Palaeozoology
Research Article

ACTA ZOOLOGICA BULGARICA
Acta zool. bulg., 68 (2), 2016: 243-264

The Rhinocerotidae and Suidae of the Middle Pleistocene from Petralona Cave (Macedonia, Greece)

Evangelia Tsoukala[1*], Claude Guérin[2]

[1]School of Geology, Aristotle University (AUTH), 54124 Thessaloniki, Greece; E-mail: lilits@geo.auth.gr
[2] UMR CNRS 5276 UCB Lyon 1-ENS (France), Département des Sciences de la Terre, Université Claude Bernard – Lyon I, 27-43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France; E-mail: claude.guerin@univ-lyon1.fr

Abstract: The Petralona Cave, well known also for its praeneanderthalian skull, has yielded 30 remains of the Rhinocerotidae, i.e. *Dicerorhinus hemitoechus* (Falconer, 1868), and 25 remains of the Suidae, i.e. *Sus scrofa priscus* Goldfuss, 1823. All these fossils of the "Old Collection" housed in the Paleontological Museum of Thessaloniki Aristotle University since 1960, correspond to a minimum of two adults or subadults, four juvenile rhinos, and a minimum of four adult boars. The dimensions and proportions of the teeth and bones of rhinoceros were compared with those of *Dicerorhinus hemitoechus*, *Dicerorhinus mercki* and *Coelodonta antiquitatis* from Europe. They confirmed that the three species were easily distinguishable and justified our determination. The remains of *Sus scrofa priscus* were compared with three European samples, one of extant *S. scrofa*, one of the upper Middle and recent Pleistocene *S. scrofa*, and one of the early Middle Pleistocene *S. s. priscus*. They corresponded to the latter subspecies. The degree of evolution of the rhino dated the site from the early Middle Pleistocene (MNQ zones 20-23), an age confirmed by recent dating and by the presence of *Sus scrofa priscus*. The presence of *D. hemitoechus* indicated forested prairie, more or less wooded. The finding of the boar strengthens confirmation of the woody dominance.

Key words: anatomy, biometry, evolution, palaeoenvironment

Introduction

The Petralona Cave was discovered in 1959, together with the first fossils in it. One year later, the well-known hominid skull was discovered by villagers. Since then, scientists from the Thessaloniki University have visited the cave and collected thousands of fossils, thus creating the "Old Collection", which is housed in the Paleontological Museum of the Geology School, Aristotle University (LGPUT). The present communication deals with the re-examination of the "Old Collection" of rhinoceros and boar. This collection has been provisionally identified by Tsoukala (1989, 1991) and re-numbered with the code PEC (Petralona Cave). On the other hand, data on a "New Collection" of rhino material from Petralona Cave have been published by Fortelius, Poulianos (1979, 1980) and Poulianos (1981), identifying *Dicerorhinus* cf. *hemitoechus*. Although we had no access to this material, the published information allowed comparisons with the fossils presented herein.

The Pleistocene mammalian fauna of Petralona Cave, associated to the pre-neanderthal hominid skull (Stringer *et al.* 1979), has been repeatedly studied since 1960 (Kanellis 1962; Sickenberg 1964, 1971; Tsoukala 1989, 1991; Koufos, Tsoukala, 2007). The palaeofauna consists of 11 species of carnivores: *Canis arnensis*, *Lycaon lycaonoides*, *Vulpes praeglacialis*, *Ursus deningeri*, *U. spelaeus*, *U. arctos*, *Pliohyaena perrieri*, *Pachycrocuta brevirostris*, *Crocuta crocuta*, *Panthera leo fossilis* and *Felis silvestris* (Baryshnikov, Tsoukala 2010); nine species of herbivores: *Equus petraloniensis* Tsoukala, 1989; *Equus* sp. (cabaline form); *Bos primigenius*

*Corresponding author: lilits@geo.auth.gr

Bojanus,1827; *Bison priscus* Bojanus,1827; *Capra ibex macedonica* Sickenberg,1971; *Pliotragus macedonica* Cregut & Tsoukala 2005; *Praemegaceros* sp.; *Cervus elaphus* Linnaeus 1758; *Dama dama* (Linnaeus 1758). These faunal remains, collected from the floor of the cave, belong to two main biostratigraphic assemblages mixed together due to the action of flowing water. The former assemblage belongs to the early Middle Pleistocene, including species with Villafranchian affinities (Crégut-Bonnoure, Tsoukala 2005), and the later belongs to the late Middle-Late Pleistocene. Based on carnivores, the collection is regarded to contain three biostratigraphic species-groups: early Middle Pleistocene, late Middle Pleistocene and Late Pleistocene group (Baryshnikov, Tsoukala 2010).

Preliminary results on the rhino and boar material from the "Old Collection" (studied here) were presented by Kanellis (1962) and Sickenberg (1964, 1971), whereas the first detailed study was presented in the doctoral thesis of Tsoukala (1989, 1991).

The aim of the present article is to provide detailed descriptions of the Rhinocerotidae and Suidae of the Middle Pleistocene from Petralona Cave, Greece.

Materials and Methods

Details of the samples studied are presented in the text about each species.

The following abbreviations are used: abs.: absolute; anat.: anatomical; ant. anterior; art.: articulation; B: breadth, width; D: dextra (right); D/: deciduous premolar; DAP: antero-posterior diameter; DDV: dorso-ventral diameter; dia.: diaphysis; dist.: distal; Right: right; DT: transversal diameter; L: length; H: height; H ant.: anterior height; i: inferior; L: length; max.: maximum; min: minimum; med.: medium; mid.: middle; M: molar; M1/: Upper, M/1: lower, Mc: metacarpal; Mt: metatarsal; n: number of specimens; P: premolar; post.: posterior; prox.: proximal; SD: standard deviation; S: sinistra (left); s: superior; sust.: sustentaculum tali; v: variation. The designation of teeth is fractional, the rank of the upper teeth is in the numerator and of the lower teeth in the denominator. All dimensions are in mm.

Results and Discussion

Three principal species of European rhinoceros are known from the second half of Middle Pleistocene until the end of Late Pleistocene (Guérin 1980): Merck's rhinoceros *Dicerorhinus mercki* (Kaup, 1841), the steppe rhinoceros *Dicerorhinus hemitoechus* (Falconer, 1868) and the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799). During the first half of the Middle Pleistocene *Dicerorhinus etruscus brachycephalus* (Schroeder, 1903) was the dominant rhinoceros in Europe, sometimes associated with Merck's rhinoceros (Guérin 1980, 2010). The steppe rhinoceros succeeded the former and all remains of the Petralona rhino correspond to *Dicerorhinus hemitoechus*.

Taxonomy

Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Family Rhinocerotidae Owen, 1845
Genus *Dicerorhinus* Gloger, 1841
***Dicerorhinus hemitoechus* (Falconer, 1868)**

Material: The "Old Collection" from Petralona Cave housed in Aristotle University with code LGPUT-PEC, comprises: Four D1/ PEC 951 left, 952 left, 953 right, 954 right; one D2/ PEC 955 right; two D3/ PEC 956 right and 957 left; one D3/ or D4/ PEC 958 right, not measurable; one D4/ PEC 959 right; one P2/ PEC 960 right; one P3/ PEC 961 right; one P4/ PEC 962 right; one M1/ PEC 963 left; three M2/ PEC 964 left, 965 right, 966 right; three fragments of upper cheek teeth PEC 967, 968, 969, completely worn, not measurable; one fragment of semimandible PEC 950, with D/2,D/3 and D/4 right; one D/1 PEC 980 left; an atlas PEC 970; one femur PEC 975 left, distal part; two ulnae PEC 973 and 974 left, and a radius PEC 972 right, all representing the two thirds of the proximal part; one tibia PEC 976 left, distal epiphysis of a juvenile, unworkable; one calcaneum PEC 978 right; an astragalus PEC 977 right; a metapodial Mt3 PEC 979 left, distal half.

The above-described samples represented 30 determinable remains, mostly isolated teeth, whereas postcranial material was very limited. All material belonged to *Dicerorhinus hemitoechus*. The only evidence to the presence of adult individuals and / or elderly were: a worn M2/, the calcaneus and the astragalus, both with the same symmetry but not articulating together. In the Petralona material there were at least two adults or sub-adults rhinoceros, and at least four juveniles at various stages of growth.

The anatomical part that was best represented was the first upper deciduous premolar; there were four specimens: two right and two left. The degree of wear was very variable; therefore they did not belong to the same individual. There were three M2/, two of them unworn; therefore belonging to juvenile individuals; the same applied for all upper premolars and M1/.

Systematics and Definitions: The classification of the genus *Dicerorhinus* Gloger, 1841 within the family Rhinocerotidae Gray, 1821, is much discussed and varies according to the various authors:

- Heissig (1973, 1989) assigned them to the subfamily Rhinocerotinae Dollo, 1885 and tribe Rhinocerotini Dollo, 1885;

- Groves (1983) assigned them to the subfamily Rhinocerotinae Dollo, 1885, tribe Rhinocerotini Dollo, 1885, subtribe Rhinocerotina Dollo, 1885;

- Prothero and Schoch (1989) assigned them to the subfamily Rhinocerotinae Owen, 1845, tribe Rhinocerotini Owen, 1845, subtribe Dicerorhinina Ringström, 1924;

- Cerdeño (1995) assigned them to the subfamily Rhinocerotinae Owen, 1845, tribe Rhinocerotini Owen, 1845, subtribe Elasmotheriina Bonaparte, 1845;

- McKenna and Bell (1997) assigned them to the subfamily Rhinocerotinae Gray, 1821, tribe Rhinocerotini Gray, 1821, subtribe Rhinocerotina Gray, 1821, infratribe Rhinoceroti Gray, 1821.

We consider (see also Guérin 1980; 1989; 2010) that *Dicerorhinus* belongs to the subfamily Dicerorhininae Simpson, 1945 (the latter taxon was often attributed by Ringström 1924), and we do not feel the need to use for this kind of taxa intermediate rank between subfamily and the genus.

Genus *Dicerorhinus* Gloger, 1841

Simplified synonymy: *Didermocerus* Brookes, 1828 (invalidated in 1977, Opinion 1080, International Commission of Zoological Nomenclature, published in a catalogue); *Ceratorhinus* Gray, 1868, junior synonym; *Stephanorhinus* Kretzoï, 1942, junior synonym; *Procerorhinus* Kretzoï, 1942, junior synonym.

Type Species: *Dicerorhinus sumatrensis* (Fischer von Waldheim, 1814)

Dicerorhinus hemitoechus (Falconer, 1868)

Simplified synonymy

Pro parte:

- *Rhinoceros leptorhinus* Owen, 1846 and not Cuvier, 1822: *R. leptorhinus sensu* Owen, originally referred to both *Dicerorhinus hemitoechus* and *D. mercki*, two Pleistocene species, frequently confused for many years, each of which renders detailed synonymy very complex. *Rhinoceros leptorhinus* sensu Cuvier in fact corresponds to the Pliocene species (Ruscinian) that is currently called *Dicerorhinus megarhinus* de Christol, 1834. Boyd Dawkins (1865, 1867) was one of the first to realise that in Europe, in the Late and Middle Pleistocene, except the "woolly" rhino *Coelodonta antiquitatis*, two other distinct species were found: *Dicerorhinus hemitoechus* and *Dicerorhinus mercki*, and he respectively designated these *Rhinoceros leptorhinus* and *Rhinoceros megarhinus*, when certainly the last pair corresponded to a Pliocene form, also distinct. About this series of confusions, see Guérin *et al.* (1969: 60-67).

- *Rhinoceros subinermis* Pomel, 1895: this is in fact the North African subspecies of *D. hemitoechus*.

- *Rhinoceros binagadensis* Dzhafarov, 1955.

Synonymy of the Petralona "Old Collection" rhino material: *Rhinoceros mercki* Jaeger (see Kanellis 1962); *Didermoceros kirchbergensis* (Jaeger) (see Sickenberg 1964); *Didermoceros* sp. (see Sickenberg 1971); *Dicerorhinus hemitoechus* (see Tsoukala 1989, 1991).

Holotype: The roof and the occipital part of skull n° 27838, figured by Falconer in 1868, pl. 15, Figs. 1-3, kept at the Natural History Museum in London. *Locus typicus and stratum typicum:* Clacton on Sea (Essex, Great Britain), zone MNQ 23.

Diagnosis: The steppe rhinoceros *Dicerorhinus hemitoechus* was a bicorn species, medium to large in size with sub-hypsodont cheek teeth, very likely following *Dicerorhinus etruscus*. Its size was about the size of *Diceros bicornis*, the extant African black rhinoceros. The skull was carried in mid-low or low position. The massive face was long, the nasal septum was ossified in its anterior part; seen in profile, the insertion of the posterior horn (frontal) was very little or not marked. The pseudo-auditory meatus was closed. The mandible with long symphysis; relatively low and narrow horizontal branch with slightly convex ventral margin. M1/ and M2/ showed ectoloph profile strongly undulated, the paracone fold constituting the strongest undulation; crochet always present, crista frequent. P3/ and P4/ showed undulated ectoloph profile through folds of the paracone and metacone, and through mesostyle; crochet normally present; crista frequent; the middle fossette rarely closed; the protocone sometimes with constriction; labial cingulum quite common. The first segment of the limb was short. The preferred habitat was open grassland with clumps of trees. Diet based on grasses, leaves, twigs and young bark, was more eclectic than that of Merck's rhino.

