicerorhinus jeanvireti* is dominated by woodland with grassy areas that consist of graminae and ferns, in a humid climate (Guérin 1980).

Order ARTIODACTYLA Owen, 1848
Sub-order SUIFORMES Jaeckel, 1911
Family Suidae Linnaeus, 1758
Genus *Sus* Linnaeus, 1758

Sus arvernensis arvernensis Croizet & Jobert, 1828

Four species of Suidae are known in the Pliocene and Early Pleistocene of Europe (Guérin 1996; Arribas & Garrido 2008): *Potamochoerus provincialis* (Gervais, 1859), exclusively of Ruscinian age, the Villafranchian *Potamochoerus magnus* Arribas & Garrido, 2008, *Sus arvernensis* Croizet & Jobert, 1828, of the Ruscinian (zones MNQ 14 and 15) and the Early Villafranchian (zone MNQ 16), and *Sus strozzii* Meneghini, 1858, F. Major, 1881, of the Villafranchian (zone MNQ 16 to 19). The Milia Suidae belongs to *S. arvernensis*.

Sus arvernensis is a small species closer to the eastern boars, with a long rostrum of *Sus verrucosus* type, than to the recent European wild boar *Sus scrofa* Linnaeus, 1758. Guérin *et al.* (1998) estimated its mass to be between 45 and 100 kg. He recognised two successive sub-species, *S. arvernensis minor* Depéret, 1890 of the Ruscinian and *S. arvernensis arvernensis* Croizet & Jobert, 1828 of the Early Villafranchian. The cheek teeth are still relatively simple and the last molars usually end in a single tubercle. Recall that the syntype of the species consists of a fragment of right maxilla bearing D2/, D3/, D4/ and M1/, and a mandible fragment bearing D/2, D/3, D/4 and M/1 on both sides, and the bud of the right M/2 (Croizet & Jobert 1828: pl. 13, figs 3-5).

The Auvergne boar is defined in France in the Early Villafranchian of Perrier-les Étouaires, it is also found in Vialette and in Trévoux-Reyrieux in Ain (Guérin *et al.* 1998); its primitive subspecies is known from the Ruscinian in the Perpignan

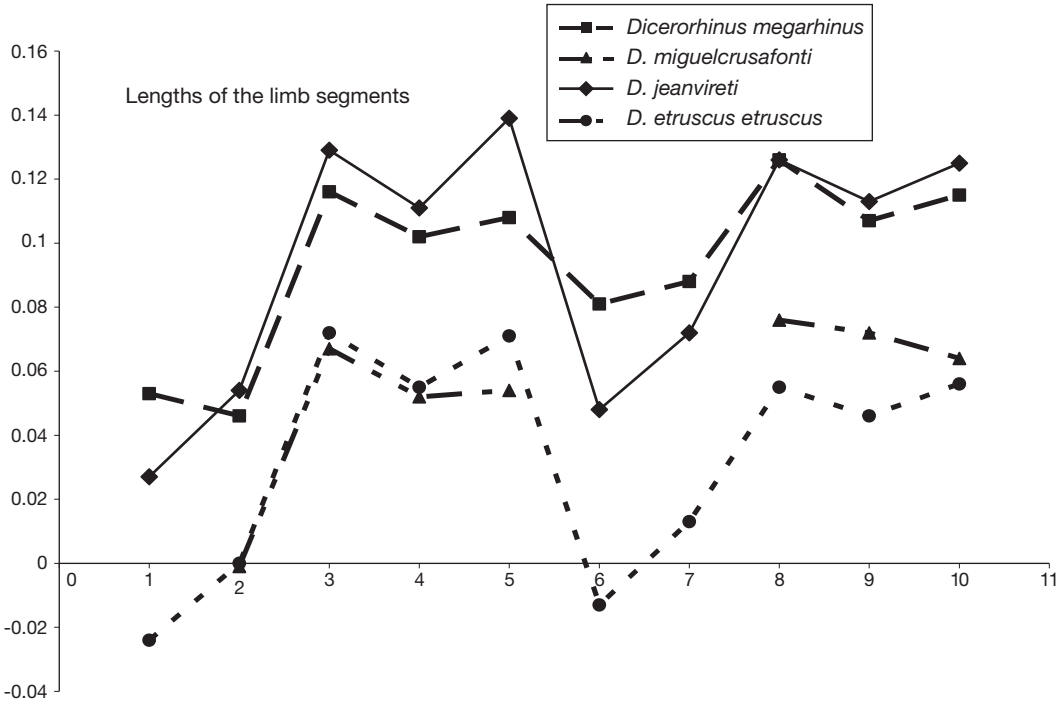

FIG. 15. — Simpson diagram of lengths of the limb segments in the *Dicerorhinus jeanvireti* Guérin, 1972, *D. megarhinus* (de Christol, 1834), *D. miguelcrusafonti* Guérin & Santafe, 1978 and *D. etruscus etruscus* (Falconer, 1859). The variables on the X axis are in order, as the average of lengths. Abbreviations: **1**, humerus; **2**, radius; **3**, Mc II; **4**, Mc III; **5**, Mc IV; **6**, femur; **7**, tibia; **8**, Mt II; **9**, Mt III; **10**, Mt. IV.

region, in Cavaillé brickfield, in Serrat d'en-Vacquer (type-site of *S. arvernensis minor*) and Mas Bruno near Saint-Estève, and Autrey near Gray in Haute-Saône (Depéret 1890; Guérin *et al.* 1998).

Guérin *et al.* (1998) pointed out that this species is also found in Great Britain (Red Crag of Suffolk), in Germany (Herbolzheim), in Hungary (Süttö), in Slovakia (Hajnacka and Ivanovca), in Moldova and probably in Georgia (Kvabébi), and in Turkey (Afyon-Dinar-Akçaköy and Çalta).

They also recall that the species is not rare in Italy (Tuscany: upper levels of Casino, Val di Pugna, Barga, Pieve Fosciana and Piedmont: Triversa, Villafranca d'Asti). Also in Italy, Campanino *et al.* (1994) described a third upper premolar of "*Sus minor*" discovered in Roatto near Villafranca d'Asti of the same age as the *Dicerorhinus jeanvireti* remains. Finally, Gliozzi *et al.* (1997) reported a *Sus* sp. of "small size", in Collepardo in Anagni Basin (Lazio), which is probably *S. arvernensis* because of its size (Guérin *et al.* 2004).

In Spain, *Sus arvernensis* is reported by Van der Made (1989-90) in Gorafe IV (MNQ 14), by Montoya *et al.* (2006) in Alcoy-Mina (MNQ 14 or 13?) and by Mazo & Torres (1989-90) in Piedrabuena (MNQ 16).

In Romania, Radulescu *et al.* (2003) and Radulescu (2005) indicate the presence of "*Sus minor*" in the Brasov Depression at Capena (MNQ 15b) and Vargha (MNQ 15b).

In Bulgaria, Spassov (2005) reported *Sus arvernensis minor* in Musselievo (Late MN 15).

Finally, with regards to Greece, *Sus arvernensis* may be present in Ptolemaida/Servia (Tobien 1981). In addition, two indeterminate suids are reported in the Ruscinian Damatria Formation of Rhodes Island, which could correspond to "*Sus" minor* according to Koufos (1986).

Material

Concerning the Auvergne boar, nine specimens have been recorded in the Milia faunal assemblage, six of which are measurable and listed as follows:
– a right upper tooth row MIL 207 with P4/-M3/;
– a left mandible fragment MIL 696, with M/2 and the roots of other cheek teeth;
– a right mandible rostral fragment with part of the canine MIL 1283;
– a right upper canine MIL 511;
– a right lower canine MIL 1485;
– a left radius proximal fragment MIL 916.

