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

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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 arvernensis 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 Viallette. 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.
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 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, fluval 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 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.

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 *arvernensis* the average lengths of the lower premolars are smaller than those of *T. terrestris* (they are the same as in *T. pinchasus*), except for P1/2 and P3/4; P2/ and P3/ which are large; the posterior widths of P3/ and P4/ 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 P3/ and P4/ is the only characteristic that seems to distinguish European Miocene and Pliocene tapirs from extant tapirs (with the exception of *T. pinchasus*). 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 strozzai* Forsyth Major, 1881 and *Dicerorhinus merckii* (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 Viallette (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* Kretzoi, 1942: 312-314, 341, junior synonym.

*Procerorhinus* Kretzoi, 1942: 315, junior synonym.

*Dicerorhinus jeannireti* Guérin, 1972

*Dicerorhinus jeannireti* 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. *Stephanorhinus 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.

*Diceroshinus jeannvireti* 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 Musselieve (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), Grosorea (MNQ 16a) and Cernatast (MNQ 16a), all three in Oltenia.

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

*Diceroshinus jeannvireti* 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 hemimandible 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 M1 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 “Ceros’’ 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 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 infrarostral foramen is above the middle of P4/; it is...
Fig. 6. — The Milia *Diceros rhinoceros 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. Jeanniverti. 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-palatal 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. Although 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, cross section of diaphysis in the middle; E, distal view; F, posterior view; G, medial view. Scale bar: 50 mm.
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 are smaller and those of 1 to 42 specimens of D. megarhinus 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 prominent 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 dl/2 or 1/2, 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...
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 ectoloph less flat than for the molars of Vialette.
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.
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 trapazoidal 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.
In posterior view (Fig. 11A), the sustentaculum 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).
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 Viallette; thus Milia could be a little more recent than Viallette, 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 Viallette 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 **SUIDIFORMES** 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 Viallette and in Trévoux-Reyrieux in Ain (Guérin *et al.* 1998); its primitive subspecies is known from the Ruscinian in the Perpignan
region, in Cavaillé brickfield, in Serrat d’en-Vacquer (type-site of *S. arvernensis minor*) and Mas Bruno near Saint-Estèze, 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).
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 three dimensions of the M/2 are close to the average of nine to ten specimens of *S. arvernensis* (Appendices, Table 13).

**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.

**Radius**

The proximal epiphysis of the Milia radius has $DT = 27.5\, \text{mm}$ for $DAP = 19\, \text{mm}$. 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 Suinae**

Because of its dimensions, in particular its upper cheek teeth, the Milia Suinae 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).

**Paleoecological 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 jeannvireti*, the latter (along with *Mammut borsoni*) being particularly well represented.

The association among *Tapirus arvernensis arvernensis*, *Dicerorhinus jeannvireti* 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. jeannvireti* 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.

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### APPENDICES

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

| Cheek Teeth | Milia 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|

| Calcaneus | Milia 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.

