

New data on the *Equus stenonis* Cocchi, 1867 from the late Pliocene locality of Sésκλο (Thessaly, Greece)

Athanassios ATHANASSIOU

University of Athens,
Department of Historical Geology and Palaeontology,
Panepistimiopolis, 157 84 Athens (Greece)
aathan@cc.uoa.gr

Athanassiou A. 2001. — New data on the *Equus stenonis* Cocchi, 1867 from the late Pliocene locality of Sésκλο (Thessaly, Greece). *Geodiversitas* 23 (3): 439-469.

ABSTRACT

The equid material from the late Pliocene locality of Sésκλο (Thessaly, Greece) is described and compared in this article. It belongs to a large and fairly stout *Equus stenonis* form, which shares many morphological characters with the species samples from Saint-Vallier, La Puebla de Valverde and Olivola, as well as with already known *Equus stenonis* samples from other Greek localities (Dafneró, Vólax). Its main features are the big skull and limbs, the short protocones and the very simple enamel plication in the teeth. Large sized and relatively robust stenonid horses are common elements of the late Pliocene faunas of Greece.

KEY WORDS

Mammalia,
Perissodactyla,
Equidae,
Equus stenonis,
late Pliocene,
Villafranchian,
Thessaly,
Greece.

RÉSUMÉ

Nouvelles données sur l'Equus stenonis Cocchi, 1867 de la localité pliocène de Sésκλο (Thessalie, Grèce).

Dans l'article présent, l'équidé de la localité pliocène de Sésκλο (Thessalie, Grèce) est décrit et comparé. Il appartient à une forme d'*Equus stenonis* large et assez robuste, qui a des caractères morphologiques communs avec les échantillons de Saint-Vallier, La Puebla de Valverde et Olivola, ainsi qu'avec des échantillons déjà connus d'autres localités grecques (Dafneró et Vólax). Ses caractères morphologiques principaux s'observent sur le crâne et sur les membres de grandes dimensions, les protocônes sont courts et l'émail dentaire est faiblement plissé. Les équidés sténoniens grands et relativement robustes sont fréquents dans les faunes grecques du Pliocène supérieur.

MOTS CLÉS

Mammalia,
Perissodactyla,
Equidae,
Equus stenonis,
Pliocène supérieur,
Villafranchien,
Thessalie,
Grèce.



Fig. 1. — Sketch map of the Thessalian area, showing the locality of Sésklo.

INTRODUCTION

The site of Sésklo (Magnesia, Thessaly, Greece) (Fig. 1) is located in a basin filled with fluvio-lacustrine clay sediments. It is situated about 10 km West of the town of Vólos, the capital of the district of Magnesia. The basement of the basin is formed of metamorphic rocks (peridotites, serpentinites and slates with marble and ophiolite intercalations) that tectonically overlie a formation of Jurassic slates and Triassic-Jurassic marbles (Müller 1983; Symeonidis & Tataris 1983; Mastoras 1985). The clays that fill the basin are red coloured, about 100 m thick and inclined to the SE. Lithologically they are very uniform; only the uppermost layers have some pebble intercalations.

A part of the basin is used by the local cement industry as a clay pit. The first findings in the site (some *Anancus* remains) were discovered in 1971 during the works in this pit (Symeonidis & Tataris 1983). Another discovery in 1982, followed by a brief excavation by Prof. N. Symeonidis (University of Athens), yielded most of the material. The present author also carried out a minor excavation in 1991. The exact location of each excavation in the site is different (Fig. 2), following the quarry development,

which brought the fossils to light. The stratigraphic relationship of the different localities is not clear, due to the petrographic uniformity of the clays and the presence of too many faults. Moreover none of these localities is available now for field studies, due to the quarry development. The fossil bones were found close to each other, forming lens-like accumulations. They were covered by a calcitic crust around their surface, which made them very difficult and time consuming to prepare.