Temporal extension: *D. hemitoechus* appeared during the MNQ 23 zone of the Middle Pleistocene (Holstein or Hoxnian) and disappeared at the end of the MNQ 26 zone (Late Pleistocene), about 12.000 to 10.000 years ago. Thus, the species existed a little less than 500.000 years.

Geographical distribution: *D. hemitoechus* was found throughout Europe (except for Ireland, Scotland and Scandinavia); Western Asia and North Africa. In the Middle East, we could verify its presence in Lebanon at Naamé, in Jordan at Azraq, in Israel and Palestine at Biq'at Quneitra, Geula, Kebara, Skhul, Tabun; it extended to Maghreb – North Africa during the Late Pleistocene, probably passing through the Strait of Gibraltar. In Greece, *D. hemitoechus* was best documented from Petralona Cave with many specimens; whereas few specimens were recorded from Megalopolis (Peloponnese), an upper third molar and two lower teeth were described by Melentis (1964,1965a); and a single specimen was found from Peneios, Larissa in Thessaly by Boessneck (1965), but its presence there is questionable (Symeonidis *et al.* 2006). The steppe rhinoceros was sometimes associated with Merck's rhinoceros (in France for example, in the Arago Cave, Pyrénées-Orientales, and at Biache-Saint-Vaast, Pas-de-Calais), more rarely with the woolly rhinoceros (e.g. in three sites in Montmaurin, Haute-Garonne, in France: the Boule, the Terrasse and the Coupe-Gorge Caves), and it seems that the three species were sympatric (La Fage, Corrèze, France). Paleolithic man has portrayed it, in the famous wall painting of the "scene of the well" in the Lascaux Cave.

Anatomy

The reference material used for the comparative diagrams was the average of 30 to 40 adult individuals of the extant *Diceros bicornis*, the African black rhinoceros (values from Guérin (1980), with additional data from newly-examined specimens, see Guérin 2010).

Upper teeth: The upper cheek teeth of the Rhinocerotidae are typically lophodonts with three blades; a transverse anterior protoloph joining protocone and paracone; a longitudinal lateral ectoloph joining paracone and metacone; and a transverse posterior metaloph joining metacone and hypocone. Interior of the three blades, internal folds can be: the end of the crista of the ectoloph, the end of the crochet of the metaloph and the end of the anticrochet of the protoloph. These folds, by fusing their extremities, may form a more or less completely closed medial fossette.

The upper cheek teeth of the Petralona material includes a total of four D1/, one D2/, two D3/, one D3,4/, one D4/, one P2/, one P3/, one P4/, one M1/, three M2/ and three indeterminable fragments. All with a rounded occlusal pattern, somewhat chagrined enamel or not, a thick cement (but it might be not very well preserved), a clear hypsodonty, and a certain lengthening of the internal folds increasing the wear surfaces. All these characters are present in *Dicerorhinus hemitoechus.*

The comparative dimensions of the upper cheek teeth from Petralona Cave are given in Table 1; all perfectly fit and within the limits of variation of *Dicerorhinus hemitoechus*. To quantify the hypsodonty for each unworn or slightly worn tooth, we calculated the hypsodonty index: 100 x H/L; the height (H), in most cases, is somewhat undervalued, especially for dental buds it is very difficult to know if they were completely developed to their base. For each category of the teeth, the really significant were the highest values. Both *Dicerorhinus* species could be distinguished from each other and from *Coelodonta antiquitatis* by the dimensions, proportions and the morphological characters of their teeth with the ectoloph profile being the most discriminating character. In *D. hemitoechus* the ectoloph of the molars was undulated (more for P3/ and P4/ in which the ripples were formed by the fold of paracone, the mesostyle and the fold of metacone). In *D. mercki*, molars were very large, their enamel was thick and smooth, the profile of their ectoloph was almost flat with a series of small vertical ripples, very soft; the premolars were also very large, P3/ and P4/ hade a flat or slightly convex profile of the ectoloph lacking sharp creases. In *Coelodonta antiquitatis* the upper cheek teeth had a more angular shape occlusal, the enamel was very chagrined and the profile of the ectoloph was different, intensely undulating with a projecting parastyle, with a small fold of paracone but clearly framed by two vertical depressions, a broad and projecting mesostyle, and a more or less divergent metastyle (Guérin 1980).

Upper deciduous teeth: Built as the permanent cheek teeth, which they differred from mainly in their brachyodonty and especially in their thin enamel.

D1/ were not rare in this species since we observed a total of 14 specimens, and four were collected at Petralona. The specimen PEC 952 was middle worn. On the intensely convex ectoloph, the fold of paracone was well marked. The crochet was strong, the crista and the anticrochet were weak. There was a continuous lingual cingulum. The protoloph was notched at its contact with the ectoloph (Fig. 1 A). D1/ PEC 951: little abraded, distinguished by the absence of the anticrochet and the closed median valley at its opening (Fig. 1 B). D1/ PEC 953: unworn, the maximum height of the ectoloph was 16.8 mm, its hypsodonty index reached 60. The only internal fold was the crochet. The lingual cingulum was discontinuous (Fig. 1 C). D1/ PEC 954: part of a juvenile tooth row (Fig. 1 N), characterised by its thin but continuous protoloph, without notch. The parastyle was very detached. Crista and crochet were present but very small. The posterior cingulum was very intense and lingually very high.

D2/: There was a single specimen, PEC 955 that was part of the juvenile tooth row of Fig. 1 N. It was middle to heavy worn. The ectoloph had undulate profile, with a strong fold of paracone. The crochet was multiple, the crista and the anticrochet were present but small. There was no constriction of protocone. The lingual cingulum was continuous.

D3/: There were two specimens, from which

PEC 956 was part of the tooth row in Fig. 1 N. The wear stage was middle. The ectoloph was strongly undulated with strong fold of paracone. The crocet was multiple, the crista rather low. The constriction of protocone was very strong, the lingual cingulum was discontinuous. PEC 957 showed no signs of wear. On the ectoloph, the fold of paracone was strong. Crista and crochet were present and distally confluent forming a closed medial fossette. The protocone was constricted. There was no lingual cingulum (Fig. 1 D). The maximum height of ectoloph was 36.5 mm, which gave an index of hypsodonty 79.3. The hypsodonty of D3/ in *D. hemitoechus* varied from 71.1 to 83, the average for seven specimens = 79.2. In two individuals of *D. mercki* this index was 72.3 and 79.3 (mean value= 75.8). In *C. antiquitatis* it varied from 68.1 to 75.3, the average for seven specimens = 71.4

D4/: There was a single specimen, PEC 959, with no trace of wear (Fig. 1 F). D4/ had the same morphological features as D3/, including an identical profile of ectoloph (Fig. 1 E). The crochet was the only internal fold. The constriction of protocone was very strong. There was a lingual discontinuous cingulum. Its height was 43 mm, giving an index of hypsodonty 84.3. The hypsodonty of D4/ in *D. hemitoechus* ranged from 74.4 to 89.6, average for 16 specimens = 81.9. For two specimens of *D. mercki* it reached 78.3 and 85.7, mean = 82. In *C. antiquitatis* it varied from 69.1 to 95.8, average for ten specimens = 82.9.

Upper premolars: The upper premolars have the same shape as molars and they are distinguished mainly by their smaller size, their stronger hypsodonty, and an opening of the lingual valley more distant from cervix.

P1/ are rare for this species: we know of only two examples: one from the Castillo cave in Spain and the other from the Gîte des Moulins in Monaco (Guérin 1980). It has not been found in Petralona. P2/: There was a single specimen, PEC 960, unworn. The profile of ectoloph was generally convex, with clear fold of paracone. The protoloph was notched in contact with ectoloph. The crochet was the only internal fold, but it is multiple. The protocone was not constricted. There was discontinuous lingual cingulum (Fig. 1 G).

The height of 40.5 mm provided an index of hypsodonty of 126.6. The hypsodonty for *D. hemitoechus* ranged from 111.6 to 133.8, average for eight specimens = 122.1. In *D. mercki*, the index was 131.6 to 149.4, average for three specimens = 142.4. In *C. antiquitatis* it varied from 117.5 to 151.7, average for 20 specimens = 133.9.

P3/: A single specimen was available, PEC 961 (Fig. 1 H). The profile of ectoloph was undulated with intense fold of paracone, weak mesostyle and small fold of metacone. With multiple crochet, but neither crista nor anticrochet. The protocone showed no sign of constriction. With continuous lingual cingulum. The height of 59.7 mm provided an index of hypsodonty of 142.1. The hypsodonty for *D. hemitoechus* was from 104.2 to 148.1, average for 16 specimens = 121.8. For *D. mercki* it varied from 127.3 to 146.9, average for four specimens = 140. In *C. antiquitatis* it varied from 128.2 to 167.1, average for 37 specimens = 147.5.

P4/: A single P4/ PEC 962 (Fig. 1 I), unworn, probably from the same individual as P3/ PEC 961. The profile of ectoloph was undulated, very similar to P3/. The crochet was the only internal fold. There was no constriction of protocone. The lingual cingulum was continuous. The dimensions of the P4/ corresponded to the average values of the species (Table 1). The height of 61.5 mm corresponded to an index of hypsodonty of 133.7. The hypsodonty for *D. hemitoechus* ranged from 113.6 to 153.5, average for 12 specimens = 134.1. In *D. mercki* it was between 114.8 and 132.8, average for four specimens = 126.9. In *C. antiquitatis* it varied from 106.8 to 169.8, average for 32 specimens = 144.6.

Upper molars: No M3/ were found in the Petralona "Old Collection".

M1/: A single specimen PEC 963, slightly worn (Fig. 1 K). The profile of ectoloph undulated, like in P3/ and P4/, with thicker and stronger mesostyle. The crochet was the only internal fold. The protocone was constricted. There was no lingual cingulum.

The height was 66.5 mm, and the hypsodonty index reached 118.8. The hypsodonty for *Dicerorhinus hemitoechus* ranged from 100 to 124.5, average for ten specimens = 111.6. In *D. mercki* the variation was of 100.8 to 113.9, 3, average for three specimens = 109.2. In *Coelodonta antiquitatis* it ranged from 94.6 to 125, average for twelve specimens = 115.2.

M2/: There were three specimens: a well abraded PEC 966 (Fig. 1 J) and two unworn PEC 964, 965 (Fig. 1 L and M respectively). M2/ was built like M1/ and had the same anatomical features: the fold of paracone was small but clear (on PEC 966, it was much stronger in 4 cm above cervix than in 2 cm), the crochet was strong, with crista, which tended to converge with the crochet occlusally resulting in almost closed (PEC 964 and 965) or completely closed (PEC 966) medial fossette; constriction of protocone variable, stronger in PEC 966. There was no lingual cingulum on PEC 966, unlike the other two M2/. The height was 72 mm for PEC 964 and 74.5 mm for PEC 965, corresponding to the hypsodonty indices 117 and 121.1, respectively. The hypsodonty in *D. hemitoechus* ranged from 103.9 to 121.8, average for eight specimens = 111.7. For *D.*

mercki variation was 92.6 to 115, average for seven specimens = 108.1. In *C. antiquitatis* it ranged from 96 to 130.6, average for 20 specimens = 118.5.

Lower teeth: As in all Rhinocerotidae, they consisted of an anterior lobe crescent (paralophid and protolophid) and a posterior lobe half-crescent (metalophid and hypolophid); in D/1 the anterior lobe was atrophied. All had smooth or slightly wrinkled enamel, cementum (that may have not been preserved), a significant hypsodonty, and a rounded occlusal contour. Molars without side cingula, bearing V-shaped valleys with enough high difference of the level between the two valleys; the anterior still being higher from cervix than the posterior one. Premolars had acute V-shaped valleys with large difference in level, and without side cingulum. Their comparative dimensions are given in Table 2.

The lower cheek teeth of the two *Dicerorhinus* differred from those of *Coelodonta* by their more rounded wear boards, their smooth or slightly wrinkled enamel and their not rare lateral cingula, whereas characteristic of *D. mercki* were the high volume of the molars that hade generally lingual U-shaped valleys and the large width of the premolars.

Lower deciduous teeth: They have the same characteristics as the lower permanent cheek teeth unless they are less hypsodont, their enamel is thinner and the two lingual valleys are sometimes U-shaped, generally with low difference of levels. In Petralona material, they comprised only an isolated D/1 and a mandible fragment of juvenile with the tooth row D/2-D/3-D/4. Their dimensions are given in Table 2.