| Cranium | Milia 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 | 308.00 |    |   |
| Minimal width of the braincase | 5 | 138 | 109 | 0 | 138 | 168 | 177 | 6.36 |
| 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 | 0|    |   |
| Dist. nasal notch-orbite | 9 | 120 | 128.5 | 1 | 117.00 |    |   |
| Dist. post. M3-cond. | 13 | 330 | 330 | 1 | 334.00 |    |   |
| Dist. nasal-orbite | 14 | 364 | 374 | 2 | 357.5 | 348 | 367 | 13.44 |
| DT major crest occip. | 15 | 172 | 188* | 0 | 188* |    |   |
| Width masto.apo. | 16 | 232 | 250 | 0 | 0|    |   |
| Width mini. frontal | 17 | 71 | 73.5 | 0 | 0|    |   |
| Width proc. post orb. | 18 | 229 | 224.5 | 0 | 224.5 |    |   |
| Width proc. above orb. | 19 | 254 | 244.5 | 0 | 244.5 |    |   |
| Width proc. ant. orb. | 20 | 266 | 0 | 1 | 221.00 |    |   |
| Width zygom. arc. | 21 | 392 | 320 | 0 | 320 |    |   |
| Width on the bottom of the nasal notch | 22 | 161 | 157 | 1 | 108.00 |    |   |
| H face occup. | 23 | 133 | 157 | 0 | 0|    |   |
| H cranium at P2 | 25 | 155.5 | 0 | 0|    |   |
| H cranium at P4-M1 | 26 | 178.5 | 0 | 0|    |   |
| H cranium at M3 | 27 | 162 | 0 | 0|    |   |
| Palatal width between P2 | 28 | 43.5 | 1 | 71.00 |    |   |
| Palatal width between P4-M1 | 29 | 82.5 | 1 | 92.50 |    |   |
| Palatal width between M3 | 30 | 102 | 1 | 100.00 |    |   |
| DT foram. occip. | 31 | 55 | 0 | 0|    |   |
| DT ext. cond. occip. | 32 | 142 | 141 | 0 | 0|    |   |
| Craneum                                      | Dicerorhinus megarhinus | Dicerorhinus etruscus etruscus |
|---------------------------------------------|-------------------------|-------------------------------|
|                                             | 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 occup.                       | 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.

| Mandible                          | Milia 162 | MIL 244 | MIL 658 | MIL 245 | MIL 1478 | MIL 281 | MIL 1477 |
|-----------------------------------|-----------|---------|---------|---------|----------|---------|----------|
| Length n° var. D                  | 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 |
|---|------|------|------|----|---|
|   | 1    | 535.00 |     |    |   |
| Length | 3 | 402.33 | 380 | 416 | 19.50 |
| Dist. post. symphysis-talon | 6 | 69.25 | 61.5 | 77 | 6.46 | 9.33 |
| H corpus between P2-P3 | 11 | 75.41 | 70 | 82 | 3.77 | 5.00 |
| H corpus between P3-P4 | 11 | 79.55 | 74 | 85 | 3.18 | 4.00 |
| H corpus between M1-M2 | 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 megahrinus**

| N | mean | min. | max. | SD | v |
|---|------|------|------|----|---|
| Length | 2 | 585.50 | 565 | 606 |     |
| Dist. post. symphysis-talon | 5 | 453.60 | 433 | 478 | 22.29 | 4.91 |
| H corpus between P2-P3 | 27 | 77.00 | 56 | 94 | 9.78 | 12.70 |
| H corpus between P3-P4 | 32 | 85.97 | 73 | 106 | 7.04 | 8.19 |
| H corpus between P4-M1 | 42 | 91.71 | 80 | 117 | 8.96 | 9.77 |
| H corpus between M1-M2 | 32 | 96.27 | 85 | 112 | 6.90 | 7.16 |
| H corpus between M2-M3 | 37 | 100.39 | 86.5 | 120 | 8.89 | 8.85 |
| H corpus after M3 | 31 | 105.90 | 87 | 127 | 8.73 | 8.24 |
| DT corpus between P4-M1 | 41 | 55.56 | 48 | 70 | 5.04 | 9.08 |
| DT corpus below ant. M3 | 40 | 58.24 | 46 | 72 | 5.83 | 10.01 |
| L symphysis | 10 | 131.95 | 113.5 | 149 | 13.16 | 9.97 |
| DAP branch at level occlusal | 12 | 160.67 | 140 | 184 | 15.37 | 9.57 |
| DT condyle | 1 | 115.00 | | | | |
| H condyle | 10 | 251.65 | 236 | 284 | 15.15 | 6.02 |
| H apo. coronoideus | 0 | | | | | |