The fossil fauna of Sésklo is already described in older studies (Symeonidis & Tataris 1983; Symeonidis 1992; Athanassiou 1996). The presence of fossil bones in the sediments is also mentioned by Müller (1983) and Mastoras (1985), who worked on the geology of the basin. The faunal list, given by Athanassiou (1996) (and, concerning the gazelles, revised by Kostopoulos & Athanassiou 1997), includes Carnivora (*Nyctereutes megamastoides* [Pomel, 1843], *Vulpes* cf. *alopecooides* Forsyth Major, 1875, *Homotherium crenatidens* [Fabrini, 1890]), Proboscidea (*Anancus arvernensis* [Croizet & Jobert, 1828], *Mammuthus meridionalis* [Nesti, 1825]), Perissodactyla (*Equus stenorhis* Cocchi, 1867, *Stephanorhinus* sp.) and Artiodactyla (cf. *Croizetoceros ramosus* [Croizet & Jobert, 1828],

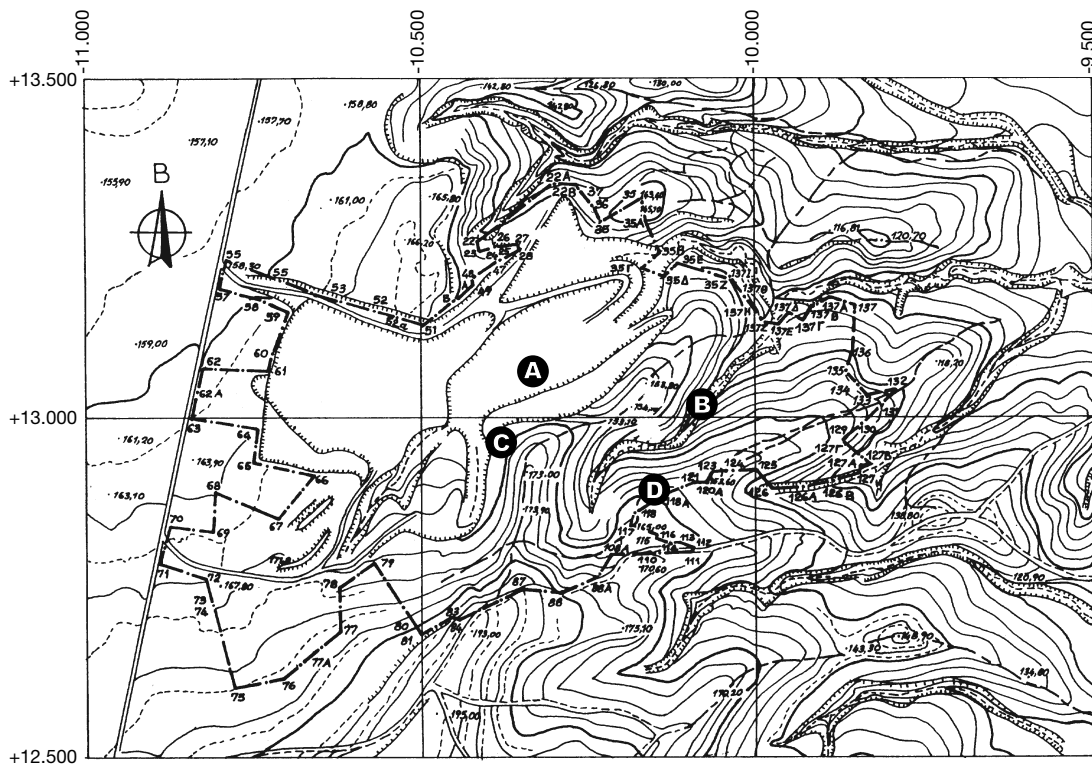


FIG. 2. — Topographical map of the clay pit of Sésklo (dated April 17, 1981), where the several collections were carried out. The letters indicate the positions of the collection sites.

cf. *Eucladoceros* sp., *Macedonitherium martinii* Sickenberg, 1967, *Gazella borbonica* Depéret, 1884, *Gazella bouvrainae* Kostopoulos, 1996, *Gazella* sp., *Gazellospira torticornis* [Aymard, 1854], as well as some unusual, mainly large sized forms, assigned to Caprini and Ovibovini). The faunal assemblage is of the so called “villafranchian type” and suggests a lower MN17 (MNQ17) age (Athassiou 1996). The equid material is abundant, being the richest *Equus stenonis* sample among those that come from the already known localities of Greece.