Description

Upper tooth row and canine

It belongs to a young adult because P4/ and M2/ display no traces of wear, and M3/, although in place, is unworn (Fig. 16A-C). The principal cusp of P4/ is not quite central, it is slightly shifted buccally; M1/ and M2/ are typical of Suinae with their four principal tubercles; they have a peripheral cingulum which for the M2/ is slightly folded behind; the M3/ has in addition to the four principal tubercles, a large posterior axial tubercle. There are many accessory cuspids on the anterior cingulum, on the posterior of the paracone and the metacone and around the metaconule; this tooth resembles the homologous tooth from Çalta (Guérin *et al.* 1998: fig. 1E).

The dimensions of the cheek teeth are given in Table 13 (see Appendices). The dimensions of the upper cheek teeth fall within the range of variation of a sample from 5 to 28 specimens of *Sus arvernensis*, the lengths are close to the maximum values measured on our comparative sample, the widths are however somewhat lower than the observed average.

The canine MIL 511 is rather slender, its crown width is about 18 mm and the length about 15 mm.

Rostral fragment of mandible

This fragment bears part of the canine, whose tip is broken (Fig. 16E, F). The lower canine has a triangular cross section, whose rounded hypotenuse covers approximately 18 mm and corresponds to the antero-lingual border. The postero-dorsal border without enamel is about 13 mm wide. The external border is about 17 mm. The inferior dihedral is acute. The cross-section and size of the canine are similar to those of the Çalta boar and as for the latter, the Milia boar approaches recent Asian *Sus verrucosus* (Guérin *et al.* 1998). The canine MIL 1485 is much stronger and its hypotenuse covers approximately 24 mm and corresponds to the antero-lingual border. The postero-dorsal border without enamel is about 18 mm wide, and the external border is about 22 mm.

M/2

It is present in a hemi-mandible fragment, in which there are also roots of P/4 and M/1, and an anterior root of M/3 (Fig. 16D). It is barely worn and its morphology requires no special comment. The three dimensions of the M/2 are close to the average of nine to ten specimens of *S. arvernensis* (Appendices, Table 13).

Radius

The proximal epiphysis of the Milia radius has DT = 27.5 mm for DAP = 19 mm. The same two dimensions are respectively 25 and 22 mm in Çalta specimens, and 26 and 19.5 mm for the two radii from Villafranca d'Asti.

Conclusion on the anatomical study of Suidae

Because of its dimensions, in particular its upper cheek teeth, the Milia Suidae belongs to the nominate subspecies *Sus arvernensis arvernensis*, *S. arvernensis minor* being smaller.

Biostratigraphic implications

Sus arvernensis arvernensis is a marker of the Early Villafranchian (zone MNQ 16).

Palaeoecological implications

Sus arvernensis was a species of open forest in relatively warm regions, well adapted to digging deep into the humid soils.

CONCLUSION ON THE MILIA FAUNA

Milia is probably the first major palaeontological site in Greece dating from the Early Villafranchian.

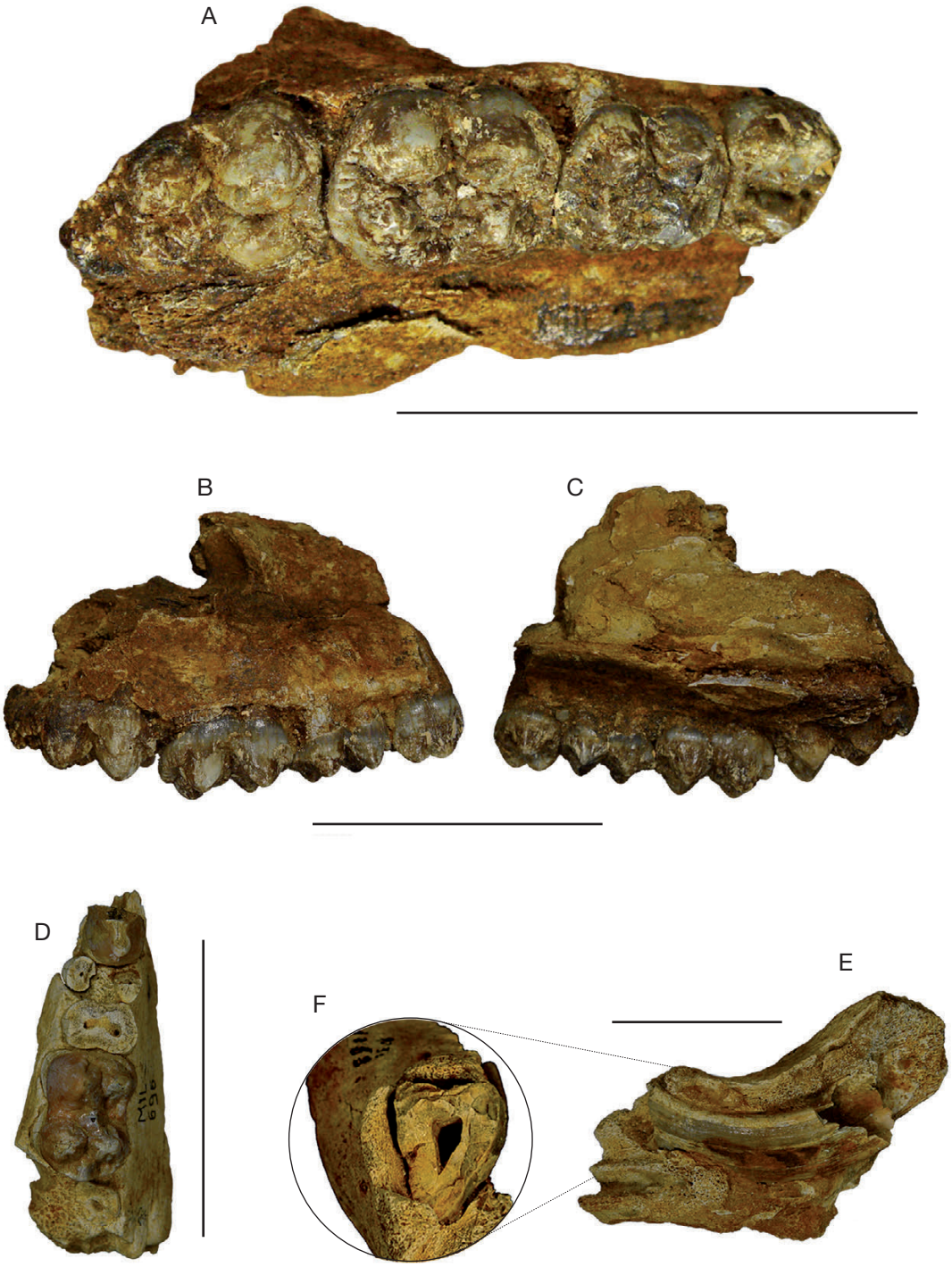

FIG. 16. — The Milia *Sus arvernensis arvernensis* Croizet & Jobert, 1828: **A**-**C**, right maxilla with P4/-M3/ MIL 207; **A**, occlusal view; **B**, lateral view; **C**, medial view; **D**, left mandible fragment with M/2 MIL 696, occlusal view; **E**, **F**, rostral fragment of mandible with part of the canine**,** MIL 1283 dex; **E**, lateral view; **F**, front view showing details of the canine section. Scale bars: 50 mm.

This is the first deposit in Greece which has yielded *Tapirus arvernensis* and *Dicerorhinus jeanvireti*, the latter (along with *Mammut borsoni*) being particularly well represented.

The association among *Tapirus arvernensis arvernensis*, *Dicerorhinus jeanvireti* and *Sus arvernensis arvernensis* characterizes the Early Villafranchian (zone MNQ 16), which lasted from a little older than 3 to 2.5 Ma (ages respectively of Vialette and Perrier-Les Étouaires, see Guérin 2007). The degree of development of the Milia *D. jeanvireti* suggests an age for the Milia site a little younger than the Vialette site.

The same faunal association is characteristic of a landscape dominated by forest vegetation, under a humid and relatively warm climate.