**Dicerorhinus etruscus etruscus**

| N | mean | min. | max. | SD | v |
|---|------|------|------|----|---|
| Length | 11 | 477.00 | 430 | 509 | 23.49 | 4.92 |
| Dist. post. symphysis-talon | 11 | 391.82 | 367 | 421 | 14.41 | 3.68 |
| H corpus between P2-P3 | 19 | 66.32 | 55.5 | 80 | 6.93 | 10.45 |
| H corpus between P3-P4 | 25 | 71.70 | 62.5 | 83.5 | 5.17 | 7.21 |
| H corpus between P4-M1 | 30 | 76.70 | 66 | 85.5 | 5.08 | 6.62 |
| H corpus between M1-M2 | 35 | 82.91 | 65 | 91 | 6.29 | 7.59 |
| H corpus between M2-M3 | 39 | 86.08 | 70 | 96.5 | 6.43 | 7.46 |
| H corpus after M3 | 38 | 91.16 | 76 | 105 | 7.13 | 7.82 |
| DT corpus between P4-M1 | 42 | 48.28 | 41 | 60 | 4.32 | 8.81 |
| DT corpus below ant. M3 | 42 | 49.02 | 41 | 60 | 4.32 | 8.81 |
| L symphysis | 15 | 110.50 | 94 | 123 | 8.15 | 7.37 |
| DAP branch at level occlusal | 17 | 143.03 | 115 | 152 | 9.39 | 6.57 |
| DT condyle | 12 | 90.46 | 77.5 | 107 | 7.41 | 8.19 |
| H condyle | 10 | 222.45 | 197 | 243 | 15.62 | 7.02 |
| H apo. coronoideus | 2 | 261.00 | 254 | 268 | | |
Table 4. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 upper cheek teeth.

| Upper teeth | MIL 162 | MIL 1476 | MIL 806 | MIL 886 | MIL 1287 | MIL 614 | MIL 1197 | MIL 1119 | MIL 1569 |
|-------------|---------|---------|--------|--------|----------|--------|----------|----------|----------|
| 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   |         |        |        |          |        |          |  52      |          |
| M 1/ B      |    56   |         |        |        |          |        |          |  57.5    |          |
| M 2/ L      |    55   |         |        |        |          |        |          |          |          |
| M 2/ B      |    63.5 |         |        |        |          |        |          |          |          |
| M 3/ L abs. |    61.5 |         |        |        |          |        |          |          |          |
| M 3/ L anat.|    45.5 |         |        |        |          |        |          |          |          |
| 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 |       |     |    | 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 | 3.33 | 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 | 6.83 | 17 | 84.79 | 74 | 97 | 6.26 | 7.38 |
| L two last P/ | 3  | 78.83 | 71 | 83.5 | 8.74 | 12 | 153.71 | 142 | 162.5 | 5.52 | 3.59 |
| 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  | 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 | 42   | 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 | 7.88 |
| 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.

|                  | 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       | 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  |         |         |         |         |         |         |         |         |         |         |
| P /4 L           | 38.5    | 38.5    | 40    |         |         |         |         |         |         |         |         |         |         |
| P /4 B           | 27      | 25.5    | 30    |         |         |         |         |         |         |         |         |         |         |
| M /1 L           | 44      | 44      | 43    |         |         |         |         |         |         |         |         |         |         |
| M /1 B           | 29      | 28.5    | 31.5  |         |         |         |         |         |         |         |         |         |         |
| M /2 L           | 48      | 47      | 47    | 47      | 47      |        |         |         |         |         |         |         |         |
| 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*    |         |       |         |         |         |         |         |         |         |         |         |         |
| 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/1B             |         |         |       |         |         |         |         |         |         |         |         |         | 11      |
| D/2L             |         |         |       |         |         |         |         |         |         |         |         |         |         |
| D/2B             |         |         |       |         |         |         |         |         |         |         |         |         |         |
| D/3L             |         |         |       |         |         |         |         |         |         |         |         |         |         |
| D/3B             |         |         |       |         |         |         |         |         |         |         |         |         |         |
| D/4L             |         |         |       |         |         |         |         |         |         |         |         |         |         |
| D/4B             |         |         |       |         |         |         |         |         |         |         |         |         |         |

|               | 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   | 4.76| 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| 5.95 |
| 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 | 3.99| 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 |

Wear + +/- to + - + + + +/- +/+++ - ++ ++ +
### Table 5. — Continuation.