D/1: It is a tooth, rarely found in *D. hemitoechus*, but there was a slightly worn specimen from the Petralona Cave material (Fig. 1 O). The anterior valley was barely outlined.

D/2: The tooth of the mandible PEC 950 was middle worn, characterised by its closed posterior valley (Fig. 1 P).

D/3: It was middle worn. Both lingual valleys were about at the same level. There was no lingual cingulum (Fig. 1 P).

D/4: The wear stage was medium to little worn. The two lingual valleys, whose transverse profile was broad V, showed clear difference in level relatively to cervix (Fig. 1 P). Without lingual cingulum.

Postcranial skeleton

Atlas: The first cervical was almost complete. Foramen magnum was large and alae well developed. The ventral arch bore a strong ventral tubercle and a well-developed dent (Fig. 2). The transverse diameter of the cranial articular facet was 130.6 mm, from the caudal was 140 mm, from the foramen magnum was 58 mm (posteriorly) and the maximum height of vertebra was 102 mm.

Femur: The distal femur was well preserved. The medial brim of the broad assymetrical trochlea was much stronger than the lateral one forming an angle of about 102°. In the middle of its distal part with distinct foramen. There was a strong latero-distal depression between the lateral brim of trochlea and the sulcus popliteus (Fig. 3). The epicondylii were intense, the medial being much stonger than the lateral. Both diameters of the distal epiphysis, transverse (137.8 mm) and anteroposterior (151.3 mm), close to the average for a sample of 11 to 18 specimens of *D. hemitoechus*, fitting perfectly in the range of variation for this species. These values were significantly lower than the averages calculated for a sample of 6-8 specimens of *D. mercki*, and 20 to 39 specimens of *C. antiquitatis* from Europe (Guérin 1980).

Ulna: The two left ulnas with preserved proximal two thirds, whereas from both, most of the olecranon tip was missing. In the middle of the assymetrical large articulation there was a deep and broad depression (Fig. 4**)**. The section of diaphysis is triangular. The transverse diameters of the proximal articular facet 82 mm for PEC 974 and 88 mm for PEC 973 which was close to the average for a sample of 10 specimens of *D. hemitoechus*, fitting perfectly in the range of variation for this species. These values were also significantly lower than the averages of the two specimens of *D. mercki*, and 30 specimens of *C. antiquitatis* from Europe (Guérin 1980).

Radius: The proximal two-thirds of a right radius were found among the remains of the Petralona rhinoceros. Guérin (1980) established as typical main characters of the proximal epiphysis of the radius for *D. hemitoechus* that the lateral articular surface for humerus was slightly extended transversely; its anterior border was set back from the anterior edge of the medial articular surface, and its posterior edge was straight and oblique; the posterior border of the entire articulation formed a widely obtuse angle; the anterior border of the humeral articulation was intensely undulating, with a strong re-entrant corresponding to the coronoid process (Fig. 5 A). In front view the proximal epiphysis bore a well-developed lateral tuberosity. On the medial side a small tuberosity also existed. The epiphysis in Petralona specimen had all these characteristics (Fig. 5 B). Both diameters of this epiphysis, transverse and anteroposterior, were slightly above the average for a sample of 21 to 22 specimens of *D. hemitoechus*, but were placed perfectly in the range of variation in this species. The transverse diameter was equal to the minimum value of a sample of 20

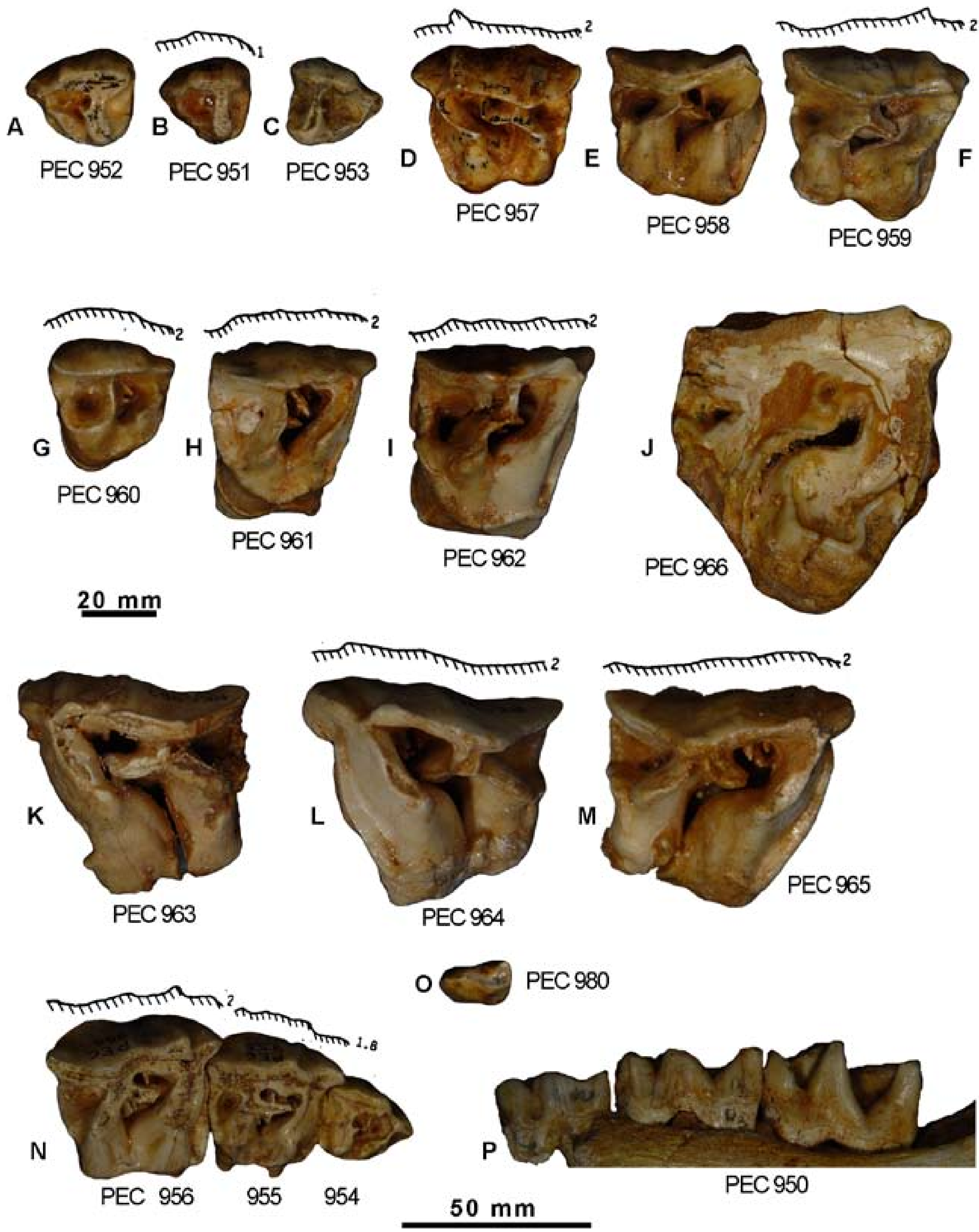

Fig. 1. Petralona *Dicerorhinus hemitoechus*, cheek teeth, occlusal view (A-O), with ectoloph profiles at the height (in cm) from the collar of the tooth noted on the right.
A: D1/ PEC 952 (left); B: D1/ PEC 951 (left); C: D1/ PEC 953 (right); D: D3/ PEC 957 (left); E: D3/ PEC 958 (right); F: D4/ PEC 959 (right); G: P2/ PEC 960 (right); H: P3/ PEC 961 (right); I: P/4 PEC 962 (right); J: M2/ PEC 966 (right); K: M1/ PEC 963 (left); L: M2/ PEC 964 (left); M: M2/ PEC 965 (right); N: Upper deciduous cheek tooth row with D2/ PEC 954, D3/ PEC 955 and D4/ PEC 956 (right). O: D/1 PEC 980 (left). Scale bar: 20 mm.
P: Mandible fragment with D/2-D/4 PEC 950 (right), lingual view. Scale bar: 50 mm

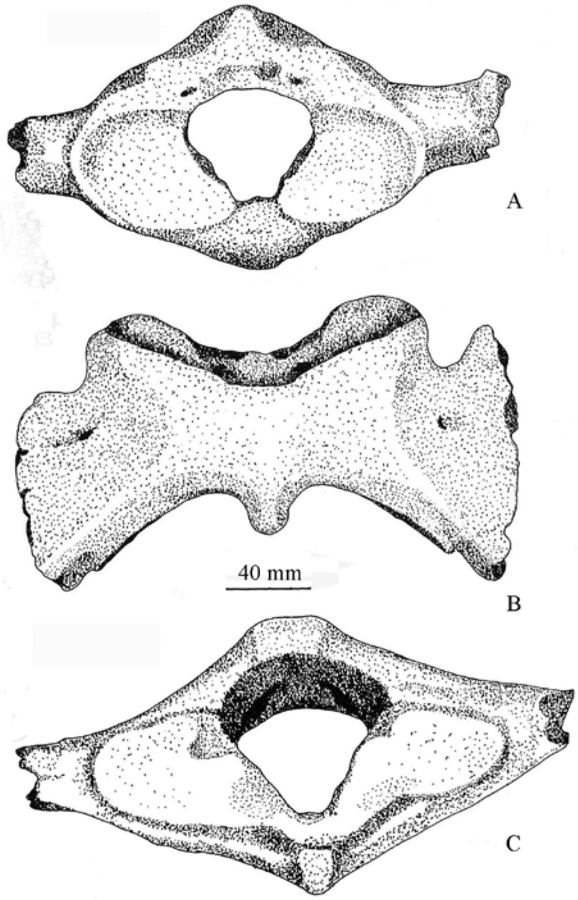

Fig. 2. Petralona *Dicerorhinus hemitoechus*. Atlas PEC 970. A. Cranial, B. Ventral, C. Caudal view. Scale bar: 40 mm

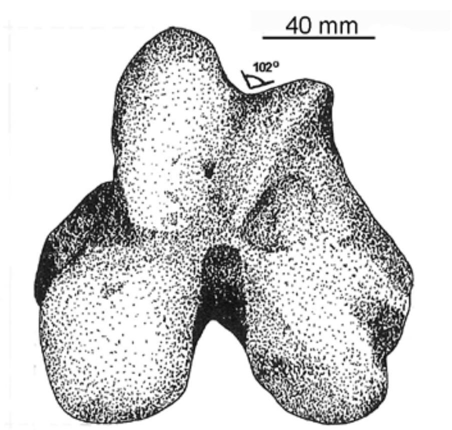

Fig. 3. Petralona *Dicerorhinus hemitoechus*. Distal femur PEC 975 (left). Distal view. Scale bar: 40 mm

specimens of *D. mercki*, whereas the anteroposterior diameter was less than the minimum value observed in 17 specimens of the same species. Finally, these values were significantly lower than the averages calculated on a sample of 109 to 111 specimens of *C. antiquitatis* from Europe, although the two dimensions of the Petralona radius were higher than the minimum values found in the woolly rhi-

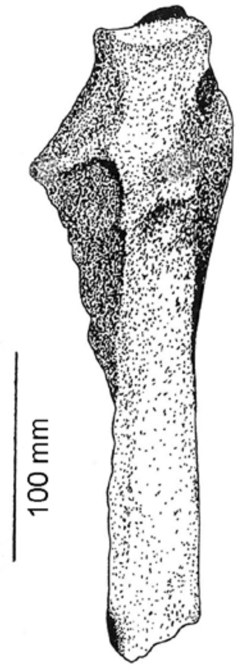

Fig. 4. Petralona *Dicerorhinus hemitoechus*. Ulna PEC 973 (left). Anterior view. Scale bar: 100 mm.

noceros (Table 3). Fig. 6 reveals the situation of the Petralona radius inside the cloud of points corresponding to *D. hemitoechus*, and shows that it was among the strongest specimens of the species; the cloud is also highly individualised and distinct from the other two species. The diagram did not distinguish *D. mercki* from *C. antiquitatis* because it did not take into account the length of the bone, which is the most discriminating variable for radius (Guérin 1980, 2010). The cloud of points corresponding to *D. etruscus brachycephalus* (39 specimens) was much more extensive than that of *D. hemitoechus*, which included completely the latter.

Calcaneum: A well-preserved calcaneus was collected from Petralona Cave. It did not articulate with astragalus and, therefore, belonged to a different individual. It presented the characteristic features of the *D. hemitoechus* calcaneum (Guérin 1980): in lateral view there was a strong difference in height between the most proximal point of the bone and the most anterior point of the tuberosity. The development of the proximal tuberosity forward was poor, much lower than that of the beak. The distal border was little developed, slightly oblique, and slightly concave. In posterior view, the axis of the sustentaculum tali was perpendicular to the axis of the corpus of the bone. The sustentaculum was well developed transversely, its end was thin and rounded (Fig. 5 C and D). The dimensions of the Petralona calcaneus were close to the average, within limits of the varia-

Fig. 5. Petralona *Dicerorhinus hemitoechus*: A, B: Radius PEC 972 (right). A: anterior, B: proximal view. C, D: Calcaneum PEC 978 (right), C: anterior, D: posterior view. Scale bar: 50 mm

tion for 24 to 33 specimens of *D. hemitoechus* (Table 4); all were lower than the average recorded for a sample of 52 to 70 specimens of *C. antiquitatis* from Europe, and less than or very close to the minimum values observed for 12-19 specimens of *D. mercki*.