Acknowledgements
The former Grevena Prefecture financed the excavations, as well as the dating projects, with the contribution of the former Municipality of Herakleotes. We deeply thank E. Vlachos, geologist MSc, for his assistance and we are much indebted to the Milia team (students and co-operators) for their participation in the excavation, the preservation and the research process. For their offer, we thank the shepherds: Thanasis Delivos, Yannis Vlachos and Thomas Tzimopoulos. We specially thank Nickos Bacharidis, who collected and preserved rhino fossils from Milia area. For their critical remarks we are deeply indebted to Martin Pickford, Annemarie Ohler and to an anonymous reviewer. For linguistic corrections we kindly thank M. Boyanides and M. Pickford.

REFERENCES

Agusti J. & Anton M. 2002. — *Mammoths, sabertooths and hominids, 65 million years of Mammalian Evolution in Europe*. Columbia University Press, New York, 313 p.

Antoine P. O. 2002. — Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). *Mémoires du Muséum national d'Histoire naturelle*, Paris, 188: 359 p.

Arribas A. & Garrido G. 2008. — A new wild boar belonging to the genus *Potamochoerus* (Suidae, Artiodactyla, Mammalia) from the Eurasian Late Upper Pliocene (Fonelas P-1, Cuenca de Guadix, Granada), *in* Arribas A. (ed.), Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas. *Cuadernos del Museo Geominero, Instituto Geológico y Minero de España* 10: 337-364.

Azzaroli A. 1963. — Rinoceronti pliocenici del Valdarno inferiore. *Paleontographia Italica* 57 (NS 27): 11-20.

Boeuf O. 1991. — *Tapirus jeanpiveteaui* nov. sp., nouvelle espèce de Tapiridae (Perissodactyla) du Pliocène de Charente (France). *Palaeontographica* A, 217, 4-6: 177-194.

Bout P. 1960. — *Le Villafranchien du Velay et du bassin hydrographique moyen et supérieur de l'Allier*. Imprimerie Jeanne d'Arc, Le Puy, 344 p.

Campanino F., Forno M. G., Mottura A., Ormezzano D. & Sala B. 1994. — *Stephanorhinus jeanvireti* (Guérin) 1972 (Rhinocerotidae, Mammalia) from Roatto near Villafranca d'Asti, NW Italy. Revision of the specimen from Dusino. *Bollettino del Museo Regionale di Scienze Naturali* 12 (2): 439-499.

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

Depéret C. 1890. — *Les animaux pliocènes du Roussillon*. Mémoires de la Société géologique de France, Paléontologie, vol. 3, 194 p.

Deperet C., Mayet L. & Roman F. 1923. — Les éléphants pliocènes. *Annales de l'Université de Lyon* nouv. ser., 1, 42: 1-221.

Durisova A. 2004. — 8. Rhinoceroses, *in* Sabol M. (ed.), Early Villanyan site of Hajnacka I (Southern Slovakia). Paleontological Research 1996-2000. *Gemer-Malohout Museum in Rimavska Sabota éd.*: 98-110.

Eisenmann V. & Guérin C. 1994. — *Tapirus priscus* Kaup from the Upper Miocene of Western Europe: palaeontology, biostratigraphy and palaeoecology. *Paleontologia i Evolució*, Sabadell, 24-25, 1992 (Proc. IX Congress of the Regional Committee, Mediterranean Neogene Stratigraphy, Barcelona, nov. 1990): 113-122.

Falconer H. 1868. — Palaeontological memoirs and notes, *in* Murchison C. (ed.), *Mastodon, Elephant, Rhinoceros, Ossiferous Caves, Primeval Man and his Cotemporaries*. Vol. II. Hardwicke, London, 675 p.

Fejfar O. 1964. — The Early-Villafranchian vertebrates from Hajnacka near Folakovo in Southern Slovakia. *Rozpravy, Ustredniho Ustavu Geologického*, 30: 115 p.

Gliozzi E., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabota C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanalda E. & Torre D. 1997. — Biochronology of selected Mammals, Molluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Rivista Italiana Paleontologia Stratigrafia* 103

(3): 369-388.

GUÉRIN C. 1972. — Une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) à Vialette (Haute-Loire, France) et dans d'autres gisements du Villafranchien inférieur européen : *Dicerorhinus jeanvireti* n. sp. *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 49: 53-150.

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 Lyon* 79: 1185 p.

GUÉRIN C. 1996. — Famille des Suidae, *in* GUÉRIN C. & PATOU-MATHIS M. (eds), *Les grands mammifères plio-pléistocènes d'Europe*. Masson édit., Paris: 40-43.

GUÉRIN C. 2004. — Les rhinocéros (Mammalia, Perissodactyla) du gisement villafranchien moyen de Saint-Vallier (Drôme), *in* FAURE M. & GUÉRIN C. (eds), Le gisement pliocène terminal de Saint-Vallier (Drôme, France). *Geobios*, Mém. spécial 26 (37): 259-278.

GUÉRIN C. 2007. — Biozonation continentale du Plio-Pléistocène d'Europe et d'Asie occidentale par les mammifères : état de la question et incidence sur les limites Tertiaire/Quaternaire et Plio/Pléistocène. *Quaternaire* 18 (1): 23-33.

GUÉRIN C. & SANTAFE LLOPIS J. V. 1978. — *Dicerorhinus miguelcrusafonti* nov. sp., une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) du gisement pliocène supérieur de Layna (Soria, Espagne) et de la formation pliocène de Perpignan (Pyrénées-orientales, France). *Geobios* 11 (4): 457-491.

GUÉRIN C. & EISENMANN V. 1994. — Les tapirs (Mammalia, Perissodactyla) du Miocène supérieur d'Europe occidentale. *Geobios* 27 (1): 113-127.

GUÉRIN C., FAURE M. & SEN S. 1998. — Le gisement de Vertébrés pliocènes de Çalta, Ankara, Turquie. 8. Suidae. *Geodiversitas* 20 (3): 441-453.

GUÉRIN C., FAURE M., ARGANT A., ARGANT J., CRÉGUT-BONNOURE E., DEBARD E., DELSON E., EISENMANN V., HUGUENEY M, LIMONDIN-LOZOUET N., MARTIN SUAREZ E., MEIN P., MOURER-CHAUVIRÉ C., PARENTI F., PASTRE J. F., SEN S. & VALLI A. 2004. — Le gisement pliocène supérieur de Saint-Vallier (Drôme, France) : synthèse biostratigraphique et paléoécologique, *in* FAURE M. & GUÉRIN C. (eds), Le gisement pliocène terminal de Saint-Vallier (Drôme, France). *Geobios*, Mémoire spécial 26 (37): 349-360.

HEINTZ E., GUÉRIN C., MARTIN R. & PRAT F. 1974. — Principaux gisements villafranchiens de France : listes fauniques et biostratigraphie. *Mémoires du Bureau de Recherches géologiques et minières*, Paris, 78 (1): 169-182.

HOLEC P. 1996. — A Plio-Pleistocene large mammal fauna from Srekov and Nova Vieska, South Slovakia. *Acta zoologia cracoviensia* 39 (1): 219-222.

HOOIJER D. A. 1981. — The first Rhinocerotid of the Pretiglian "Black Bones" fauna from the Netherlands. *Netherlands Journal of Zoology* 31 (2): 472-475.

HOOIJER D. A. 1985. — Plio/Pleistocene Elephantid, Equid and Rhinocerotid remains from dredging operations at Linden and Maren-Kessel (Noord-Brabant, The Netherlands). *Lutra* 28: 31-37.

HÜRZELER J. 1967. — Nouvelles découvertes de mammifères dans les sédiments fluvio-lacustres de Villafranca d'Asti. Coll. intern. CNRS n° 163: 633-636.

JANSTOVA M. 2004. — 9. Tapirs, *in* SABOL M. (ed.), Early Villanyan site of Hajnacka I (Southern Slovakia). Paleontological Research 1996-2000. *Gemer-Malohout Museum in Rimavska Sabota édit.*: 111-123.

KOTSAKIS T. 1986. — Elementi di paleobiogeographia dei mammiferi terziari dell' Italia. *Hystrix*, Roma, 1 (1): 25-68.