|                | Dicerorhinus etruscus etruscus | Dicerorhinus miguelcrusafonti |
|----------------|-------------------------------|--------------------------------|
|                | N    | mean | min. | max. | SD  | v  | N    | mean | min. | max. |
| P /1 L         | 1    | 22.00|      |      |     |    | 1    | 30.50|      |      |
| P /1 B         | 1    | 11.00|      |      |     |    |      |      |      |      |
| P /2 L         | 15   | 29.97| 25   | 33   | 1.87| 6.23| 1    | 34.75| 33.5 | 36   |
| 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    | 25.00| 25   | 25   |
| 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| 1    | 103.00|      |      |
| 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.**

| Mc III | MIL 1587 | MIL 902 |
|--------|----------|---------|
| L      | 215      |         |
| DT prox. | 64       | 62      |
| DAP prox. | 51       | 51      |
| DT dia. | 53       | 55.5    |
| DAP dia. | 21.4     | 22.5    |
| DT distal | 63.5      |         |
| DT dist. art. | 51.3      |         |
| DAP dist.art. | 46.2      |         |

**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**

| N | mean | min. | max. | SD | v |
|---|------|------|------|----|---|
| L | 10 | 225.00 | 213 | 243 | 8.44 | 3.75 |
| DT prox. | 13 | 67.65 | 60 | 75 | 4.13 | 6.10 |
| DAP prox. | 11 | 54.73 | 48 | 58 | 3.10 | 5.67 |
| DT dia. | 10 | 60.35 | 51.5 | 68 | 5.73 | 9.49 |
| DAP dia. | 8 | 22.25 | 18.5 | 25 | 2.17 | 9.76 |
| DT distal | 9 | 70.11 | 60 | 80 | 6.88 | 9.81 |
| DT dist. art. | 10 | 56.20 | 49 | 63 | 5.01 | 8.92 |
| DAP dist.art. | 9 | 49.72 | 45.5 | 53 | 2.28 | 4.58 |

**Dicerorhinus etruscus etruscus**

| N | mean | min. | max. | SD | v |
|---|------|------|------|----|---|
| L | 20 | 202.03 | 194 | 220.5 | 6.43 | 3.18 |
| DT prox. | 25 | 53.52 | 48.5 | 58 | 2.40 | 4.48 |
| DAP prox. | 22 | 45.93 | 42.5 | 51 | 2.11 | 4.60 |
| DT dia. | 23 | 48.83 | 45 | 53.5 | 2.45 | 5.02 |
| DAP dia. | 20 | 20.70 | 18.5 | 24.5 | 1.39 | 6.71 |
| DT distal | 21 | 56.79 | 49 | 61 | 2.56 | 4.51 |
| DT dist. art. | 21 | 46.19 | 43 | 50 | 1.93 | 4.19 |
| DAP dist.art. | 17 | 40.68 | 35 | 43 | 1.97 | 4.84 |

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

| Tibia | MIL 819 | 1582 | 1642 | 1645 |
|-------|---------|------|------|------|
| L     | 415     |       |      |      |
| DT prox. | 134*   | 126  |      |      |
| DAP prox. | 65     | 60.5 |      |      |
| DT distal | 104   | 81   | 102 | 107 |
| DT distal art. | 85 | 81   | 79.5 | 87 |
| DAP distal art. | 64 | 64   | 64  | 70  |