Fig. 7 represents a Simpson diagram of the Petralona calcaneus compared to extreme values for *D. hemitoechus* and averages for *D. mercki*, *C. antiquitatis* and *D. etruscus brachycephalus*; all individual variables were within *D. hemitoechus* variation; it was close to the average values observed in the latter. The Petralona specimen was near the average values of *D. e. brachycephalus* (23-29 specimens), but its height and the DT of the tuberosity (variable 1 and 5, Fig. 7) were greater, whereas the DAP, its tuberosity and the DT above the sustentaculum tali (variables 2 and 6, Fig. 7) were lower.

Astragalus: Only a single, well preserved specimen. It had the morphological characteristics that were retained by Guérin in 1980 as features of the *D. hemitoechus* astragalus: anteriorly trochlea was not very wide but deep (Fig. 8 A); the slope of the medial lip was intense, the axis of the trochlea was well oblique. In medial aspect, the distal massive tubercle was poorly individualised, near the distal border and posteriorly. In distal aspect (Fig. 8 B), the front edge of the distal articulation was weakly depressed in the center. The articular facet for cuboid was not longer than the articular facet for navicular and its front edge was just barely shifted forward. The maximum width of the bone was slightly lower than the average of a sample of *D. hemitoechus* of 48 specimens to a height greater than the average of 51 specimens; the other variables were close to the average of 41 to 53 individuals of the species (Table 5). Except for the height, these dimensions were well below the average of a sample of 81 to 109 specimens of *C. antiquitatis* from Europe. All were below the minimum values of 33-43 astragali of *D. mercki*.

Fig. 9 is a Simpson diagram of the Petralona astragalus compared to extreme values for *D. hemitoechus* and averages for *D. mercki*, *C. antiquitatis* and *D. etruscus brachycephalus*; for all variables the Petralona astragalus was placed within the limits of variation of *D. hemitoechus*, but its height was relatively higher, among others with respect to the average profiles of *D. mercki* and *C. antiquitatis*. The average values of *D. etruscus brachycephalus* (31-39 specimens) were close to those of the Petralona specimen but the latter was higher, and its distal transverse diameters were stronger (variables 2, 5 and 7, Fig. 9); however the DAP at the medial lip and the distance of the summits of the two brims in frontal view (variables 3 and 6, Fig. 9) were weaker in Petralona specimen than in *D. e. brachycephalus*.

Metapodial: Only a distal part from middle diaphysis of the third metatarsal was preserved, with the distal articulation little eroded (Fig. 10 A). The section of diaphysis semi-elliptical with anterior border slightly convex and posterior slightly concave (Fig. 10 B). The tranverse diameter 2.3 times larger than the anteroposterior. Both diameters of the distal robust epiphysis, transverse (56.18 mm) and anteroposterior (47.4 mm) were close or exceeded slightly the maximum values for a sample of 14 to 16 specimens of *D. hemitoechus*. These values were significantly lower than the averages calculated in a sample of 10 to 11 specimens of *D. mercki*, and were close to the averages of 76 to 74 specimens of *C. antiquitatis* from Europe (Guérin 1980).

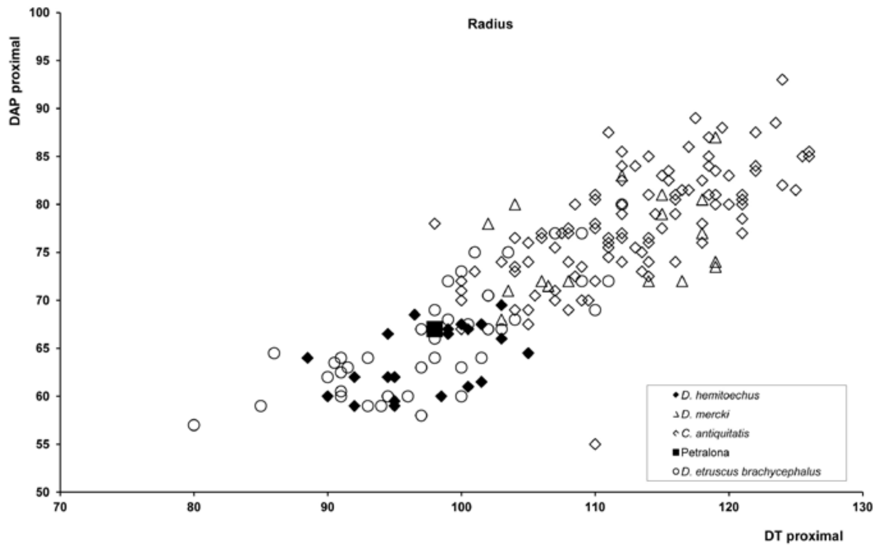

Fig. 6. Dispersal diagram of radius, proximal diameters (transverse to antero-posterior): solid square: Petralona; solid rhomb: *Dicerorhinus hemitoechus* (Falconer, 1868); open triangle: *Dicerorhinus mercki* (Jaeger 1839, Kaup 1841), open rhomb: *Coelodonta antiquitatis* (Blumenbach, 1799) and open circle: *Dicerorhinus etruscus brachycephalus* (Schroeder 1903)

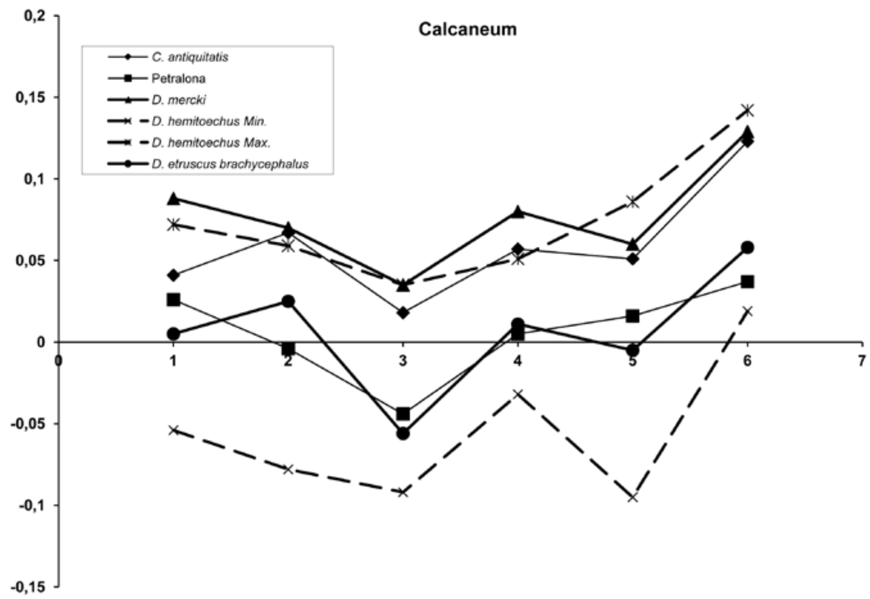

Fig. 7. Simpson diagram of calcaneum: mean values of the Petralona *Dicerorhinus hemitoechus* (Falconer, 1868), compared with minimum and maximum values of *D. hemitoechus*, average values of *Dicerorhinus mercki* (Jaeger 1839), *Coelodonta* antiquitatis (Blumenbach, 1799) and *Dicerorhinus etruscus brachycephalus* (Schroeder, 1903). The variables on the X axis are the same and in the same order as in Table 4 (see Appendix). For reference population, see Guerin 1980, updated here

Conclusion of the anatomical study

All morphological and biometric characters of the Petralona rhinoceros allowed attributing it to *Dicerorhinus hemitoechus*, a species that was widespread in the Mediterranean area, Southern Europe, (Lacombat 2005).

Within this species, Guérin (1980) recognised two evolutionary stages Middle and Late Pleistocene age, perhaps corresponding to two successive subspecies (Azzaroli 1963). Currenttly, there is no sufficient material available to support any of the two hypotheses.

Due to the limited amount of the anatomical material found in Petralona, the trends between the Middle and the Late Pleistocene are the following:

- Reduction of the width and the length of the upper premolars, increasing the size of the upper molars;

- Significant reduction of the width of the lower premolars and significant increase in the length of the lower molars;

- Elongation of the calcaneus with enlargement of tuber and stretching its beak forward; these three dimensions correspond to the least significant differences (Fig. 7);

- Highly significant increase of the height and width of the astragalus (Fig. 9).

This is the form of Middle Pleistocene that the remains of the Petralona *D. hemitoechus* are attributed to.

Remarks

Fortelius, Poulianos (1979) described other rhino remains from Petralona Cave, which are not stored at the Paleontological Museum of Thessaloniki University, but in the exhibitional place next to the cave, with no access. They fall into two groups: "Crenian", which would be equivalent to Cromerian (MNQ 21), and "Petralonian", which is equivalent to Mindel (MNQ 22). This is essentially a large fragment of the skull (badly and incorrectly reconstructed) with the skull roof retained behind the frontal horn up to the large occipital crest and with part of the maxilla with P4/ – M3/ left and M1/ – M3/ right. The teeth are much worn and show an elderly individual; a left maxilla fragment with D2/ -D4/ of juvenile; three complete isolated cheek teeth a D3/, a P/3 and a M2/; a right mandible fragment; a radius left proximal fragment; a femur right distal fragment; three tibiae, one of which a complete right; a complete left calcaneus. This additional material corresponds to at least two adult individuals and two juveniles (Fortelius, Poulianos 1980, Poulianos 1981**).** Fortelius *et al.* (1993) continued to interpret the rhino Petralona as belonging to "*Stephanorhinus*" *hemitoechus*. Later, most authors, notably Tsoukala (1989, 1991) and Symeonidis *et al.* (2006) considered that it pertained to the latter species.

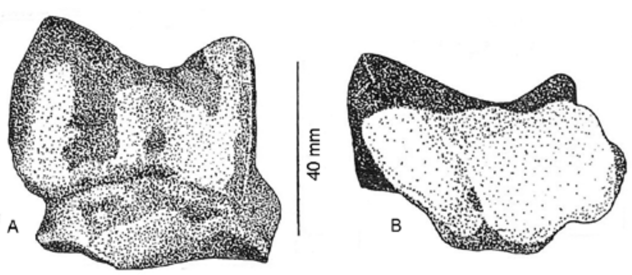

Fig. 8. Petralona *Dicerorhinus hemitoechus*. Astragalus PEC 977 (right). A. anterior, B. distal view. Scale bar: 40 mm

Order Artiodactyla Owen, 1848
Suborder Suiformes Jaeckel, 1911
Family Suidae Gray, 1821
Genus *Sus* Linnaeus, 1758
***Sus scrofa* Linnaeus, 1758**
***Sus scrofa priscus* Goldfuss, 1832**

Material: One M3/ PEC 921 left; one M3/ frag. PEC 922 left, anterior lobe; Cs PEC 933 left; two I1/: PEC 932 and 934 right; one lower tooth row PEC 920 with P/3-M/3 left; one P/3 PEC 931 left; one M/1 PEC 930 right; three M/2: PEC 927 right,

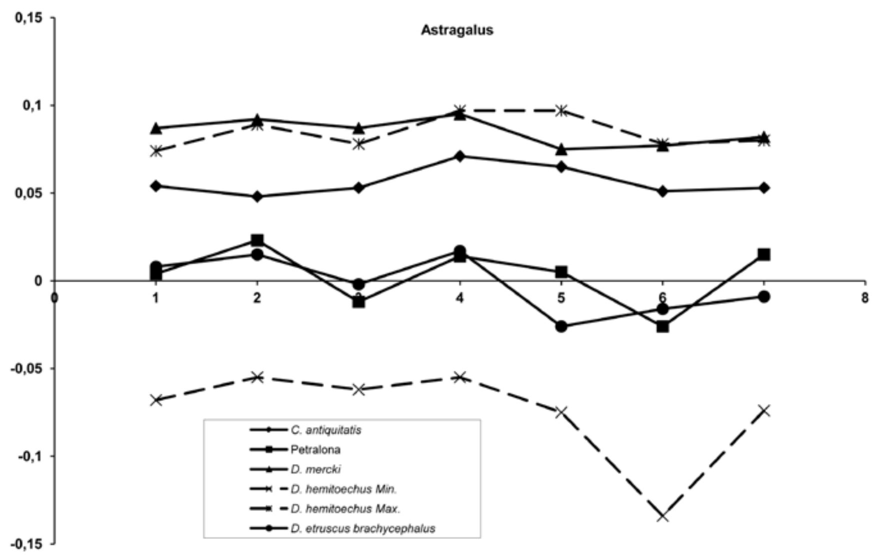

Fig. 9. Simpson diagram of astragalus: mean values of the Petralona *Dicerorhinus hemitoechus* (Falconer, 1868), compared with minimum and maximum values of *D. hemitoechus*, average values of *Dicerorhinus mercki* (Jaeger 1839, Kaup 1841), *Coelodonta* a*ntiquitatis* (Blumenbach, 1799) and *Dicerorhinus etruscus brachycephalus* (Schroeder, 1903). The variables on the X axis are the same and in the same order as in Table 5 (see Appendix). For reference population see Guerin 1980, updated here

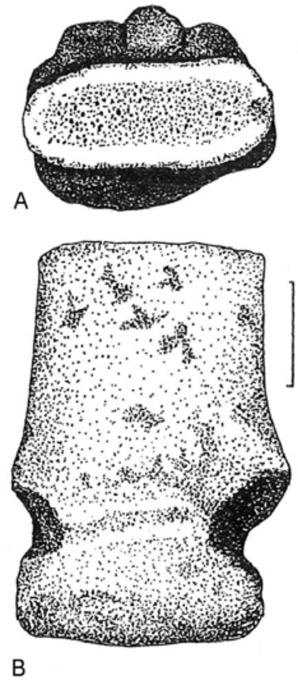

Fig. 10. Petralona *Dicerorhinus hemitoechus*. Distal Mt3 PEC 979 (left). A. Cross section at about the middle of diaphysis, B. anterior view. Scale bar: 20 mm

928 left and 929 right; three M/3 right: PEC 923, 924 and 926; four Ci PEC 935, 937 right and 936, 1606 left; two I/2: PEC 938 left and 939 right; three I/1: PEC 940, 941 left, 942 right; one distal humerus PEC 949 right; one axial phalanx I PEC 948.