KOUFOS G. D. 1986. — The presence of *Sus strozzii* in the Villafranchian (Villanyan) of Macedonia (Greece). *Paläontologische Zeitschrift* 60: 341-351.

KRETZOÏ M. 1942. — Bermerkungen zum System der nachmiozänen Nashorn-Gattungen. *Földtany Közlöny* 72: 309-318.

LACOMBAT F. & MÖRS T. 2008. — The northernmost occurrence of the rare Late Pliocene rhinoceros *Stephanorhinus jeanvireti* (Mammalia, Perissodactyla). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 294: 157-165.

MAZO A. V. 1995. — *Stephanorhinus etruscus* (Perissodactyla, Mammalia) en el Villafranquiense inferior de Las Higueruelas, Alcolea de Calatrava (Ciudad Real). *Estudios Geologicos* 51: 285-290.

MAZO A. V. & TORRES T. 1989-90. — El Pozo de Piedrabueno, un nuevo yacimiento de vertebrados pliocenos en el Campo de Calatrava (Ciudad Real). *Paleontologia i Evolució* 23: 213-222.

MCKENNA M. C. & BELL S. K. 1997. — *Classification of Mammals above the species level*. Columbia University Press, New York, 631 p.

MICHAUX J., SIGÉ B. & SUDRE J. 1976. — Présence de *Tapirus arvernensis* (Mammalia, Perissodactyla) dans le Pliocène supérieur de Bassan (Hérault). *Comptes Rendus sommaires de la Société géologique de France* 1: 9-11.

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.

PARASKEVAIDIS E. 1977. — Säugetierreste aus Griechenland. *Proc. VI Coll. Geol. Aegean Region, Athens II*: 1143-1154.

PICTET F. J. 1853. — *Traité de Paléontologie, ou histoire naturelle des animaux fossiles considérés dans leurs rapports zoologiques et géologiques*. 2nde édition. T. 1. J. B. Baillière, Paris, 584 p.

POMEL A. 1852-53. — *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans*

la vallée de son affluent principal l'Allier. J.B. Baillière, Paris, 193 p.

RADULESCU C. 2005. — Artiodactyles du Pliocène et du Pléistocène inférieur de Roumanie. *Quaternaire* HS 2: 191-200.

RADULESCU C., SAMSON P.M., PETCULESCU A. & TIUCA E. 2003. — Pliocene large Mammals of Romania. *Colloquios de Paleontologia* 53: 1-10.

ROOK L. & RUSTIONI M. 1991. — *Tapirus* cf. *arvernensis* remains from the Late Turolian Baccinello V3 faunal assemblage (Grosseto, Tuscany). *Bollettino della Societa Paleontologica Italiana* 30 (3): 325-327.

RUSTIONI M. 1992. — On Pliocene tapirs from France and Italy. *Bollettino della Societa Paleontologica Italiana* 31 (3): 269-294.

SACCO F. 1895. — *Le rhinocéros de Dusino*. Archives du Muséum d'Histoire naturelle de Lyon, 6, 31 p.

SCHMIDT Z. & HALOUZKA R. 1970. — New vertebrate fauna of the Villafranchian from Strekov in the Hronska Pahorkatina (Danube Lowland). *Geologicke Prace* 51: 173-784.

SPASSOV N. 2005. — Brief review of the Pliocene ungulate fauna of Bulgaria. *Quaternaire*, HS 2: 201-212.

THENIUS E. 1955. — Die Verknöcherung des Nasenscheidewand bei Rhinocerotiden und ihr systematischer Wert zum Geschlechtsdimorphismus fossile Rhinocerotiden. *Schweitzerische Palaeontologische Abhandlungen* 71: 1-17.

TOBIEN H. 1981. — *Mammals of the Neogene/Quaternary boundary in the Eastern Mediterranean Area and from the Upper Siwaliks*. Proceedings of Field Conference on Neogene/Quaternary Boundary (India, 1979), Calcutta: 185-197.

TSOUKALA E. 2000. — Remains of a Pliocene *Mammut borsoni* (Hays, 1834), from Milia (Grevena, W. Macedonia, Greece). *Annales de Paléontologie* 86 (3): 165-191.

TSOUKALA E. & LISTER A. 1998. — Remains of straight-tusked elephant *Elephas* (*Palaeoloxodon*) *antiquus* Falc. & Caut., 1847, ESR-dated to oxygen isotope stage 6 from Grevena (W. Macedonia, Greece). *Bolletino della Societa Paleontologica Italiana* 37 (1): 117-139.

VAN DER MADE J. 1989-1990. — A range-chart for European Suidae and Tayassuidae. *Paleontologia i Evolució* 23: 99-104.

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, 200 p.

Submitted on 9 February 2011;
accepted on 4 May 2012;
published on 28 June 2013.

APPENDICES

TABLE 1. — Comparative dimensions of the lower cheek teeth and the calcaneum of the Milia *Tapirus arvernensis arvernensis* Croizet & Jobert, 1828.

	Tapirus						
	Milia	***Tapirus arvernensis***					
Cheek Teeth	MIL 649	**N**	**mean**	**min.**	**max.**	**SD**	**v**
D/4 L	21	2	18.5	18	19		
D/4 B ant.	15	2	12	11.5	12.5		
D/4 B post.	15	2	12	11.5	12.5		
M/1 L	20	13	19.4	18	21	1.02	5.2
M/1 B ant.	16	11	14.6	13	16	1	6.8
M/1 B post.	15	11	13.8	12.5	15	0.84	6.1
	Milia	***Tapirus arvernensis***					
Calcaneus	MIL 1282	**N**	**mean**	**min.**	**max.**	**SD**	**v**
H	105	10	87.50	86	88.5	0.97	1.11
DT prox.	26	10	21.85	20	24	1.29	5.91
DAP prox.	40.5	9	32.22	31	35	1.30	4.04
DT middle	17.5	10	14.70	13.5	16.5	0.92	6.25
DAP max.	46	10	34.05	30.5	40	3.01	8.85
DT max.	42	9	37.00	33	40	2.35	6.34

TABLE 2. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 skulls.

	Milia			***Dicerorhinus jeanvireti***					
Cranium	n° var.	MIL 1501	MIL 162	**N**	**mean**	**min.**	**max.**	**SD**	**v**
Length occipito-nasal	2	727	705	1	637.00				
Dist. nasal-chignon	3	736	750	1	692.00				
L nasal notch	4	249	237	2	172.50	168	177	6.36	
Minimal width of the braincase	5	138	109	0					
Length supraoccipital crest – postorbital process	6	343	340	1	308.00				
Length supraoccipital crest – supraorbital process	7	363	370	1	308.00				
Length supraoccipital crest – antorbital process	8	415	400	0					
Dist. nasal notch-orbite	9	120*	128.5	1	117.00				
Dist. post. M3-cond.	13		330	1	334.00				
Dist. nasal-orbite	14	364	374	2	357.50	348	367	13.44	
DT major crest occip.	15	172	188*	0					
Width masto.apo.	16	232	250	0					
Width mini. frontal	17	71	73.5	0					
Width proc. post orb.	18	229	224.5	0					
Width proc. above orb.	19	254	244.5	0					
Width proc. ant. orb.	20		266	1	221.00				
Width zygom. arc.	21	392	320	0					
Width on the bottom of the nasal notch	22	161	157	1	108.00				
H face occip.	23	133	157	0					
H cranium at P2	25		155.5	0					
H cranium at P4-M1	26		178.5	0					
H cranium at M3	27		162	0					
Palatinal width between P2	28		43.5	1	71.00				
Palatinal width between P4-M1	29		82.5	1	92.50				
Palatinal width between M3	30		102	1	100.00				
DT foram. occip.	31		55	0					
DT ext. cond. occip.	32	142	141	0					

TABLE 2. — Continuation.