**Dicerorhinus jeanvireti**

| N | mean | min. | max. | SD | v |
|---|------|------|------|----|---|
| L | 8    | 409.63 | 375 | 431 | 20.06 | 4.90 |
| DT prox. | 10  | 134.90 | 123 | 140 | 5.34 | 3.96 |
| DAP prox. | 8 | 131.88 | 123 | 137.5 | 5.81 | 4.41 |
| DT dia. | 13 | 65.23 | 61 | 70 | 2.83 | 4.33 |
| DAP dia. | 12 | 62.88 | 56 | 69 | 3.54 | 5.62 |
| DT distal | 10 | 109.60 | 102 | 118 | 5.44 | 4.96 |
| DT dist. art. | 9 | 79.06 | 75 | 83.5 | 3.02 | 3.81 |
| DAP dist.art. | 7 | 64 | 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 | Astragalus | MIL 367 | MIL 181 | MIL 852 | Dicerorhinus miguelcrusafonti |
|-------|------------|---------|---------|---------|-----------------------------|
|       | S          | D       | S       |         | N mean min. max.             |
| DT max. | 98.5       | 92      | 99      |         | 3 85.67 85                   |
| H       | 87         |         | 92*     |         | 3 89.67 89                   |
| 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

|                          | 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

|                          | mean min. max. SD v |
|--------------------------|---------------------|
| DT max.                  | 32 101.73 92.5 113 4.58 4.50 |
| H                        | 32 97.31 88 110 5.66 5.82 |
| DAP int.                 | 32 67.13 59 75 4.27 6.36 |
| DT dist.art.             | 31 81.74 71 91 4.58 5.61 |
| DAP dist.art.            | 25 49.56 45.5 58 3.00 6.05 |
| Dist. 2 brims            | 33 69.91 53 81 5.25 7.51 |
| DT dist.                 | 31 87.19 78 99 4.74 5.43 |

### Dicerorhinus etruscus etruscus

|                          | mean min. max. SD v |
|--------------------------|---------------------|
| DT max.                  | 48 80.95 73 88 3.45 4.26 |
| H                        | 48 77.22 71 84 3.26 4.22 |
| DAP int.                 | 47 53.39 47 58 2.53 4.74 |
| DT dist.art.             | 44 65.74 57 75 3.98 6.05 |
| DAP dist.art.            | 44 40.69 36 45.5 2.39 5.88 |
| Dist. 2 brims            | 50 55.58 49 62 3.14 5.65 |
| DT dist.                 | 44 70.05 60 78 3.71 5.29 |
### Table 9. — Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Guérin, 1972 calcaneum.

| Milia                      | Dicerorhinus miguelcrusafonti |
|----------------------------|--------------------------------|
| **Calcaneum**              | **N** | **min.** | **max.** | **SD** | **v** |
| MIL 1703                   |       |          |          |        |      |
| Height                     | 139   |          |          |        |      |
| DAP tuber                  | 76.1  |          |          |        |      |
| DAP bec                    | 76    |          |          |        |      |
| DT sust.                   | 80    |          |          |        |      |
| DT tuber                   | 56    |          |          |        |      |
| DT middle                  | 43    |          |          |        |      |

| **Dicerorhinus jeanvireti** | **N** | **mean** | **min.** | **max.** | **SD** | **v** |
|-----------------------------|-------|----------|----------|----------|--------|-------|
| Height                      | 12    | 139.08   | 128.5    | 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     | 4.22   | 5.80  |

| **Dicerorhinus megarhinus** | **N** | **mean** | **min.** | **max.** | **SD** | **v** |
|-----------------------------|-------|----------|----------|----------|--------|-------|
| Height                      | 14    | 148.54   | 133      | 163      | 8.03   | 5.40  |
| DAP tuber                   | 16    | 78.84    | 67       | 87.5     | 5.05   | 6.40  |
| DAP bec                     | 19    | 78.16    | 69       | 84       | 3.63   | 4.65  |
| DT sust.                    | 10    | 84.40    | 72       | 98       | 7.12   | 8.44  |
| DT tuber                    | 18    | 56.14    | 48       | 63       | 4.26   | 7.59  |
| DT middle                   | 16    | 43.72    | 38.5     | 51       | 4.23   | 9.68  |

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

| Milia                      | Dicerorhinus miguelcrusafonti |
|----------------------------|--------------------------------|
| **Cuboid**                 | **N** | **min.** | **max.** | **SD** | **v** |
| MIL 1665                   |       |          |          |        |      |
| Length                     | 63.3  |          |          |        |      |
| Breadth                    | 47.8  |          |          |        |      |
| Height                     | 68    |          |          |        |      |
| L art.surf.sup.            | 46.4  |          |          |        |      |
| B art.surf.sup.            | 44    |          |          |        |      |
| H ant.face                 | 44.8  |          |          |        |      |

| **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.