Systematic and definitions: The classification of the genus *Sus* Linnaeus, 1758 within the family Suidae Gray, 1821 is an object of a consensus. All authors place the genus into the subfamily Suinae Gray, 1821.

Genus *Sus* Linnaeus, 1758

Simplified synonymy: Grubb (1993) gave a list of eight generic synonyms; all are unutilised for a long time.

Type-species: Sus scrofa Linnaeus, 1758

Sus scrofa Linnaeus, 1758

Simplified synonymy: Grubb (1993) provided a long list of specific synonyms. Many correspond in fact to the geographical extant sub-species of *Sus scrofa*, whose distribution area is huge.

Holotype: Not designated.

Sus scrofa priscus Goldfuss, 1832

Simplified synonymy: *Sus scrofa mosbachensis* Küthe, 1933, recent synonym.

Synonymy of Petralona "Old Collection" suid material: *Sus choeroides* Pomel (see Kanellis 1962); *Sus* sp. (see Sickenberg 1964); "*Sus scrofa priscus*?" (see Sickenberg 1971); *Sus scrofa scrofa* Linnaeus, 1758 (see Tsoukala 1989; 1991).

Holotype: The skull, described and figured by M. de Serres Dubreuil et Jeanjean (1835-1839, p. 134-142, pl. XI) and preserved at the University of Montpellier, constitutes the lectotype. *Locus typicus and stratum typicum:* Lunel-Viel Caves (Hérault), early Middle Pleistocene, zone MNQ 23.

Diagnosis: Wild hog of large size, which differs from the recent forms mainly by its stronger and simpler cheek teeth.

Spatio-temporal extension: The modern Eurasian wild hog *Sus scrofa* first appeared in the beginning of Middle Pleistocene (zone MNQ 20) as the primitive subspecies *Sus scrofa priscus* Goldfuss, 1832 (see also de Serres Dubreuil et Jeanjean, 1835-1839). We verified the presence of *Sus scrofa priscus* in many localities around Europe, and Hünermann (1969) has reported a few others:

- France: at Le Vallonnet (Alpes-Maritimes, MNQ 20), in Châlon-Saint-Cosme (Sâone-et-Loire, MNQ 20 ?), Ceyssaguet (Haute-Loire, MNQ 20), at Abbeville in the Carpentier quarry (white marl, MNQ 21) (Antoine *et al.* 2015), in the Caune de l'Arago at Tautavel (Pyrénées-Orientales, MNQ 22), in La Nautérie at La Romieu (Gers, MNQ 22 ?), in Lunel-Viel (Hérault, MNQ 23), in Montsaunès (Haute-Garonne, MNQ 23 ?). Hünermann (1969) also indicated Sainte-Suzanne and Saint-Didier;
- Great-Britain: Forest Bed, especially at Corton (Suffolk), Pakefield, East Runton, West Runton (Norfolk), Sidestrand, Trimingham. All these sites are mainly from the MNQ 21 biozone;
- the bottom of the North Sea (drainage by trawlers): between 51, 35, 49° and 51, 38, 49° of latitude North and 3, 01, 39° and 3, 08, 35° E;
- Germany: at Mauer (MNQ 21), Mosbach (MNQ 20 and 22), Süssenborn, Voigtstedt and Untermassfeld (Guérin, Faure 1997), at Weimar-Ehringsdorf (Hünermann 1975), Taubach (Hünermann 1977), Burgtonna (Hünermann 1978) and in the valley of Lippe (Rhine, MNQ 22). Hünermann (1969) had already indicated Sundwig, too;
- Italy: Palombara Marcellina (Hünermann 1969);
- Hungary: Beremend and Gombaszög (Hünermann 1969);
- Greece: Megalopolis (Peloponnese) (Melentis 1965b).

Anatomy

The suid material represented 25 determinable remains, mostly isolated teeth; postcranial material was very limited. All material belonged to *Sus scrofa priscus*.

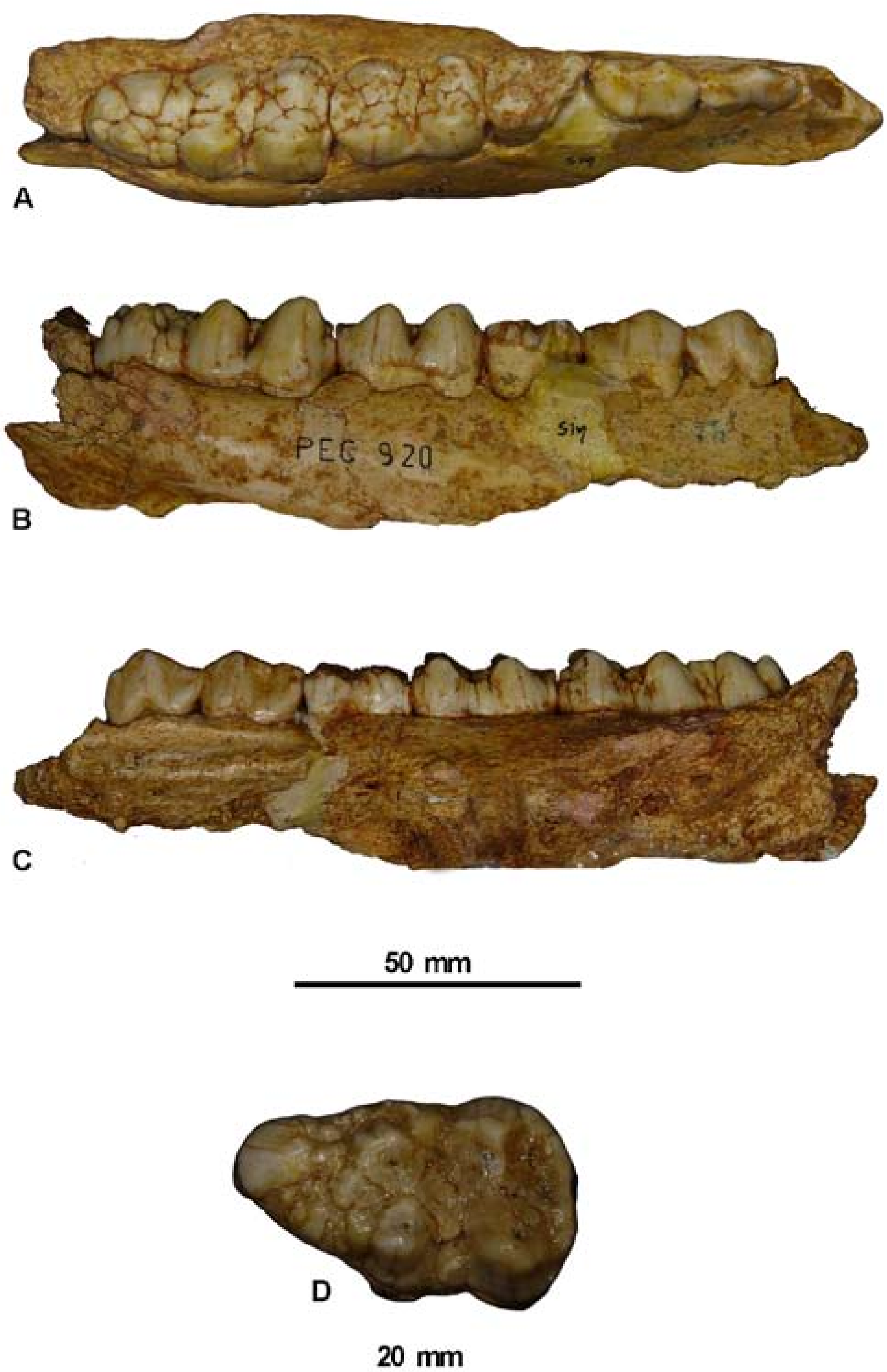

Fig. 11. Petralona *Sus scrofa priscus.* Cheek teeth. A-C: mandible fragment with P/3-M/3 PEC 920 (left). A: occlusal view. B: labial view. C: lingual view. D: M3/ PEC 921 (left), occlusal view

Upper cheek teeth: One complete and one anterior fragment of the last molar, the former, an isolated left M3/ PEC 921 (Fig. 11 D) was slightly worn and characterised by five principal tubercles arranged in two successive pairs followed by a single caudal tubercle shifted lingually. The secondary tubercles were numerous, distributed between the rows of the main tubercles and on the anterior and lingual cingula.

The length of the tooth was 40.4 mm and its anterior width was 25 mm. These values were respectively 40.6 and 23.61 mm (averages for 18 individuals) in *S. scrofa priscus*, 38.23 and 21.18 mm for 77 and 76 specimens of *Sus scrofa* from the upper Middle and Late Pleistocene of Western Europe, 35.92 and 21.27 mm for 45 specimens of extant *Sus scrofa* from Europe and the Middle East.

Lower cheek teeth: The tooth row in the mandible fragment PEC 920 (Fig. 11 A-C) was well preserved. In the scatter plot diagram (Fig. 12) of the length of the last two premolars as a function of the length of the "molar" segment, demonstrated the large dimensions of the tooth row, including a particularly long segment of the last two premolars, the largest among all *Sus scrofa* (extant 65 specimens, 39 specimens of Late and upper Middle Pleistocene and six specimens of lower Middle Pleistocene) we have measured.

No P/2 had been found in Petralona "Old Collection".

P/3: There was only one, in the tooth row PEC 920. It was laminar, with a strong axial tubercle almost medial and slightly worn with dimensions given in Table 6. Its length was equal to that of the largest specimen of fossil *S. scrofa* we had measured; its width was however smaller than the average of the three samples for comparison.

P/4: The two teeth were slightly worn. The crown, compressed transversely, was high and narrow, and showed a clear vertical syncline on its labial surface. There was a small tubercle in the postero-labial angle (Fig. 11 A and C). The morphology was identical to that of Untermassfeld P/4 (Guérin, Faure 1997); the dimensions (Table 6) showed a similar length but a narrower crown.

M/1: There were two specimens, quite heavily abraded, including that of the tooth row PEC 920. As with all Suinae, the tooth had two successive pairs of main tubercles, the lingual ones of each pair being shifted towards the rear. The length was equal to the average of those of *S. scrofa* fossils; the width was a little greater (Table 6).

M/2: The construction plane was identical to that of M/1. That of the tooth row PEC 920 was moderately worn, and only one of three isolated specimens (PEC 927) was little worn. The lengths were greater than the average of all three comparison samples, the widths were relatively higher (Table 6).

M/3: Four specimens were available, two of which slightly worn. Three-lobed: each one of the first two lobes with a pair of main tubercles whose lingual ones were shifted rearwardly; the posterior lobe was complex with no less than eight tubercles bundled together, the stronger of which was placed in the middle of the labial surface of this lobe; with two small tubercles on the posterior side, the labial being much stronger than the lingual (Fig. 11 A). There was a strong anterior cingulum. Small accessory cuspids were on the labial border of the valley between the first and the second lobe. The dimensions (Table 6) were similar as for the previous molar: rather similar in length, significanty larger in breadth.

Fig. 13 presents a scatter plot of the length of the M/3 as a function of its anterior width. The Petralona four M/3 were placed perfectly in the cloud of points of *S. scrofa priscus*, and it was entirely within the cloud of the upper Middle and Late Pleistocene *S. scrofa*.