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
Cranium	**N**	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
Length occipito-nasal	2	743.75	700	787.5	61.87	8.32	11	612.64	530	648	32.32	5.28
Dist. nasal-chignon	3	756.00	690	808	60.23	7.97	10	618.70	530	655	37.97	6.14
L nasal notch	4	266.25	245	297	22.77	8.55	15	191.50	138	209.5	18.34	9.58
Minimal width of the braincase.	1	144.00					14	101.07	79	126	13.23	13.09
Length supraoccipital crest – postorbital process	4	376.25	345	399	22.88	6.08	10	278.05	247	290	13.07	4.70
Length supraoccipital crest – supraorbital process	1	413.00					4	323.63	314	340	11.40	
Length supraoccipital crest – antorbital process	2	414.25	385	443.5			2	340.50	334.5	346.5		
Dist. nasal notch-orbite	5	115.50	105	125	7.35	6.36	19	105.47	90	123	11.16	10.58
Dist. post. M3-cond.	3	340.67	321	351	17.04		11	287.91	252.5	320	23.00	7.99
Dist. nasal-orbite	3	387.00	360	411	25.63		9	298.39	236	327	27.03	9.06
DT major crest occip.	2	175.00	165	185			8	136.00	101	154	16.24	11.94
Width masto.apo.	2	262.50	243	282			11	190.32	158	212	16.91	8.89
Width mini. frontal	3	58.17	43.5	69	13.18		10	47.50	34	60.5	10.94	23.04
Width proc. post orb.	2	244.00	226	262			1	188.00				
Width proc. above orb.	1	238.00					3	205.00	188	227	19.97	
Width proc. ant. orb.	2	221.00	210	232			8	200.75	162	224	19.39	9.66
Width zygom. arc.	0						9	293.11	255	324	21.71	7.41
Width on the bottom of the nasal notch	3	171.50	150.5	212	35.08		12	118.33	100	134	11.17	9.44
H face occip.	2	184.50	184	185			9	127.44	117	142	8.08	6.34
H cranium at P2	2	216.00	167	265			14	159.54	124	178	16.36	10.26
H cranium at P4-M1	4	215.00	171.5	266.5	42.03	19.55	14	163.04	127	202	21.65	13.28
H cranium at M3	2	220.50	176	265			14	169.96	138	206	19.81	11.65
Palatinal width between P2	0						6	54.17	46	67	8.28	15.29
Palatinal width between P4-M1	0						6	77.08	61.5	90	12.10	15.70
Palatinal width between M3	0						5	77.60	68	88	7.23	9.32
DT foram. occip.	1	72.00					12	49.71	40	57.5	4.93	9.92
DT ext. cond. occip.	1	158.00					14	121.71	103	134	8.24	6.77

TABLE 3. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 mandibles.

	Milia	MIL 162	MIL 244	MIL 658	MIL 245	MIL 267	MIL 1478	MIL 281	SGP 1	MIL 1477
Mandible	n° var.	D	D	double	D	D			double	
Length	1		497							
Dist. post. symphysis-talon	2		390							
H corpus between P2-P3	3									
H corpus between P3-P4	4									
H corpus between P4-M1	5		81	85			77	82	75.5	
H corpus between M1-M2	6									
H corpus between M2-M3	7	104.5	84.5		91			93	79	82.5
H corpus after M3	8	104.5			96					
DT corpus between P4-M1	9	61	54	47			47.5	47	47	
DT corpus below ant. M3	10	56.5	55		50			49.5	52	50.5
L symphysis	11		125	117					> 112	
DAP branch at level occlusal	13	144	140			131*				
DT condyle	14	102.5				88				
H condyle	15	225	224							
H apo. coronoideus	16	>300								

	Dicerorhinus jeanvireti					
	N	**mean**	**min.**	**max.**	**SD**	**v**
Length	1	535.00				
Dist. post. symphysis-talon	3	402.33	380	416	19.50	
H corpus between P2-P3	6	69.25	61.5	77	6.46	9.33
H corpus between P3-P4	11	75.41	70	82	3.77	5.00
H corpus between P4-M1	11	79.55	74	85	3.18	4.00
H corpus between M1-M2	11	84.23	71	92	5.31	6.30
H corpus between M2-M3	14	89.75	77	99	6.18	6.88
H corpus after M3	8	96.81	90	105	5.36	5.54
DT corpus between P4-M1	11	52.50	45	60.5	4.50	8.57
DT corpus below ant. M3	14	52.11	43.5	69	7.51	14.41
L symphysis	5	120.40	114	133	7.36	6.11
DAP branch at level occlusal	4	144.38	135.5	163	12.62	8.74
DT condyle	6	105.00	92	115	8.07	7.69
H condyle	5	241.60	220	270	19.30	7.99
H apo. coronoideus	2	302.00	286	318		

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
Length	2	585.50	565	606			11	477.00	430	509	23.49	4.92
Dist. post. symphysis-talon	5	453.60	433	478	22.29	4.91	11	391.82	367	421	14.41	3.68
H corpus between P2-P3	27	77.00	56	94	9.78	12.70	19	66.32	55.5	80	6.93	10.45
H corpus between P3-P4	32	85.97	73	106	7.04	8.19	25	71.70	62.5	83.5	5.17	7.21
H corpus between P4-M1	42	91.71	80	117	8.96	9.77	30	76.70	66	85.5	5.08	6.62
H corpus between M1-M2	32	96.27	85	112	6.90	7.16	35	82.91	65	91	6.29	7.59
H corpus between M2-M3	37	100.39	86.5	120	8.89	8.85	39	86.08	70	96.5	6.43	7.46
H corpus after M3	31	105.90	87	127	8.73	8.24	38	91.16	79	105	7.13	7.82
DT corpus between P4-M1	41	55.56	48	70	5.04	9.08	34	48.28	41	60	4.47	9.27
DT corpus below ant. M3	40	58.24	46	72	5.83	10.01	42	49.02	41	60	4.32	8.81
L symphysis	10	131.95	113.5	149	13.16	9.97	15	110.50	94	123	8.15	7.37
DAP branch at level occlusal	12	160.67	140	184	15.37	9.57	17	143.03	115	152	9.39	6.57
DT condyle	1	115.00					12	90.46	77.5	107	7.41	8.19
H condyle	10	251.65	236	284	15.15	6.02	10	222.45	197	243	15.62	7.02
H apo. coronoideus	0						2	261.00	254	268		

TABLE 4. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 upper cheek teeth.

	Milia									
	MIL 162	MIL 1476	MIL 806	MIL 868	MIL 880	MIL 1287	MIL 614	MIL 1197	MIL 1119	MIL 1569
Upper teeth	double	D	S	D	S	D	S	S	D	D
P 2/ L	36									
P 2/ B	41									
P 3/ L	43	42.5	43							
P 3/ B	53.5	53.5	48.5							
P 4/ L	45			41.5	46.5	44				
P 4/ B	57.5			54.5	57.5	58.5				
M 1/ L	52						56			52
M 1/ B	56						58			57.5
M 2/ L	55							56		
M 2/ B	63.5							63		
M 3/ L abs.	61.5								57.5	
M 3/ L anat.	45.5								45	
M 3/ B	59								54.5	
L P2/-M3/	253.5									
L P/	116.5									
L two last P/	84									
L M/	149									
wear		+	0	+/-	-to +/-	+	-	+/- to +	++	+/-

	Dicerorhinus jeanvireti					*Dicerorhinus megarhinus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
P 1/ L	1	24.00										
P 1/ B	1	20.00										
P 2/ L	4	34.13	31	37	2.46	7.22	18	38.31	31	41	2.50	6.54
P 2/ B	4	37.88	35	39	1.93	5.10	24	42.25	35.5	46	2.54	6.01
P 3/ L	4	41.00	40	42.5	1.08	2.63	23	43.59	39	48.5	2.67	6.12
P 3/ B	5	48.70	45	50.5	2.28	4.68	32	53.97	48	59.5	3.11	5.77
P 4/ L	8	42.19	40.5	44	1.13	2.68	29	47.26	43	57	3.30	6.98
P 4/ B	10	53.00	46	56.5	4.05	7.64	41	58.56	52.5	67	3.51	6.00
M 1/ L	7	49.43	48.5	51	0.84	1.70	24	55.56	47.5	64	4.02	7.23
M 1/ B	7	53.50	50	57.5	3.32	6.20	31	62.35	54	70	3.89	6.24
M 2/ L	7	53.14	51	55.5	1.55	2.91	23	60.17	50.5	65.5	4.18	6.95
M 2/ B	9	58.50	51.5	61	3.89	6.65	37	65.86	57	73	3.50	5.31
M 3/ L abs.	4	56.75	53	59	2.63	4.63	34	59.91	53	70	3.28	5.48
M 3/ L anat.	2	55.50	53	58			33	50.86	43.5	62	4.67	9.17
M 3/ B	5	50.30	46	56	4.44	8.82	35	58.20	50	67	3.90	6.70
L P2/-M3/	1	248.00					8	265.38	256	274	6.19	2.33
L P/	2	115.50	114	117			10	118.70	105.5	128	6.72	5.66
L two last P/	3	78.83	71	83.5	6.83		17	84.79	74	97	6.26	7.38
L M/	4	136.00	120	146	11.89	8.74	12	153.71	142	162.5	5.52	3.59

TABLE 4. — Continuation.