Plio-Pleistocene stenonid horses are known from several localities in Greece: Kos (Airaghi 1928; Desio 1931), Líbakos, Polýlakkon, Aliákmon basin (Steensma 1988), Krímni, Gerakaróu, Ríza, Ravin of Voulgarákis (Koufos 1992), Dafneró (Koufos & Kostopoulos 1993) and Vólax (Koufos & Vlachou 1997). Some scanty equid

materials are also probably referable to *Equus stenonis*: Paraskevaidis (1953) described some remains of a stenonid horse from Attica. Van der Meulen & Van Kolfshoten (1988) referred some equid remains from Pýrgos to *E. cf. stenonis* and *E. cf. stehlini* Azzaroli, 1965. A horse with stenonid affinities, but probably of younger age, is also reported from Vaterá (Lésbos Island, Dermitzakis *et al.* 1991). A recent excavation in another site of this locality (Site F) yielded an interesting Plio-Pleistocene fauna that includes a large but slender stenonid horse (Eisenmann in press).

The stenonid horses are the most common fossils in the European larger Mammal faunas of the villafranchian type. Several local samples have been described until now, usually referred to as subspecies of *Equus stenonis*. Some well known of them are those from Saint-Vallier, Senèze,

Chilhac and Venta Micena, which have been assigned to distinct subspecies, *E. s. vireti* Prat, 1964, *E. s. senezensis* Prat, 1964, *E. s. guthi* Boeuf, 1983 and *E. s. granatensis* Marin, 1987, respectively, while the samples from the sites in Valdarno and neighbouring localities (e.g., Olivola, Matassino) are usually referred to the nominal subspecies (De Giuli 1972). The common practice of erecting subspecies based on local samples has been well-criticised by Groves (1986), and recently by Forsten (1998, 1999), since they have a point-like distribution in space and time and they may not represent geographically isolated populations of the same species. However, the use of the subspecies category is still broadly accepted in the fossil horse studies. Recently, Caloi (1997) made the rather exaggerated suggestion that every good *E. stenorionis* samples should be distinguished from the others by a sub-specific name, stressing its particular palaeoecological adaptations.

Some authors doubted the attribution of some of the above-mentioned samples to *Equus stenorionis*, as this species name has been used collectively for most of the Plio-Pleistocene stenorionid horses and, therefore, presents relatively high metrical and morphological variation. Caloi & Palombo (1987) and Forstén (1999) refer the Venta Micena horse to *Equus altidens* von Reichenau, 1915 or *E. cf. altidens*, while, according to a recent study by Eisenmann (1999), it should be given a full specific rank (*Equus granatensis*). Forsten (1999) tentatively groups the small and/or gracile forms of southern Europe (including the horse material from the Greek localities Líbakos, Krímni and Gerakaroú, previously attributed to *E. stenorionis mygdoniensis* Koufos, 1992) under *E. cf. stehlini* or *E. cf. altidens*. The raised taxonomical problem is difficult to solve, as it is almost impossible to draw objective metrical boundaries between *E. stehlini/altidens* and *E. stenorionis*. The discussion on the specific attribution of the slender stenorionid forms is beyond the scope of this study. To avoid any confusion, I will use the locality names instead of the several taxonomical names proposed, when comparing the available samples.