Front teeth: The twelve isolated canines and incisors were from both male and female individuals. The upper canine was middle worn, strong, of a

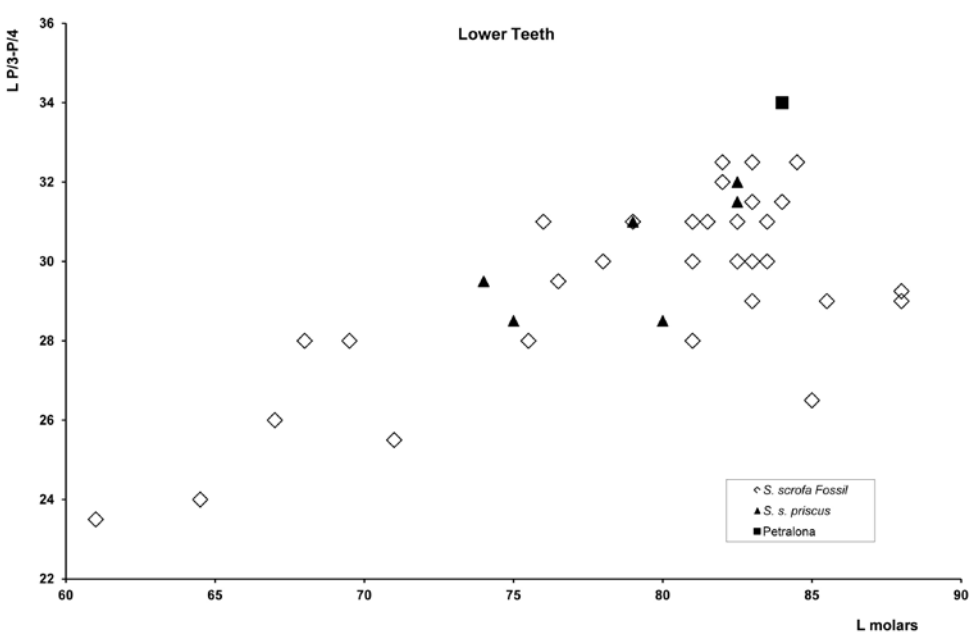

Fig. 12. Scatter diagram of the lengths of the tooth rows P/3-P/4 to molars. Solid square: Petralona; solid triangle: *Sus scrofa priscus;* open rhomb: fossil *Sus scrofa*

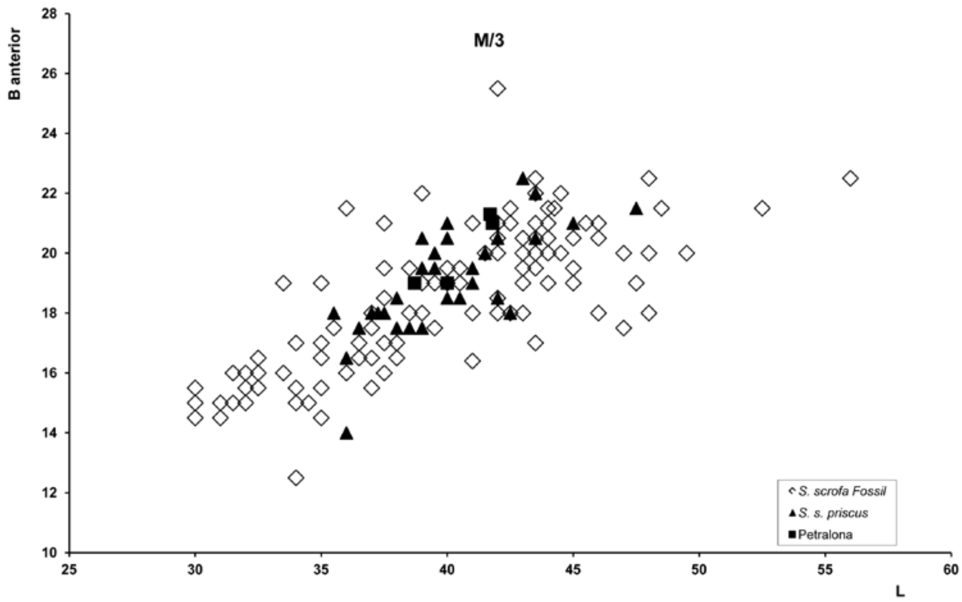

Fig. 13. Scatter diagram of length to anterior breadth of M/3. Solid square: Petralona; solid triangle: *Sus scrofa priscus*; open rhomb: fossil *Sus scrofa*

male individual. Of the four lower canines two were attributed to male, and two to female individuals. The former were more worn than the latter that were little to middle worn. Both right first upper incisors were little worn, probably belonging to male individuals. All five lower incisors were little worn and strong, probably of male individuals too.

Post-cranial skeleton

Humerus: The distal part with epiphysis of a right humerus was preserved. The dimensions were: DT dist. = 54.5 mm and DAP dist. = 53 mm. This was a rather large-sized specimen, as the maximum values measured on a sample of 10 specimens of extant *S. scrofa* were 55 and 48 mm respectively.

Phalanx I, central: Ph1 PEC 148: length L = 45.5 mm, proximal epiphysis DT = 23 mm, and DAP = 23.5 mm.

Biostratigraphical implications: *Sus scrofa priscus*, which sometimes is considered as a distinct species (*Sus priscus*), is characteristic form of the early Middle Pleistocene (zones MNQ 20-23) in Western, Central and South-eastern Europe. On the other hand, the occurrence of *Sus strozzi* Forsyth Major, 1881, of Late Villafrancian was noted by Koufos (1986) and Kostopoulos, Koufos (1994) in Gerakarou and Vassiloudi sites, north of the Petralona area.

Paleoecological implications: The extant *Sus scrofa* was very ubiquitous; it lived in the fields, bushy undergrowth, and almost in all types of forests and plains in mountains. Its diet was particularly varied and included roots, tubers, fallen fruits, vegetable sprouts, small rodents, snakes, gastropods, insect larvae, newborn deer, carrions (Groves 1981, Hainard 1988).

Taphonomical remarks: The best represented anatomical specimen was the lower third molar: there were four specimens: three right and one left. The specimen PEC 923 right could be matched with the M/3 of the left tooth row in mandible PEC 920. Similarly, there were four M/2, two right and two left, but no matching was possible. Deciduous teeth had not been recognised. Thus, there were a minimum of four hogs, all adults, in the Petralona "Old Collection".

Conclusions

The Petralona Cave, with its rich paleo-faunal remains, is the most important Middle Pleistocene cave of Greece. It was used as a den by carnivores, which brought the herbivore remains into the cave, excluding their accidental presence. There is no evidence that it was a settlement of humans, since none of the specimens of the "Old Collection", except for the skull belonging to hominids.

The Petralona rhinoceros belongs to a primitive evolutionary stage of *Dicerorhinus hemitoechus*, therefore it could be dated as early Middle Pleistocene. The same applies for *Sus scrofa priscus*.

Their paleoenvironment most likely corresponded to forested meadow.

Further research and excavations in the Petralona Cave will give accurate evidence to study about the stratigraphy and palaeontology of this important cave.

Acknowlegements: We thank Dr. E. Vlachos, geologist-paleontologist, for his contribution and assistance to the graphics, as well as the anonymous reviewers, who helped with their comments to improve the ms.

References

Antoine P., M.-H. Moncel, J.-L.Locht, N. Limondin-Lozouet, P. Auguste, E. Stoetzel, J. Dabkowski, P. Voinchet, J.-J. Bahain and C. Falguères 2015. Dating the earliest human occupation of Western Europe: new evidence from the fluvial terrace system of the Somme basin (Northern France). – *Quaternary International*, **370**: 77-99.

Azzaroli A. 1963. Validita della species *Rhinoceros hemitoechus* Falc. – *Paleontographia Italica*, **57** (NS 27): 21-34.

Baryshnikov G. F., E. Tsoukala 2010. New analysis of the Pleistocene carnivores from Petralona Cave (Macedonia, Greece) based on the Collection of the Thessaloniki Aristotle University. – *Geobios*, **43**: 389-402, +15p. tables.

Blumenbach J.F. 1799. Handbuch der Naturgeschichte. Dieterich, Göttingen,708 p.,

Boessneck J. 1965. Die jungpleistozänen Tierknochenfunde aus dem Peneiostal bei Larissa in Thessalien. – In: Milojzic, V. (Ed.): Paläolithicum um Larissa in Thessalien. Beitrage zur ur- und frühgesch. Archäolog. Mittelmeer-Kulturraumes, R.H. Verlag, Bonn.

Bojanus L.H. 1825 [1827]. De Uro nostrate eiusque sceleto Commentatio. Scripsit et *Bovis primigenii* sceleto auxit. Verhandlungen der Kaiserlichen Leopoldinisch – *Carolinischen Akademie der Naturforscher*, Bonn, **13** (2): 411-478.

Bonaparte C.L. 1845. Systema vertebratorum. – Transactions of the Linnean Society of London, **18**: 31-41.

Boyd Dawkins W. 1865. On the dentition of *Rhinoceros megarhinus*. – *Natural History Review*, **19**: 399-414, London.

Boyd Dawkins W. 1867. On the dentition of *Rhinoceros leptorhinus* Owen. – *Quarterly Journal of the Geological Society of London*, **23**: 213-227.

Brookes J. 1828. Catalogue of the anatomical and zoological Museum of Joshua Brookes, 76 p., London.

Cerdeño E. 1995. Cladistic analysis of the family Rhinocerotidae (Perissodactyla). – *American Museum Novitates*, **3143**: 1-25.

Christol J. de 1834. Recherches sur les caractères des grandes espèces de Rhinocéros fossiles. J. Martel Ainé (Ed.), 70 p., Montpellier (et 1835). – *Annales des Sciences Naturelles Zoologie*, 2s. **IV**: 44-112, Paris.

Crégut-Bonnoure E., E. Tsoukala 2005. The Pleistocene Bovids from the Petralona cave (Macedonia, Greece): New interpretations and biogeographical implications. – *Quaternaire, Hors-serie*, **2**: 161-178, Paris.

Cuvier G. 1822. Recherches sur les ossements fossiles, nouvelle édition II, première partie. Dufour et d'Ocagne, 648 p. Paris.

Dollo L. 1885. Rhinocéros vivants et fossiles. – *Revue des questions scientifiques*, Bruxelles, **17**: 293-300.

Dzhafarov R. D. 1955. A new representative of the Quaternary rhinoceros *(Rhinoceros binagadensis* sp. nova) in the Binagadinsk fauna. – *Akademia Nauk Azerbaijan SSR*, **10**: 65-88, Bakou.

Falconer H. 1868. Palaeontological memoirs and notes, vol. II. R. Hardwicke, London, 675 p.

Fischer von Waldheim G. 1814. *Zoognosia: tabulis synopticis illustrata in usum praelectionum.* Academiae imperialis medico-chirurgicae Mosquensis Edita. – *Nicolai Sergeidis Vsevolozsky*, Moscow, **3**: 694 p.

Fortelius M., N.A. Poulianos 1979. *Dicerorhinus* cf. *hemitoechus* (Mammalia, Perissodactyla) from the Middle Pleistocene cave at Petralona Chalkidiki, N. Greece. Preliminary report. – *Anthropos*, **6**: 15-43. Athens.

Fortelius M., N.A. Poulianos 1980. Errata of: *Dicerorhinus* cf. *hemitoechus* (Mammalia Perissodactyla) from the Middle Pleistocene cave at Petralona. – *Anthropos*, **7**: 324-325. Athens.

Fortelius M., P. Mazza, B. Sala 1993. *Stephanorhinus* (Mammalia, Rhinocerotidae) of the Western European Pleistocene, with a special revision of *Stephanorhinus etruscus* (Falconer 1868). – *Paleontographia Italica*, **80**: 63-155.

Gloger C.W.L. 1841. Gemeinnützіges Hand- und Hilfsbuch der Naturgeschichte. – *Aug. Schultz und Comp*., Breslau, **1**: 495 p.

Goldfuss A. 1823. Osteologische Beiträge zur Kenntnis verschiedener Säugethiere der Vorwelt. – *Nova Acta Academiae Cesareae Leopoldino-Carolinae, naturae curiosum*, **11**: 2: 482 p.

Gray J.E. 1821. On the natural arrangement of vertebrose animals. – *London Medical Repository*, **15** (1): 296-310.

Groves C. 1981. Ancestors for the pigs: taxonomy and phylogeny of the genus *Sus*. Tech. Bull. 3, Depart. Prehist. Research School of Pacific Studies, Australian National University Press, Canberra, A.C.T., 96 p.

Groves C. 1983. Phylogeny of the living species of Rhinoceros. Zeitschrift für Zoologische. – *Systematic und Evolutionforschung*, **21** (4): 293-313.

Grubb P. 1993. Order Artiodactyla. – In: Wilson D.E., D.A. Reeder (Eds.): Mammal species of the world, a taxonomic and geographic reference. Smithsonian Institution Press,

Guérin C. 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. – *Documents des Laboratoires de Géologie de Lyon*, **79**: 1185 p.