	Dicerorhinus etruscus etruscus						*Dicerorhinus miguelcrusafonti*	
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**
P 1/ L	5	24.30	23	27.5	1.82	7.50		
P 1/ B	5	24.30	21	26	2.08	8.56		
P 2/ L	12	32.29	29	35	2.38	7.37		
P 2/ B	23	37.93	32	42.5	3.07	8.10		
P 3/ L	13	39.19	35	43.5	2.36	6.02	1	45.5
P 3/ B	26	48.73	42	54	3.48	7.15	1	45
P 4/ L	12	42.04	37	49	3.88	9.23	1	43
P 4/ B	25	54.82	45	63	4.19	7.64	1	59
M 1/ L	15	49.10	45	54	2.19	4.46	1	55.5
M 1/ B	25	55.50	48	60.5	3.62	6.52	1	60
M 2/ L	13	50.35	45.5	57	3.45	6.86	1	56.5
M 2/ B	21	57.02	48	65.5	4.38	7.68		
M 3/ L abs.	16	53.47	47	59	2.91	5.45		
M 3/ L anat.	21	46.55	38.5	54	4.74	10.17		
M 3/ B	22	51.89	46	56.5	2.91	5.61		
L P2/-M3/	13	229.50	215	245	8.68	3.78		
L P/	17	109.79	100	137	10.51	9.57		
L two last P/	18	75.17	67	83.5	4.61	6.13		
L M/	14	135.14	126.5	145	6.00	4.44		

TABLE 5. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 lower cheek teeth.

	Milia												
	MIL 162	MIL 244	SGP 1	MIL 658	MIL 245	MIL 281	MIL 1145	MIL 1343	MIL 837	MIL 425	MIL 245	MIL 1324	MIL 1478
Lower teeth	D	D	double	double	D	D	D	S	D	D	S	D	D
P /2 L			30	29		27							
P /2 B			17	17		18							
P /3 L			37	33		37							
P /3 B			24.5	23.5		25.5					34		
P /4 L			38.5	38.5		40					40		
P /4 B			27	25.5		30					31		
M /1 L			44	44		43			42.5			40	43.5
M /1 B			29	28.5		31.5			29.5			30	29.5
M /2 L	48	47	48.5		47	47.5							
M /2 B	32.5	30	30		32.5	31							
M /3 L	52	49	46.5*		48.5	51.5	53	52					
M 3/B	31.5	29.5			31	29.5	28.5	29.5					
L P/2-M/3			246*			238							
L /P			106.5	97		102							
L two last/P		78*	77	68.5		73.5							
L /M		133	140			138							
D/1L										22			
D/1lB										11			
D/2L													
D/2B													
D/3L													
D/3B													
D/4L													
D/4B													
wear	+	+/- to +	-	+	+	+	+/-	+/-	+++	-	++	++	+

	Dicerorhinus jeanvireti						*Dicerorhinus megarhinus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
P /2 L	8	30.19	27	32	2.02	6.68	18	34.42	29.5	43	3.63	10.54
P /2 B	8	19.31	16.5	21	1.53	7.94	20	21.23	16.5	25.5	2.37	11.17
P /3 L	6	35.08	33	38	1.74	4.97	36	40.39	35	47	2.55	6.31
P /3 B	6	25.17	23	27	1.33	5.28	42	27.67	22	32	2.07	7.50
P /4 L	10	38.90	37	40.5	1.22	3.14	35	43.71	37.5	48	2.60	5.95
P /4 B	10	28.40	24	31	2.16	7.60	42	31.73	27.5	38	2.28	7.19
M /1 L	10	43.35	40	47	2.19	5.04	48	47.49	38.5	53	3.11	6.55
M /1 B	13	30.88	25	34	2.66	8.62	70	33.56	28.5	40	2.82	8.41
M /2 L	15	47.47	43	53.5	2.99	6.30	52	51.19	43	57.5	3.07	6.01
M /2 B	17	30.88	27	34.5	1.97	6.39	61	34.44	31	39	2.28	6.61
M /3 L	10	48.15	43.5	54	3.06	6.36	48	53.85	48	62	3.39	6.29
M 3/B	9	29.94	26	33	1.86	6.22	53	32.73	29.5	37	1.96	5.98
L P/2-M/3	4	238.75	234	242	3.40	1.43	23	264.15	228	293	16.17	6.12
L /P	4	102.75	98	106	3.59	3.50	23	115.13	101	136	8.28	7.19
L two last/P	9	73.39	69.5	77	2.58	3.52	41	81.05	71	92	4.94	6.09
L /M	11	133.55	127	138	3.08	2.30	42	149.77	134	165	7.71	5.15

TABLE 5. — Continuation.

	Dicerorhinus etruscus etruscus						*Dicerorhinus miguelcrusafonti*			
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**
P /1 L							1	22.00		
P /1 B							1	11.00		
P /2 L	15	29.97	25	33	1.87	6.23	1	30.50		
P /2 B	16	18.97	16	22	1.81	9.55	1	20.50		
P /3 L	15	34.67	31.5	37.5	1.92	5.55	2	34.75	33.5	36
P /3 B	19	23.55	21.5	29	1.73	7.35	2	25.00	25	25
P /4 L	21	37.81	35	42.5	1.83	4.85	1	36.50		
P /4 B	28	26.68	22	31	2.15	8.07	1	28.50		
M /1 L	29	41.79	36	50	3.43	8.21	1	41.00		
M /1 B	41	29.11	26.5	33	1.59	5.48	1	33.50		
M /2 L	33	45.77	40	54	3.41	7.45	2	48.75	47.5	50
M /2 B	44	29.65	27	34	1.96	6.60	2	32.75	32.5	33
M /3 L	39	45.96	41	52	2.51	5.46	1	52.00		
M 3/B	38	28.66	26	33	1.59	5.56	1	34.00		
L P/2-M/3	13	231.65	210	251.5	14.56	6.29				
L /P	12	99.79	87	108	8.06	8.08	1	103.00		
L two last/P	24	70.21	63	80.5	5.25	7.47	1	70.50		
L /M	32	129.91	121	143	6.15	4.74				

TABLE 6. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 Mc III.