MATERIAL AND METHODS

The studied material comes from a single site (Site B in Fig. 2, excavation of the year 1982). The Site D (Fig. 2, excavation of the year 1991) also yielded an inadequate number of badly preserved equid remains (mainly a proximal and a distal tibia fragment) that do not differ either morphologically or metrically from those of the Site B. However, they have been excluded from the statistical sample, as they possibly come from a different level. The morphological and metrical comparisons are based mainly on equid material from the collections of the Natural History Museum of Basel, Switzerland, and on bibliographical data. The studied specimens are described and measured according to the suggestions of Eisenmann *et al.* (1988). All measurements are given in mm, with an accuracy of one decimal digit. Inaccurate measurements (in case of bad preservation) are given without decimals and/or in parentheses. The Greek locality names are transcribed accented, to help to their correct pronunciation.

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
 Family EQUIDAE Gray, 1821
 Subfamily EQUINAE Gray, 1821
 Genus *Equus* Linnaeus, 1758

Equus stenorionis Cocchi, 1867

MATERIAL EXAMINED. — Isolated teeth and fragmentary material are not given in the list. Cranium part with the M3 sin. (Σ -104); cranium part (cranial roof, zygomaticum, nasals) (Σ -246); cranium part with C sin., I2-I3 sin., I2-I3 dex., P2-M3 sin., P2-P4 dex. (Σ -203); part of maxilla with M3 sin. (Σ -71); maxilla with P2-M2 sin. (Σ -170); maxilla with P2-M3 sin. (Σ -194); maxilla with P2-M3 dex. (Σ -199); ossa praemaxillaria (Σ -299); maxilla with DM1-PM2 sin. (Σ -380); maxilla with DM1-DM4 dex. and DM2-DM4 sin. (Σ -383); part of maxilla with C sin. (Σ -404); maxilla with PM3-M3 dex. (Σ -946); ossa praemaxillaria (Σ -947); part of maxilla with M3 dex. (Σ -953); ossa praemaxillaria with I1-I3 dex., I1-I3 sin. and C sin. (Σ -1028); maxilla with P3-M1 dex. (Σ -1029); maxilla with M1-M2 sin. (Σ -1203); part of maxilla with M3 sin. (Σ -1207); maxilla with P3-M3 sin. (Σ -1220); right