Guérin C. 1989. La famille des Rhinocerotidae (Mammalia, Perissodactyla): systématique, histoire, évolution, paléoécologie. – *Cranium*, **6**: 2, 3-14.

Guérin C. 2010. *Coelodonta antiquitatis praecursor* (Rhinocerotidae) du Pléistocène moyen final de l'Aven de Romain-la-Roche (Doubs, France). In: Guérin C., Malvesy T. (Eds.). L'aven pléistocène moyen final de Romain-la-Roche (Doubs, France). – *Revue de Paléobiologie Genève*, **29** (2): 697-746.

Guérin C., Faure M. 1997. The Wild Boar (*Sus scrofa priscus*) from the Post-Villafranchian Lower Pleistocene of Untermassfeld. – In: Kahlke R.D. (Ed.): Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), Teil 1.- Monographien Römisch-Germanisches Zentralmuseum für Vor- und Frühgeschichte, Bonn, **40** (1): 375-383.

Guérin C., R. Ballesio and H. Méon-Vilain 1969. Le *Dicerorhinus megarhinus* (Mammalia, Rhinocerotidae) du Pliocène de Saint-Laurent-des-Arbres (Gard.). – *Documents des Laboratoires de Géologie de Lyon*, **31**: 55-145.

Hainard R. 1988. Mammifères sauvages d'Europe, 4ème édition, 2. Delachaux and Niestlé, Neuchâtel, 347 p.

Heissig K. 1973. Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). – *Säugetierkunde Mitteilungen*, München, **40** (21): 25-30.

Heissig K. 1989. The Rhinocerotidae. – In: Prothero D.R., R.M. Schoch (Eds.). The Evolution of Perissodactyls. Oxford University Press, New-York: 399-417.

Hünermann K.A. 1969. *Sus scrofa priscus* Goldfuss im Pleistozän von Süssenborn bei Weimar. – *Paläontologische Abhandlungen, Abt*., Berlin, A, **III**, 3/4: 611-616,

Hünermann K.A. 1975. *Sus scrofa* Linné aus dem Pleistozän von Weimar-Ehringsdorf. – *Paläontologische Abhandlungen*, **23**: 251-263.

Hünermann K.A., 1977. *Sus scrofa* L. aus dem Jungpleistozän von Taubach bei Weimar in Thüringen. – *Quartärpaläontologie*, **2**: 225-235.

Hünermann K.A. 1978. Das Wildschwein (*Sus scrofa* L.) aus dem Jungpleistozän von Burgtonna in Thüringen. – *Quartärpaläontologie*, **3**: 123-127.

Jaeckel OMJ. 1911. Die Wirbeltiere. Eine Übersicht über die fossilen und lebenden Formen. Gebrüder Bornträger, 252 p.

Jaeger G.F. 1839. Über die fossilen Säugethiere welche in Württemberg in verschiedenen Formationen aufgefunden worden sind, nebst geognotischen Bemerkungen über diese Formationen. Carl Erhard (Ed.), Stuttgart, 214 p.

Kanellis A. 1962. Die Höhle von Petralona. To Vouno: "Das Gebirge". – *Zeitschrift fur Deusche-Griechische Bergsteiger-Verbandes*, Athens, **227**: 91-102.

Kaup J.J. 1841. Akten der Urwelt oder Osteologie der urweltlichen Säugethiere und Amphjbien. Darmstadt, 10 p.

Kostopoulos D.S., G.D. Koufos 1994. The Plio-Pleistocene Artiodactyls of Macedonia and their biostratigraphic significance. Preliminary report. – *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris*, **318** (2): 1267-1272.

Koufos G. 1986. The presence of *Sus strozzii* in the Villafranchian (Villanyian) of Macedonia (Greece). – *Paläontologische Zeitschrift*, **60**: 341-351.

Koufos G., E. Tsoukala 2007. Petralona cave. Aristotle University Ed., Thessaloniki, 134 p.

Kretzoï M. 1942. Bermerkungen zum System der nachmiozänen Nashorn-Gattungen. – *Földtani Közlöny, Budapest*, **72**: 309-318.

Küthe K. 1933. Study of *Sus scrofa mosbachensis* from the Mosbach sand (Quaternary) and comparison with recent forms. – *Notizbl. Hesse Geol. L.-Amt Darmstadt* (V), **14**: 117-124.

Lacombat F. 2005. Les rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif central. Paléontologie et implications biochronologiques. – *British Archaeological Research International Series*, **1419**: 175 p.

Linnaeus C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Salvius, Holmiæ, **4**: 824 p.

Mckenna M.C., S.K. Bell 1997. Classification of Mammals above the species level. Columbia University Press, New York, 631 p.

Melentis J. 1964. Die fossilen Rhinocerotiden, Hippopotamiden und andere Säugertiere aus dem Becken von Megalopolis im Peloponnes (Griechenland). – *Praktika Akadimias Athinon*, **39**: 388-400.

Melentis J. 1965a. Studien über fossile Vertebraten Griechenlands: 4. Die pleistozänen Nashörner des Beckens von Megalopolis im Peloponnes (Griechenland). – *Annales Géologiques des Pays Helléniques*, **16**: 363-402.

Melentis J. 1965b. Studien über fossile Vertebraten Griechenlands: 6. *Sus scrofa* L. aus dem Jungpleistozän des Beckens von Megalopolis im Peloponnes (Griechenland). – *Annales Géologiques des Pays Helléniques*, **16**: 436-445.

Owen R. 1845. Odontography or a treatise on comparative anatomy of the teeth, their physiological relation, mode of development, and microscopic structure in the vertebrate animals. Baillères, London, 655 p.

Owen R. 1846. A history of British fossil Mammals and Birds. – In: van Voorst J. (Ed.), 561 p., London.

Owen R. 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N. W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. – *Quarterly Journal of the Geological Society London*, **4**: 103-41.

Pomel A. 1895. Les rhinocéros quaternaires. – Carte géologique de l'Algérie, Paléontologie, Monographies, Alger, 49 p.

Poulianos N.A. 1981. New Rhino findings from the Crenian Period of Petralona Cave. – *Anthropos*, **8**: 84-90, Athens.

Prothero D.R., R.M. Schoch 1989. Classification of the Perissodactyls. In: Prothero D.R., R.M. Schoch (Eds.): The Evolution of Perissodactyls (IVth Theriological Congress, Edmonton, Alberta, 1985). Oxford University Press, New York, 530-539 p.

Ringström T. 1924. Nashörner der Hipparion-Fauna Nord Chinas. Paleontologica Sinica, **C (1,4, 4)**: 157 p.

Schroeder H. 1903. Die Wirbeltier-Fauna der Mosbacher Sandes. I: Gattung *Rhinoceros*. – *Abhandlungen der Königlich Preussischen Geologischen Landesanstalt*, Berlin, NF, **18**: p. 141; **1**: atlas 14 pl.

Serres M. de Dubreuil Jeanjean, 1839. Recherches sur les ossemens humatiles des cavernes de Lunel-Viel. Boehm et Cie Montpellier, 275 p.

Sickenberg O. 1964. Die Säugetierfauna der Höhle Petralona bei Thessaloniki (Vor. Mit.). – *Geological and Geophysical Research*, Athens, **9**: 1-16.

Sickenberg O. 1971. Revision der Wirbeltier fauna der Höhle Petralona (Griech., Mazedonien). – *Annales Géologiques des Pays Helléniques*, **23**: 230-264.

Simpson G.G. 1945. The principles of classification and a classification of mammals. – *Bulletin of the American Museum of Natural History*, New York, **85**: 350 p.

Stringer C., F.C. Howell and J. Melentis, 1979. The significance of the fossil hominid skull from Petralona, Greece. – *Journal of Archeological Sciences*, **6**: 235-253.

Symeonidis N.K., I.X. Giaourtsakis, R. Seemann and V.I.Giannopoulos 2006. Aivaliki, a new locality with fossil Rhinoceroses near Alistrati (Serres, Greece). – *Beitrage zur Paläontologie*, Wien, **30**: 437-451.

Tsoukala E. 1989. Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave, Chalkidiki (N. Greece). Ph.D. Thesis, Aristotle University of Thessaloniki, School of Geology. – *Scientific Annals*, **8**: 1-360, 62 pl. (In Greek with English summary).

Tsoukala E. 1991. Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave, Chalkidiki (N. Greece). Preliminary report. – *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris*, **312** (2): 331-336.

Wood H.E. 2nd 1937. Perissodactyl suborders. – *J. Mammal*, **18**: 106.

Received: 13.08.2015
Accepted: 21.10.2015

APPENDIX

Table 1. Comparative dimensions of the Petralona *Dicerorhinus hemithoecus* upper cheek teeth (in mm) (see abbrev.)

Upper teeth	Petralona			
P1/				
P 1/L				
P 1/B				
P2/	PEC 960 D			
P 2/L	32			
P 2/B	34			
P3/	PEC 961 D			
P 3/L	42			
P 3/B	47.5			
P3/				
P 3/L				
P 3/B				
P4/	PEC 962 D			
P 4/L	46			
P 4/B	53.5			
M1/	PEC 963 S			
M1/L	56			
M1/B	60			
M2/	PEC 964 S	PEC 965 D	PEC 966 D	
M2/L	61.5	61.5	62	
M2/B	62.5	65.5	72	
M3/				
M3/L abs				
M3/L anat				
M3/B				
D1/	PEC 954 D	PEC 953 D	PEC 951 S	PEC 952 S
D1/ L	26	28	23	28
D1/ B	22	20	21.5	24.5
D2/	PEC 955 D			
D 2/L	36.5			
D 2/B	36.5			
D3/	PEC 956 D	PEC 957 S		
D 3/L	46.5	46		
D 3/B	44.5	42		
D4/	PEC 959 D			
D 4/L	51			
D 4/B	50			

Coelodonta antiquitatis							***Dicerorhinus hemitoechus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
P 1/L							1	23.50				
P 1/B							1	19.50				
P 2/L	37	30.95	20.5	37	4.23	13.67	39	33.47	29	40	2.152	6.43
P 2/B	50	33.64	27.5	42	3.79	11.26	52	36.32	27	44	2.987	8.22
P 3/L	70	37.65	24.5	55	3.92	10.42	55	41.48	34	49	2.861	6.90

Table 1. Continued

P 3/B	85	41.68	35	51	3.08	7.39	78	48.40	43	57	2.559	5.29
P 4/L	67	43.34	35.5	58	4.18	9.65	52	44.23	37	51	2.510	5.67
P 4/B	83	48.49	41.5	60	3.41	7.02	65	55.18	47	62	2.642	4.79
M 1/L	63	50.85	33.5	58.5	4.23	8.33	59	54.37	43.5	63.5	3.917	7.20
M 1/B	84	53.32	43.5	63	3.46	6.48	71	58.97	52.5	68	3.457	5.86
M 2/L	88	56.24	47	65.5	3.76	6.69	43	59.76	46.5	66.5	3.960	6.63
M 2/B	98	55.73	45	63	3.25	5.83	48	62.51	56	72	3.640	5.82
M 3/L abs.	112	57.29	42.5	70	5.02	8.77	66	63.23	50	77	5.635	8.91
M 3/L anat.	104	52.07	43	61	4.15	7.97	65	53.55	41.5	64	5.046	9.42
M 3/B	107	50.13	40	61	3.70	7.39	71	55.03	41	65	4.543	8.25
D1/L	6	22.58	21	25	1.66	7.33	11	25.05	21	29	1.993	7.96
D1/B	6	18.25	17	20.5	1.17	6.43	10	22.00	20	24.5	1.563	7.11
D2/L	33	30.65	28	33	1.44	4.71	19	35.18	33	37.5	1.320	3.74
D2/B	36	29.57	26	38	2.04	6.89	24	34.73	32	38.5	1.320	3.80
D3/L	32	41.91	31	45.5	3.19	7.62	24	42.96	39	48	1.960	4.55
D3/B	37	36.91	31.5	41	2.03	5.50	23	41.85	37	45	2.110	5.05
D4/L	30	48.82	44	57	3.12	6.39	24	47.90	44	51.5	2.400	5.00
D4/B	33	43.17	39	50	2.60	6.02	24	46.60	42	56	2.970	6.37
Dicerorhinus mercki							***Dicerorhinus etruscus brachycephalus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
P 1/L	2	28.25	28	28.5								
P 1/B	2	26.00	23.5	28.5								
P 2/L	16	38.69	33	43.5	3.10	8.02	27	35.72	28.5	45	3.061	8.57
P 2/B	28	42.43	35	50.5	3.66	8.62	40	40.04	31	52.5	4.279	10.69
P 3/L	18	46.64	40.5	51	2.68	5.75	20	42.80	38	47.5	2.623	6.13
P 3/B	31	56.69	50	63	3.55	6.26	28	50.89	43.5	58	3.586	7.05
P 4/L	34	51.84	44	66	3.96	7.63	32	45.14	39	54	3.572	7.91
P 4/B	44	63.67	54	70	4.26	6.68	50	55.42	47.5	61.5	3.166	5.71
M 1/L	20	56.98	48.5	63.5	4.24	7.44	35	51.56	44	60	3.846	7.46
M 1/B	34	63.59	55	71.5	4.80	7.54	41	56.30	44.5	63.5	4.062	7.21
M 2/L	37	66.73	53	71	4.06	6.08	48	54.59	47	63	3.359	6.15
M 2/B	50	68.11	62	78.5	3.74	5.49	63	58.84	52	67	3.279	5.57
M 3/L abs.	46	65.72	54	75	4.46	6.79	44	54.57	45	66	3.916	7.18
M 3/L anat.	41	55.94	48	75	5.53	9.89	44	48.38	40.5	56	4.177	8.63
M 3/B	50	59.99	47.5	68.5	5.28	8.79	59	50.31	41.5	60	4.074	8.10
D1/L	3	29.00	26	32			8	28.06	25.5	30	1.761	6.28
D1/B	3	25.33	23	29			8	24.31	21	28	2.120	8.72
D2/L	7	36.93	34	39.5	2.34	6.32	7	37.86	34	41	2.340	6.18
D2/B	8	37.38	31	42	3.57	9.56	9	36.17	32.5	39	2.165	5.99
D3/L	9	45.89	41.5	50.5	3.30	7.18	8	42.38	36	46.5	3.215	7.59
D3/B	10	46.85	42	54.5	3.99	8.51	10	42.10	33.5	46.5	3.430	8.15
D4/L	6	53.83	48	57	3.13	5.81	12	48.50	44	58	4.528	9.34
D4/B	8	52.81	48	57.5	3.06	5.79	15	46.83	43.5	56.5	3.614	7.72

Table 2. Comparative dimensions of the Petralona *Dicerorhinus hemithoecus* lower cheek teeth (in mm) (see abbrev.)