	Milia		*Dicerorhinus miguelcrusafonti*			
	MIL 1587	MIL 902				
Mc III	D	S	N	mean	min.	max.
L	215		2	200.25	195	205.5
DT prox.	64	62	3	63.17	61.5	65
DAP prox.	51	51	3	46.50	44	49
DT dia.	53	55.5	2	57.25	56.5	58
DAP dia.	21.4	22.5	1	24.00		
DT distal	63.5		2	63.50	60	67
DT dist. art.	51.3		1	48.00		
DAP dist.art.	46.2		2	44.50	43	46

	Dicerorhinus jeanvireti					
	N	mean	min.	max.	SD	v
L	8	229.38	219	237	7.31	3.19
DT prox.	11	63.91	57	69	4.13	6.47
DAP prox.	10	54.65	48	58	3.67	6.71
DT dia.	11	57.55	51	63	3.83	6.66
DAP dia.	8	21.88	20	24	1.22	5.57
DT distal	9	65.83	60	71	4.09	6.22
DT dist. art.	11	53.45	48	58.5	3.07	5.74
DAP dist.art.	11	47.77	42	53.5	3.80	7.95

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
L	10	225.00	213	243	8.44	3.75	20	202.03	194	220.5	6.43	3.18
DT prox.	13	67.65	60	75	4.13	6.10	25	53.52	48.5	58	2.40	4.48
DAP prox.	11	54.73	48	58	3.10	5.67	22	45.93	42.5	51	2.11	4.60
DT dia.	10	60.35	51.5	68	5.73	9.49	23	48.83	45	53.5	2.45	5.02
DAP dia.	8	22.25	18.5	25	2.17	9.76	20	20.70	18	24.5	1.39	6.71
DT distal	9	70.11	60	80	6.88	9.81	21	56.79	49	61	2.56	4.51
DT dist. art.	10	56.20	49	63	5.01	8.92	21	46.19	43	50	1.93	4.19
DAP dist.art.	9	49.72	45.5	53	2.28	4.58	17	40.68	35	43	1.97	4.84

TABLE 7. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 tibia.

	Milia				*Dicerorhinus jeanvireti*					
	MIL 819	MIL 1582	MIL 1642	MIL 1645						
Tibia	D	S	S	S	**N**	**mean**	**min.**	**max.**	**SD**	**v**
L	415				8	409.63	375	431	20.06	4.90
DT prox.	134*				10	134.90	123	140	5.34	3.96
DAP prox.	126				8	131.88	123	137.5	5.81	4.41
DT dia.	65				13	65.23	61	70	2.83	4.33
DAP dia.	60.5				12	62.88	56	69	3.54	5.62
DT distal	104		102	107	10	109.60	102	118	5.44	4.96
DAP distal	81	80	71	78.8	9	79.06	75	83.5	3.02	3.81
DT distal art.	85		79.5	87						
DAP distal art.	64		64	70						

TABLE 7. — Continuation.

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
L	13	424.31	392	448	17.72	4.18	21	357.33	334	389	14.37	4.02
DT prox.	11	142.50	123	157	11.38	7.99	20	109.90	102	115	3.76	3.42
DAP prox.	8	138.06	123	144.5	6.67	4.83	16	109.19	100	117.5	4.88	4.47
DT dia.	22	69.55	56	80	6.21	8.93	28	53.46	43.5	61.5	4.02	7.52
DAP dia.	21	64.64	54	76	5.09	7.87	28	51.98	43	63	4.71	9.06
DT distal	25	112.82	101.5	127	6.81	6.04	31	90.85	80	105	6.53	7.19
DAP distal	25	81.02	70	89	4.47	5.52	32	64.39	58	72	3.92	6.09

TABLE 8. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 astragalus.

	Milia			*Dicerorhinus miguelcrusafonti*			
	MIL 367	MIL 181	MIL 852				
Astragalus	S	D	S	**N**	**mean**	**min.**	**max.**
DT max.	98.5	92	99	3	85.67	85	
H	87		92*	3	89.67	89	86
DAP int.	64	56.5	61.5*	1	59.00		90
DT dist.art.	76	80	79	2	71.50	71	
DAP dist.art.	51	46.5		1	43.50		72
Dist. 2 brims	68	65	65	3	63.17	60	
DT dist.	84.5	84	88	2	78.50	78.5	66

	Dicerorhinus jeanvireti					
	N	**mean**	**min.**	**max.**	**SD**	**v**
DT max.	15	99.70	92	107.5	5.28	5.30
H	13	91.04	87	104	4.36	4.79
DAP int.	11	65.18	62	72	3.03	4.64
DT dist.art.	8	77.69	70	85	6.28	8.09
DAP dist.art.	8	48.19	46	52	2.03	4.22
Dist. 2 brims	11	65.18	62	69	3.00	4.61
DT dist.	10	85.25	77	94	6.55	7.68

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
DT max.	32	101.73	92.5	113	4.58	4.50	48	80.95	73	88	3.45	4.26
H	32	97.31	88	110	5.66	5.82	48	77.22	71	84	3.26	4.22
DAP int.	32	67.13	59	75	4.27	6.36	47	53.39	47	58	2.53	4.74
DT dist.art.	31	81.74	71	91	4.58	5.61	44	65.74	57	75	3.98	6.05
DAP dist.art.	25	49.56	45.5	58	3.00	6.05	44	40.69	36	45.5	2.39	5.88
Dist. 2 brims	33	69.91	53	81	5.25	7.51	50	55.58	49	62	3.14	5.65
DT dist.	31	87.19	78	99	4.74	5.43	44	70.05	60	78	3.71	5.29

TABLE 9. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 calcaneum.

	Milia											
	MIL 1703						***Dicerorhinus miguelcrusafonti***					
Calcaneum	S						N	mean				
Height	139						1	128.5				
DAP tuber	76.1						1	69				
DAP bec	76											
DT sust.	80											
DT tuber	56						1	49				
DT middle	43											
	Dicerorhinus jeanvireti											
	N	**mean**	**min.**	**max.**	**SD**	**v**						
Height	12	139.08	128	149.5	8.01	5.76						
DAP tuber	13	73.92	66	83.5	4.16	5.62						
DAP bec	12	73.13	67	83	4.28	5.85						
DT sust.	11	81.36	75	89	4.43	5.44						
DT tuber	14	53.61	48	61	4.55	8.48						
DT middle	10	38.15	35	43.5	2.21	5.80						
	Dicerorhinus megarhinus						***Dicerorhinus etruscus etruscus***					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
Height	14	148.54	133	163	8.03	5.40	23	118.72	109	130	6.21	5.23
DAP tuber	16	78.84	67	87.5	5.05	6.40	25	63.64	57.5	71	3.70	5.81
DAP bec	19	78.16	69	84	3.63	4.65	25	59.94	54	70	3.92	6.53
DT sust.	10	84.40	72	98	7.12	8.44	23	67.61	60	75	3.98	5.88
DT tuber	18	56.14	48	63	4.26	7.59	23	43.89	39.5	49	2.58	5.89
DT middle	16	43.72	38.5	51	4.23	9.68	21	34.98	31	39	2.31	6.60

TABLE 10. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 cuboid.

	Milia											
	MIL 1665						***Dicerorhinus miguelcrusafonti***					
Cuboid	D						**N**	**mean**	**min.**	**max.**	**SD**	**v**
Length	63.3						1	70.00				
Breadth	47.8						1	40.00				
Height	68						3	61.17	55.5	67	5.75	9.40
L art.surf.sup.	46.4						3	40.17	37	43.5	3.25	8.10
B art.surf.sup.	44						2	44.75	44.5	45	0.35	0.79
H ant.face	44.8						1	39.50				
	Dicerorhinus jeanvireti											
	N	**mean**	**min.**	**max.**	**SD**	**v**						
Length	7	67.43	63	71	2.51	3.72						
Breadth	8	50.63	48	54	2.08	4.11						
Height	9	63.28	56	73	6.13	9.69						
L art.surf.sup.	7	45.29	36	51	4.82	10.64						
B art.surf.sup.	2	47.50	40	55								
H ant.face	4	48.75	45	52	2.99	6.13						

TABLE 10. — Continuation.

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
Length	12	71.63	63.5	76.5	4.19	5.85	24	58.77	53.5	67	3.44	5.85
Breadth	11	53.50	47.5	60	3.88	7.25	23	41.22	36	48	3.30	8.01
Height	12	68.54	59	75	5.63	8.21	21	55.90	51	62	2.74	4.90
L art.surf.sup.	10	49.05	43.5	54	3.62	7.39	22	39.86	34	47	2.80	7.02
B art.surf.sup.	8	50.44	43.5	55.5	3.61	7.16	13	40.08	31.5	43	2.82	7.04
H ant.face	10	48.30	45	52	2.29	4.74	22	39.80	36	42.5	2.34	5.89

TABLE 11. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 Mt III.