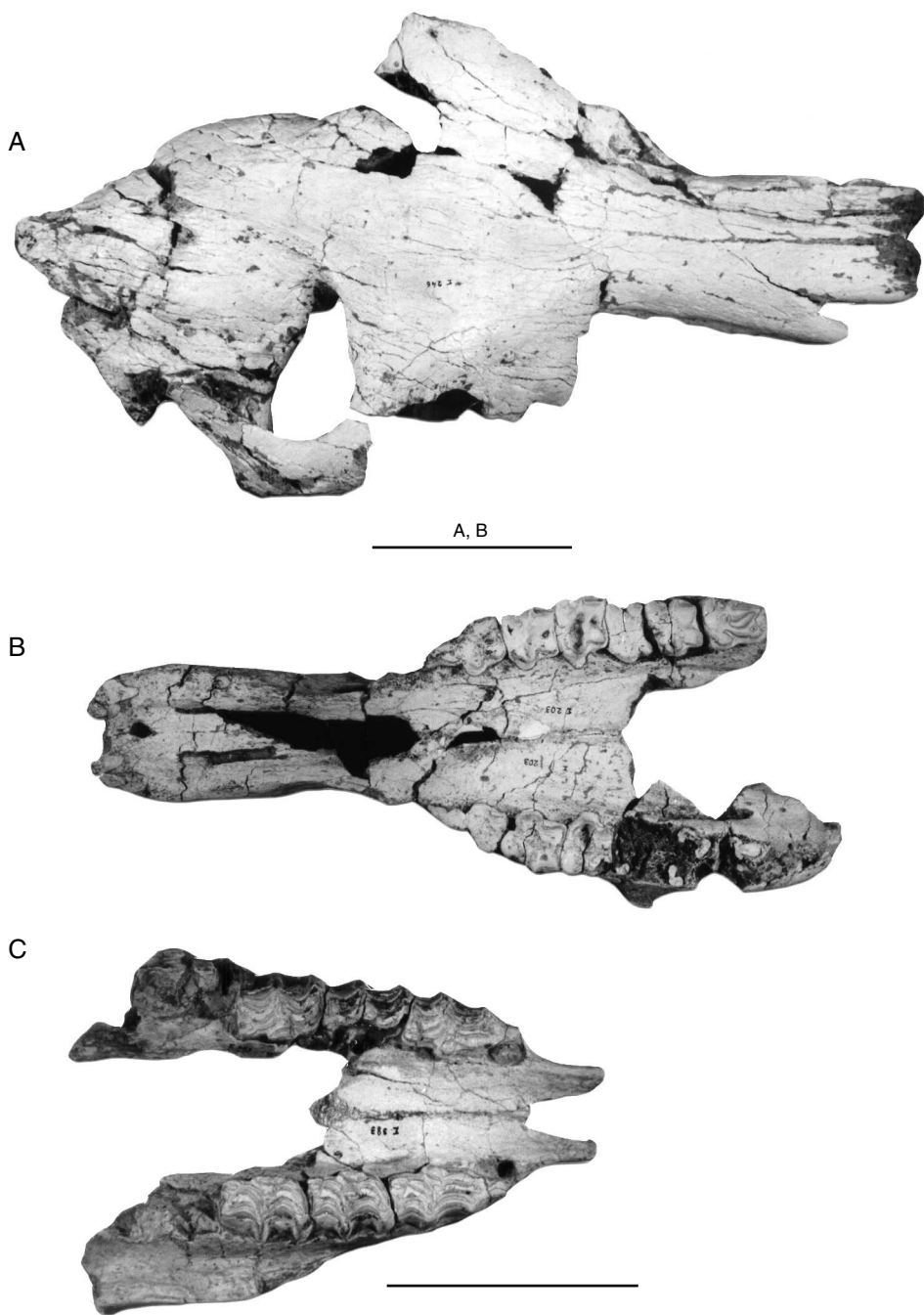


FIG. 3. — *Equus stenonis* from Sésklo; **A**, cranium part (Σ-246), dorsal view; **B**, cranium part of a very aged individual (Σ-203), ventral view; **C**, maxilla of a juvenile individual (Σ-383), ventral view. Scale bars: 100 mm.