| Milia | Dicerorhinus megarhinus | Dicerorhinus etruscus etruscus |
|-------|-------------------------|-------------------------------|
|       | N | mean | min. | max. | SD  | N | mean | min. | max. | SD  | v   |
|       |   |     |     |     |     |   |     |     |     |     |     |     |
| Length| 12| 71.63| 63.5| 76.5| 4.19| 24| 58.77| 53.5| 67  | 3.44| 5.85|
| Breadth | 11| 53.50| 47.5| 60  | 3.88| 23| 41.22| 36  | 48  | 3.30| 8.01|
| Height | 12| 68.54| 59  | 75  | 5.63| 21| 55.90| 51  | 62  | 2.74| 4.90|
| L art.surf.sup. | 10| 49.05| 43.5| 54  | 3.62| 22| 39.86| 34  | 47  | 2.80| 7.02|
| B art.surf.sup. | 8 | 50.44| 43.5| 55.5| 3.61| 13| 40.08| 31.5| 43  | 2.82| 7.04|
| H ant.face | 10| 48.30| 45  | 52  | 2.29| 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 |
|-------|--------------------------------|
|       | N | mean | min. | max. | SD  | N | mean | min. | max. | SD  | v   |
|       |   |     |     |     |     |   |     |     |     |     |     |     |
| Mt III |       |     |     |     |     |   |     |     |     |     |     |     |
| D | 200 |     |     |     |     |   |     |     |     |     |     |     |
| S | 58  | 57.5|     |     |     |   | 40.07| 40.5| 41  |     |     |     |
| DAP prox. | 6 | 47.83| 44  | 52  | 3.25| 2 | 45.25| 45  | 45.5|     |     |     |
| DAP dia. | 11 | 49.36| 46  | 53  | 2.35| 2 | 24.75| 24.5| 25  |     |     |     |
| DAP dia. | 8  | 24.06| 21  | 25  | 1.43| 3 | 58.17| 56  | 60  | 2.02|     |     |
| DAP dist. | 6 | 61.83| 58  | 65.5| 2.70| 3 | 46.50| 45  | 47.5| 1.32|     |     |
| DAP dist. | 9  | 50.17| 45  | 54  | 2.54| 3 | 38.83| 38  | 40  | 1.04|     |     |

| Milia | Dicerorhinus jeanvireti |
|-------|-------------------------|
|       | N | mean | min. | max. | SD  | N | mean | min. | max. | SD  | v   |
|       |   |     |     |     |     |   |     |     |     |     |     |     |
| L | 7  | 205.29| 200 | 212 | 4.39| 24| 175.92| 165 | 187 | 6.02| 3.42|
| DT prox. | 10 | 57.00| 53  | 60.5| 2.64| 24| 48.54| 43  | 56  | 3.56| 7.34|
| DAP prox. | 6  | 47.83| 44  | 52  | 3.25| 24| 41.86| 38  | 47  | 2.79| 6.67|
| DAP dia. | 11 | 49.36| 46  | 53  | 2.35| 19| 50.13| 48  | 59  | 2.72| 5.21|
| DAP dia. | 8  | 24.06| 21  | 25  | 1.43| 18| 42.28| 39  | 46  | 2.13| 5.04|
| DAP dist. | 6 | 61.83| 58  | 65.5| 2.70| 14| 36.86| 32  | 40  | 2.13| 5.77|
| DAP dist. | 9  | 50.17| 45  | 54  | 2.54| 14| 36.86| 32  | 40  | 2.13| 5.77|
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**Table 12.** Comparative dimensions of the Milia *Dicerorhinus jeanvireti* Mt IV.