	Milia		*Dicerorhinus miguelcrusafonti*				
	MIL 368	MIL 710					
Mt III	D	S	**N**	**mean**	**min.**	**max.**	**SD**
L	200		3	186.83	186	187.5	0.76
DT prox.	58	57.5	4	52.00	51.5	52.5	0.41
DAP prox.	48		2	40.75	40.5	41	
DT dia.	51.5		2	45.25	45	45.5	
DAP dia.	27		2	24.75	24.5	25	
DT distal	59.5		3	58.17	56	60	2.02
DT dist. art.	50		3	46.50	45	47.5	1.32
DAP dist.art.	46		3	38.83	38	40	1.04

	Dicerorhinus jeanvireti					
	N	**mean**	**min.**	**max.**	**SD**	**v**
L	7	205.29	200	212	4.39	2.14
DT prox.	10	57.00	53	60.5	2.64	4.62
DAP prox.	6	47.83	44	52	3.25	6.80
DT dia.	11	49.36	46	53	2.35	4.75
DAP dia.	8	24.06	21	25	1.43	5.92
DT distal	6	61.83	58	65.5	2.70	4.36
DT dist. art.	9	50.17	45	54	2.54	5.06
DAP dist.art.	9	43.44	40	45	1.81	4.17

	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
L	18	202.53	190	213.5	5.76	2.84	18	175.92	165	187	6.02	3.42
DT prox.	19	60.03	53	65	3.38	5.63	24	48.54	43	56	3.56	7.34
DAP prox.	14	47.93	42.5	55	3.64	7.60	18	41.86	38	47	2.79	6.67
DT dia.	22	56.16	45	63	5.08	9.04	19	40.18	33.5	45	3.01	7.50
DAP dia.	22	25.55	22	34	2.82	11.04	15	22.90	21.5	25	1.11	4.83
DT distal	16	65.47	57	72	3.97	6.06	16	52.13	48	59	2.72	5.21
DT dist. art.	19	53.26	46.5	59	3.22	6.05	18	42.28	39	46	2.13	5.04
DAP dist.art.	18	43.92	37.5	48	2.49	5.68	14	36.86	32	40	2.13	5.77

TABLE 12. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Mt IV.

	Milia											
	MIL 204						*Dicerorhinus miguelcrusafonti*					
Mt IV	S						**N**	**mean**	**min.**	**max.**		
L	178.5						1	156.50				
DT prox.	56						2	37.75	37	38.5		
DAP prox.	51.5						1	35.00				
DT dia.	36.5						1	29.00				
DAP dia.	35.5						1	29.50				
DT distal	43						1	35.00				
DT dist. art.	43						1	33.50				
DAP dist.art.	45						1	34.50				
	Dicerorhinus jeanvireti						**Hajnacka I (Durisova 2004)**					
	N	**mean**	**min.**	**max.**	**SD**	**v**						
L	7	180.43	168	188.5	7.12	3.95		188	186			
DT prox.	10	49.00	44	52	2.58	5.27		49	50			
DAP prox.	10	44.15	40.5	49	2.97	6.73		44.2	44			
DT dia.	10	35.00	31	38	2.07	5.91		34	37			
DAP dia.	9	28.56	23	36	4.61	16.15		27	32			
DT distal	5	41.60	40	44	1.52	3.65		40	46			
DT dist. art.	7	39.86	37	45	2.61	6.55		38.5	43			
DAP dist.art.	7	45.00	41	49.5	2.66	5.91		40.5	43			
	Dicerorhinus megarhinus						*Dicerorhinus etruscus etruscus*					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
L	8	176.19	164	182	5.88	3.34	16	153.69	146	163	5.54	3.61
DT prox.	10	49.65	42	55	4.44	8.93	25	37.58	30	42	2.99	7.96
DAP prox.	11	47.55	38	53.5	4.20	8.84	22	36.32	33	41	2.10	5.77
DT dia.	12	34.29	32	37	1.51	4.42	18	26.25	22	31	2.52	9.59
DAP dia.	12	31.08	22	35	4.19	13.49	18	24.03	20	28	2.22	9.24
DT distal	9	40.22	39	42	1.23	3.05	14	33.32	29	41.5	3.17	9.52
DT dist. art.	9	38.72	35.5	42	1.89	4.88	15	32.10	28.5	35	2.20	6.85
DAP dist.art.	8	44.81	40.5	47	2.10	4.69	15	35.93	33	39	2.21	6.15

TABLE 13. — Comparative dimensions of the Milia *Sus arvernensis arvernensis* Guérin, 1972 cheek teeth.

Sus	**Milia**	***Sus arvernensis***				
Teeth	MIL 205	**N**	**mean**	**min.**	**max.**	**SD**	**v**
P 4/ L	13	13	11.85	10.5	13.5	0.75	6.30
P 4/ B	15	13	14.27	12.5	16.5	1.35	9.45
M 1/ L	18	13	15.69	13.5	17.5	1.09	6.95
M 1/ B ant.	14	12	14.67	13	16	1.07	7.32
M 1/ B post.	15.5	14	15.11	14	16	0.90	5.97
M 2/ L	21.5	14	20.11	18	21.5	0.88	4.38
M 2/ B ant.	17.5	14	17.82	16	19.5	1.08	6.09
M 2/ B post.	17.5	14	17.50	14.5	19.5	1.34	7.68
M 3/ L	29	26	27.13	24.5	31	1.66	6.11
M 3/ B ant.	17.5	28	18.09	16	20.5	1.42	7.86
M 3/ B mid.	15	27	16.07	14.5	18	1.04	6.50
M 3/ B post.	10.5	17	10.24	8	14	1.95	19.01
L M/	64.5	5	61.40	59	64.5	2.27	3.70
	MIL 696						
M/2 L	20	10	19.95	18	22.5	1.48	7.42
M/2 B ant.	14.5	9	14.33	13	15	0.83	5.78
M/2 B post.	14.5	9	15.11	14	17	0.93	6.14

	Potamochoerus provincialis						***Sus strozzii***					
	N	**mean**	**min.**	**max.**	**SD**	**v**	**N**	**mean**	**min.**	**max.**	**SD**	**v**
P 4/ L	3	15.33	14.5	16	0.76	4.98	10	13.85	12	15.5	1.16	8.35
P 4/ B	3	17.50	17	18	0.50	2.86	10	17.70	15.5	19	1.09	6.13
M 1/ L	2	19.00	19	19	0.00	0.00	13	18.85	17	22	1.59	8.42
M 1/ B ant.	2	17.00	17	17	0.00	0.00	6	17.25	16.5	19	0.88	5.10
M 1/ B post.	2	17.25	17	17.5	0.35	2.05	6	18.08	17	20	1.50	8.28
M 2/ L	7	24.71	22	26.5	1.52	6.16	15	27.63	25	30.5	1.46	5.27
M 2/ B ant.	7	22.21	20	25	2.04	9.18	15	22.87	21	24.5	0.97	4.25
M 2/ B post.	7	21.50	19	23.5	1.80	8.39	16	22.59	21	25	0.92	4.06
M 3/ L	12	37.25	29	45	3.93	10.56	22	42.86	33.5	49	3.40	7.92
M 3/ B ant.	13	25.15	22.5	27.5	1.51	5.98	23	26.50	24	29	1.38	5.21
M 3/ B mid.	13	21.88	19	23	1.10	5.04	22	23.91	21	27	1.49	6.25
M 3/ B post.	12	12.96	9.5	19	2.48	19.15	18	17.28	13	21	1.96	11.33
L M/	1	79.50					10	86.60	80.5	92	3.33	3.85
M/2 L	17	25.09	22	27	1.24	4.94	22	26.18	24.5	28	1.08	4.11
M/2 B ant.	17	17.94	15.5	20	0.97	5.39	22	17.66	16	19	0.76	4.31
M/2 B post.	17	17.59	16.5	19	0.75	4.29	22	18.52	16.5	20	0.76	4.12