Lower teeth	Petralona
D/1	PEC 980 S
D/1 L	18.5
D/1B	11
D/2	PEC 950 S
D/2 L	30
D/2 B	17.5
D/3	PEC 950 S
D/3 L	40
D/3 B	21
D/4	PEC 950 S
D/4 L	43
D/4 B	22

Coelodonta antiquitatis							***Dicerorhinus hemitoechus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
D/1L	3	24.67	17.5	32.5			3	17.83	17	19		
D/1B	3	13.50	12	14.5			2	11.25	10.5	12		
D/2L	16	26.69	20.5	29.5	2.04	7.64	16	30.06	27.5	35	2.089	6.95
D/2B	17	16.00	11.5	18.5	1.46	9.11	17	16.71	15	18.5	1.105	6.61
D/3L	30	36.97	32	41.5	1.87	5.06	22	41.16	37.5	45.5	2.101	5.1
D/3B	34	20.28	17	24	1.46	7.19	28	22.07	20.5	25	1.223	5.54
D/4L	22	42.59	37	51	3.18	7.47	19	43.47	37	50.5	2.951	6.79
D/4B	23	22.28	19	25.5	1.99	8.92	22	24.41	22	27.5	1.386	5.68
Dicerorhinus mercki							***Dicerorhinus etruscus brachycephalus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
D/1L	2	20.25	17.5	23			4	19.00	17	23.5		
D/1B	1	14.00					4	11.88	11	13		
D/2L	8	33.00	28	38	3.15	9.55	9	31.78	27.5	34	2.063	6.49
D/2B	9	19.28	16.5	21.5	1.58	8.21	9	18.50	17.5	20	0.866	4.68
D/3L	13	42.15	38	44.5	1.59	3.76	16	41.88	30	47	3.931	9.39
D/3B	15	23.40	21	28.5	1.93	8.24	16	22.66	18	28.5	2.535	11.19
D/4L	11	45.91	42	51	2.71	5.90	16	42.38	36	47	2.969	7.01
D/4B	11	27.09	23	31	2.51	9.26	16	25.22	22.5	31	2.280	9.04

Table 3. Comparative dimensions of the Petralona *Dicerorhinus hemithoecus* radius (in mm) (see abbrev.)

	Petralona
Radius	PEC 972 D
DT prox.	98
DAP prox.	67

Coelodonta antiquitatis							***Dicerorhinus hemitoechus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
DT prox.	111	113.05	98	126	6.57	5.81	22	97.57	88.5	105.0	4.55	4.66
DAP prox.	109	77.78	55	93	5.90	7.59	23	63.93	59	69.5	3.31	5.18
Dicerorhinus mercki							***Dicerorhinus etruscus brachycephalus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
DT prox.	20	111.28	102	119	6.11	5.49	39	98.06	80	112	7.318	7.46
DAP prox.	17	75.97	68	87	5.18	6.81	39	66.14	57	80	5.936	8.97

Table 4. Comparative dimensions of the Petralona *Dicerorhinus hemithoecus* calcaneum (in mm)(see abbrev.)

	Petralona
Calcaneum	PEC 978 D
1. H	125.0
2. DAP tuber	64.0
3. DAP beak	62.5
4. DT sust.	72.0
5. DT tuber	51.0
6. DT middle	36.5

Coelodonta antiquitatis							***Dicerorhinus hemitoechus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
H	67	129.48	117.5	141	5.57	4.30	25	121.02	104	139	8.460	6.99
DAP tuber	63	75.10	60	90	6.71	8.94	24	63.00	54	74	4.723	7.50
DAP beak	63	71.93	59.5	86.5	6.11	8.49	33	66.59	56	75	4.759	7.15
DT sust.	65	80.94	65	93	6.63	8.19	30	74.38	66	80	4.516	6.07
DT tuber	70	55.25	45	66	4.46	8.07	24	50.10	39.5	60	5.002	9.98
DT middle	52	44.39	35	59	4.43	9.99	25	39.54	35	46.5	3.307	8.36
Dicerorhinus mercki							***Dicerorhinus etruscus brachycephalus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
H	19	144.34	130.5	152.5	7.07	4.90	28	119.16	110.0	131	6.149	5.16
DAP tuber	16	75.88	69	86.5	5.40	7.11	23	68.41	55.5	77	4.673	6.83
DAP beak	18	75.00	69	80.5	3.82	5.09	24	60.75	54.0	68	4.019	6.62
DT sust.	15	85.53	76	94	5.12	5.99	27	72.94	64.0	80	4.382	6.01
DT tuber	18	56.53	51	61	2.73	4.82	29	48.60	43.0	58	3.764	7.74
DT middle	12	45.13	40	51	4.01	8.89	28	38.29	32.5	44	3.489	9.11

Table 5. Comparative dimensions of the Petralona *Dicerorhinus hemithoecus* astragalus (in mm) (see abbrev.)

	Petralona
Astragalus	PEC 977 D
1. DT max.	85.5
2. H	82
3. DAP int.	54.5
4. DT dist. art.	71
5. DAP dist. art.	44.5
6. Dist. 2 brims	59
7. DT dist.	78

Coelodonta antiquitatis							***Dicerorhinus hemitoechus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
DT max.	112	96.02	84	112	5.03	5.24	48	85.34	72.5	100.5	6.167	7.23
H	112	86.96	77	102	4.45	5.12	51	81.33	68.5	95.5	6.082	7.48
DAP int.	81	63.22	52	72	4.85	7.67	47	57.49	48.5	67.0	4.416	7.68
DT dist. art.	111	80.99	68	91	4.65	5.74	45	68.48	60.5	86.0	5.376	7.85
DAP dist. art.	92	51.15	42	59	3.34	6.54	40	44.09	37	55.0	4.430	10.05
Dist. 2 brims	103	70.61	60	83	4.17	5.91	54	59.46	46	7.0	5.609	9.43
DT dist.	109	85.22	76	97	4.38	5.13	41	73.88	63.5	90.5	5.413	7.33
Dicerorhinus mercki							***Dicerorhinus etruscus brachycephalus***					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
DT max.	43	103.57	93	116.5	6.10	5.89	39	86.38	76	107	6.522	7.55
H	40	96.26	88.5	105	4.10	4.26	39	80.47	72	89	5.113	6.35
DAP int.	33	68.36	60	83	5.08	7.43	35	55.69	46	68	4.683	8.41
DT dist. art.	40	85.46	74	93	4.87	5.70	33	71.41	59.5	85	6.036	8.45
DAP dist. art.	36	52.28	43	60	3.84	7.34	31	41.40	35	52	3.953	9.55
Dist. 2 brims	39	74.88	63.5	91	5.48	7.32	38	60.41	52	71	4.853	8.03
DT dist.	40	90.91	80	102	5.13	5.64	36	73.85	61	82	5.253	7.11

Table 6. Comparative dimensions of the Petralona *Sus scrofa priscus* lower cheek teeth (in mm) (see abbrev.)

Sus	**Petralona**								
Lower teeth	PEC 920 S								
L P/3-M/3	129								
L P/3-P/4	34								
L molars	84								
P/3 L	17								
P/3 B	7				PEC 931 S				
P/4 L	17.6				16.6				
P/4 B	10.3				9.5				
						PEC 930 D			
M/1 L	17.3					18			
M/1 B ant						12.7			
M/1 B post	13.7					12.4			
							PEC 928 S	PEC 929 D	PEC 927 D
M/2 L	26						25	25	26
M/2 B ant.	17.6						16.2	16.3	15.5
M/2 B post	17.7						11	16.4	16.5
		PEC 926 D	PEC 923 D	PEC 924 D					
M/3 L	41.7	38.7	41.8	40					
M/3 B ant	21.3	19	21	19					
M/3 B med	19.4	17.5	19.4	18.8					
M/3 B post	16.3	15.5	16.6	16					

***Sus scrofa* recent**							***Sus scrofa* upper Middle – Late Pleistocene**					
	N	mean	min.	max.	SD	v	N	mean	min.	max.	SD	v
L P/3-M/3	64	113.55	86	148	10.766	9.48	20	116.88	97	127.5	10.069	8.62
L P/3-P/4	65	28.1	22	31.5	2.342	8.34	39	29.15	22.5	33	2.586	8.87
L molars	63	74.14	54	85.5	6.829	9.21	44	79.42	61	88	6.609	8.32
P/3 L	63	13.68	7.5	16	1.498	10.95	43	14.09	11	17	1.398	9.92
P/3 B	63	7.55	5.5	13.5	1.23	16.3	43	7.88	6	17.5	1.832	23.23
P/4 L	63	14.63	8.5	17.5	1.629	11.14	63	15.56	12.5	18	1.306	8.39
P/4 B	63	9.76	7	12.5	1.114	11.41	62	10.2	7.5	13	1.301	12.75
M/1 L	61	16.28	13	19	1.596	9.81	71	17.32	13.5	23.5	1.538	8.88
M/1 B ant	59	11.08	8.5	15	1.074	9.70	64	11.47	9	15	1.126	9.82
M/1 B post	60	12.13	9.5	18	1.321	10.89	66	12.5	10	16.5	1.301	10.41
M/2 L	63	21.59	14	25	2.156	9.99	90	23.22	17	28.5	2.066	8.90
M/2 B ant	63	14.68	10.5	17.5	1.389	9.46	88	15.69	11.5	19	1.626	10.37
M/2 B post	62	15.59	11	22.5	1.796	11.52	90	16.37	11	20	2.015	12.31
M/3 L	62	37.45	25	44.5	4.245	11.34	124	39.92	30	56	5.345	13.39
M/3 B ant	62	17.26	12	21	1.896	10.99	119	18.48	12.5	25.5	2.401	12.99
M/3 B med	60	16.21	9.5	20	2.691	16.60	107	17.69	12	21	2.083	11.78
M/3 B post	35	13.54	9.5	21	2.041	15.07	114	14.32	10	19	1.889	13.19

***Sus scrofa* lower Middle Pleistocene**						
	N	mean	min.	max.	SD	v
L P/3-M/3	5	119.6	115	125	4.492	3.76
L P/3-P/4	6	30.17	28.5	32	1.538	5.1
L molars	9	79.94	74	91	5.253	6.57
P/3 L	7	14.71	13.5	16	0.859	5.84
P/3 B	7	7.43	6.5	8.5	0.787	10.59
P/4 L	11	15.91	15	17	0.701	4.4
P/4 B	11	10.32	8	12.5	1.505	14.58
M/1 L	16	17.59	13.5	20	1.744	9.91
M/1 B ant	17	11.68	10	14	1.015	8.69
M/1 B post	17	12.97	11.5	15	1.243	9.59
M/2 L	20	24.62	22	26.5	1.459	5.92
M/2 B ant	18	16.53	15	18.5	1.021	6.18
M/2 B post	18	17.22	15.5	20	1.468	8.52
M/3 L	32	40.02	35.5	47.5	2.772	6.93
M/3 B ant	34	18.99	14	22.5	1.756	9.25
M/3 B med	20	18.17	15	21	1.633	8.98
M/3 B post	29	15.24	13	18	1.177	7.72