| Milia       | Dicerorhinus miguelcrusafonti |
|-------------|-------------------------------|
| Mt IV       |                               |
| MIL 204     |                               |

| Measurement | Milia MIL 204 | Dicerorhinus miguelcrusafonti |
|-------------|---------------|-------------------------------|
| L           | 178.5         | 156.50                        |
| DT prox.    | 56            | 37.75 37 38.5                 |
| DAP prox.   | 51.5          | 35.00                         |
| DT dia.     | 36.5          | 29.00                         |
| DAP dia.    | 35.5          | 29.50                         |
| DT distal   | 43            | 35.00                         |
| DT dist. art| 43            | 33.50                         |
| DAP dist.art| 45            | 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 | 42 | 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      |
| 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 | 8.64 | 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 | 9.99 |
| 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 | 13.0 | 16.0 | 1.07 | 7.32 |
| M 1/ B post. | 15.5 | 14 | 15.11 | 14.0 | 16.0 | 0.90 | 5.97 |
| M 2/ L | 21.5 | 14 | 20.11 | 18.0 | 21.5 | 0.88 | 4.38 |
| M 2/ B ant. | 17.5 | 14 | 17.82 | 16.0 | 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 | 31.0 | 1.66 | 6.11 |
| M 3/ B ant. | 17.5 | 28 | 18.09 | 16.0 | 20.5 | 1.42 | 7.86 |
| M 3/ B post. | 15 | 27 | 16.07 | 14.5 | 18.0 | 1.04 | 6.50 |
| M 3/ B mid. | 10.5 | 17 | 10.24 | 8.0  | 14.0 | 1.95 | 19.01 |
| L M/ | 64.5 | 5  | 61.40 | 59.0 | 64.5 | 2.27 | 3.70 |
|     | MIL 696 |     |     |     |     |     |     |
|     | M/2 L | 20 | 10 | 19.95 | 18.0 | 22.5 | 1.48 | 7.42 |
|     | M/2 B ant. | 14.5 | 9 | 14.33 | 13.0 | 15.0 | 0.83 | 5.78 |
|     | M/2 B post. | 14.5 | 9 | 15.11 | 14.0 | 17.0 | 0.93 | 6.14 |

**Potamochoerus provincialis**

| Sus strozzii |
|--------------|
|     | Teeth | MIL 205 |
|     | N   | mean | min. | max. | SD  | v  |
| P 4/ L | 3  | 15.33 | 14.5 | 16.0 | 0.76 | 4.98 |
| P 4/ B | 3  | 17.50 | 17.0 | 18.0 | 0.50 | 2.86 |
| M 1/ L | 2  | 19.00 | 19.0 | 19.0 | 0.00 | 0.00 |
| M 1/ B ant. | 2 | 17.00 | 17.0 | 17.0 | 0.00 | 0.00 |
| M 1/ B post. | 2 | 17.25 | 17.5 | 17.5 | 0.35 | 2.05 |
| M 2/ L | 7  | 24.71 | 22.0 | 26.5 | 1.52 | 6.16 |
| M 2/ B ant. | 7 | 22.21 | 20.5 | 25.0 | 2.04 | 9.18 |
| M 2/ B post. | 7 | 21.50 | 19.0 | 23.5 | 1.80 | 8.39 |
| M 3/ L | 12 | 37.25 | 29.0 | 45.0 | 3.93 | 10.56 |
| M 3/ B ant. | 13 | 25.15 | 22.5 | 27.5 | 1.51 | 5.98 |
| M 3/ B mid. | 13 | 21.88 | 19.0 | 23.0 | 1.10 | 5.04 |
| M 3/ B post. | 12 | 12.96 | 9.5  | 19.5 | 2.48 | 19.15 |
| L M/  | 1  | 79.50 |     |     |     |     |
| M/2 L  | 17 | 25.09 | 22.0 | 27.0 | 1.24 | 4.94 |
| M/2 B ant. | 17 | 17.94 | 15.0 | 20.0 | 0.97 | 5.39 |
| M/2 B post. | 17 | 17.59 | 16.5 | 19.0 | 0.75 | 4.29 |