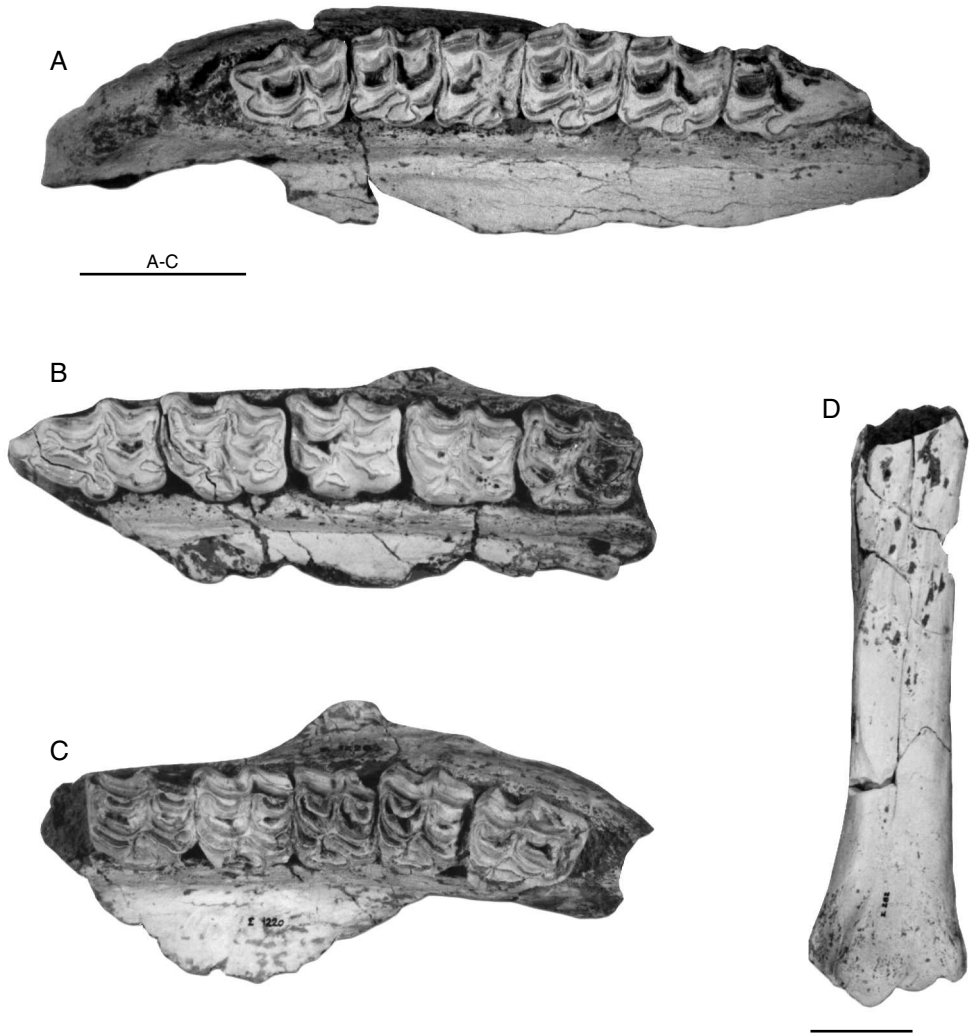


FIG. 4. — *Equus stenonis* Cocchi, 1867 from Sésklo; **A**, right maxilla (Σ -199) with P2-M3; **B**, left maxilla (Σ -170) with P2-M2; **C**, left maxilla (Σ -1220) with P3-M3; **D**, right tibia (Σ -282). Scale bars: 50 mm.

mandibular ramus with dm4-m1 (Σ -441); part of left mandibular ramus with dm3/4 (Σ -951); mandibula with il-i3, c, p2-m3 (Σ -1026); left mandibular ramus with dm1-dm3 (Σ -1027); right mandibular ramus with dm3-dm4 (Σ -1130); left mandibular ramus with dm2-dm3 (Σ -1226); atlas (Σ -39, Σ -248, Σ -1304, Σ -1314, Σ -1324); atlas, epistropheus (Σ -16, Σ -253); vertebrae cervicales (Σ -102, Σ -251, Σ -949, Σ -1301, Σ -1303, Σ -1306, Σ -1310); part of scapula, proximal part of humerus sin. (Σ -1237); proximal part of humerus sin. (Σ -1236, Σ -1247); distal part of humerus sin. (Σ -166, Σ -210, Σ -281, Σ -315, Σ -342); distal part of humerus dex. (Σ -209, Σ -211, Σ -265,

Σ -666, Σ -667, Σ -668, Σ -1031, Σ -1235); parts of humerus, radius and ulna sin. (Σ -99, Σ -356); proximal part of radius sin. (Σ -352, Σ -672, Σ -1238, Σ -1241); proximal part of radius dex. (Σ -333, Σ -671, Σ -673, Σ -1032); distal part of radius sin. (Σ -86, Σ -373, Σ -375, Σ -376, Σ -663, Σ -665, Σ -930); distal part of radius dex. (Σ -662, Σ -664, Σ -1240, Σ -376); distal part of radius, os capitatum, os trapezoideum dex. (Σ -468); distal parts of radius and ulna, ossa carpi dex. of a juvenile individual (Σ -477); os lunatum sin. (Σ -621); ossa metacarpalia II, III, IV dex. (Σ -87); proximal parts of ossa metacarpalia II, III, IV sin. (Σ -336, Σ -578); proximal parts of ossa metacarpalia II, III, IV dex. (Σ -206);

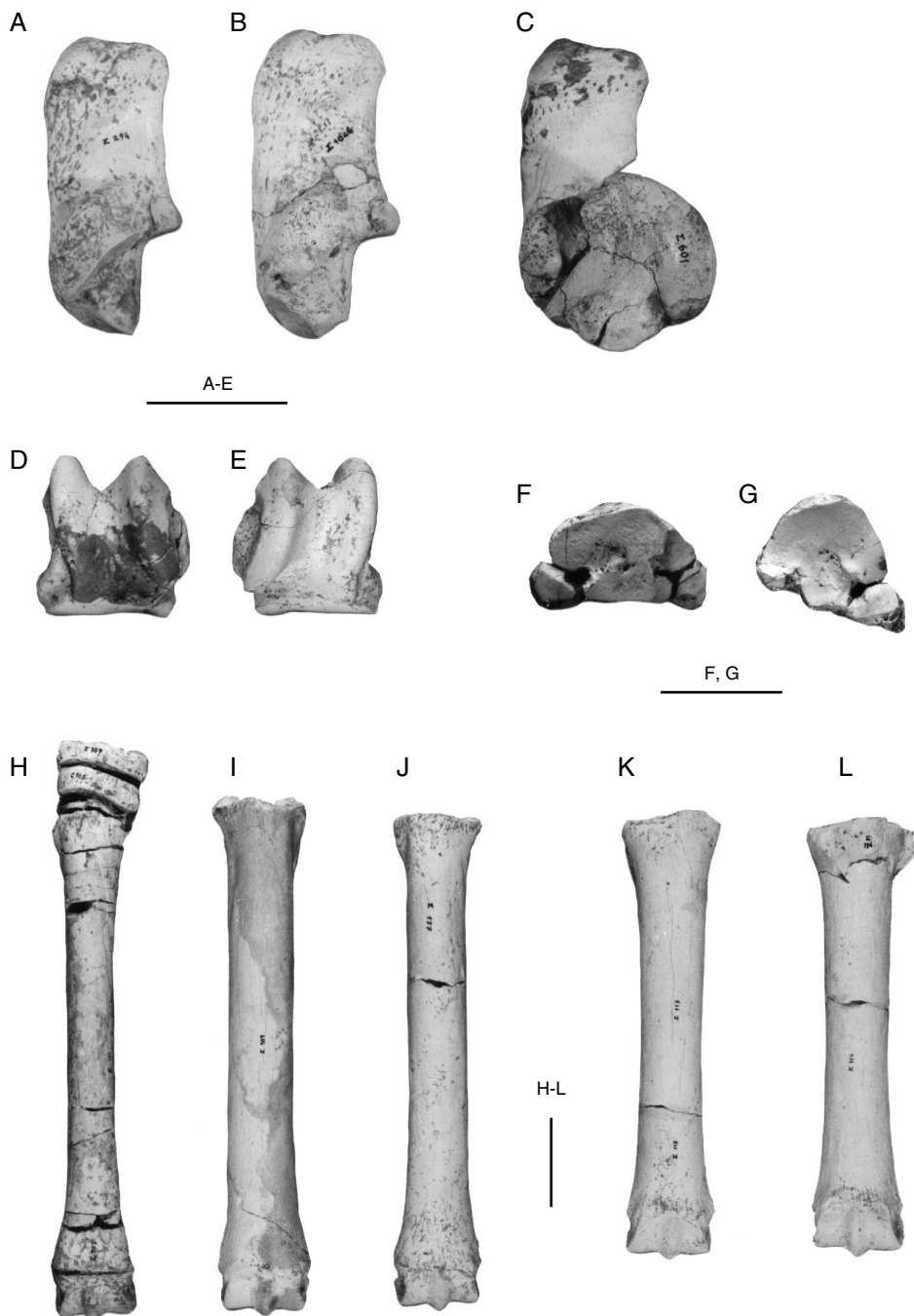


FIG. 5. — *Equus stenonis* Cocchi, 1867 from Sésklo; **A**, left calcaneum (Σ -294); **B**, left calcaneum (Σ -1046); **C**, left calcaneum and astragalus (Σ -601); **D**, left astragalus (Σ -188); **E**, right astragalus (Σ -615); **F**, proximal articulation of the right metacarpals II-IV (Σ -206); **G**, proximal articulation of the right metatarsals III-IV (Σ -244); **H**, right tarsals (navicular, cuboid and cuneiforms) and metatarsals II-IV of a juvenile individual (Σ -107); **I**, left metatarsals II-IV (Σ -109); **J**, right metatarsal III (Σ -177); **K**, left metacarpals II-III (Σ -113); **L**, left metacarpals III-IV (Σ -114). Scale bars: 50 mm.

ossa metacarpalia II, III sin. (Σ-108, Σ-113); ossa metacarpalia III, IV sin. (Σ-114); proximal parts of ossa metacarpalia II, III sin. (Σ-125, Σ-128, Σ-143); proximal parts of ossa metacarpalia II, III dex. (Σ-36, Σ-309, Σ-551); proximal parts of ossa metacarpalia III, IV sin. (Σ-142, Σ-147); proximal part of os metacarpale III sin. (Σ-69, Σ-127, Σ-137, Σ-138, Σ-329, Σ-409, Σ-588, Σ-1253, Σ-1254, Σ-1255); proximal part of os metacarpale III dex. (Σ-64, Σ-140, Σ-310, Σ-579, Σ-964); distal part of os metacarpale III sin. (Σ-118, Σ-119, Σ-121, Σ-122, Σ-123, Σ-124, Σ-130, Σ-164, Σ-317, Σ-1219); distal part of os metacarpale III dex. (Σ-106, Σ-117, Σ-134, Σ-165, Σ-205, Σ-303, Σ-307, Σ-311, Σ-583, Σ-584, Σ-585); distal part of os metacarpale III (Σ-120); distal part of os metacarpale III, phalanx proximalis, phalanx media, phalanx distalis sin. (Σ-153); os sesamoideum phalangis proximalis (Σ-624); phalanx proximalis sin. (Σ-353); phalanx proximalis dex. (Σ-88, Σ-1005); phalanx proximalis (Σ-1003); distal part of phalanx proximalis (Σ-622); phalanx media sin. (Σ-204); phalanx media dex. (Σ-89); phalanx media, phalanx distalis sin. (Σ-979); phalanx media, phalanx distalis dex. (Σ-180); phalanx distalis dex. (Σ-604, Σ-634); os coxae dex. (Σ-45, Σ-59, Σ-219, Σ-941, Σ-963, Σ-1336, Σ-1338, Σ-1344); os coxae sin. (Σ-51, Σ-220, Σ-1050, Σ-1313, Σ-1330); proximal part of femur dex. (Σ-231, Σ-351); distal part of femur sin. (Σ-705); distal part of femur dex. (Σ-212, Σ-374, Σ-1246); proximal part of tibia sin. (Σ-234, Σ-1244, Σ-2016); distal part of tibia sin. (Σ-61, Σ-223, Σ-264, Σ-332, Σ-334, Σ-360, Σ-361, Σ-378, Σ-381, Σ-650, Σ-653, Σ-654, Σ-655, Σ-657, Σ-659, Σ-660, Σ-661, Σ-1250, Σ-2012); distal part of tibia dex. (Σ-52, Σ-237, Σ-282, Σ-316, Σ-348, Σ-349, Σ-362, Σ-606, Σ-651, Σ-652, Σ-656, Σ-658); distal part of tibia, astragalus sin. of a juvenile individual (Σ-18); distal part of tibia, astragalus, calcaneum dex. of a juvenile individual (Σ-345); distal part of tibia, astragalus, calcaneum, os naviculare, os cuboideum, os cuneiforme mediale, os cuneiforme laterale, ossa metatarsalia II, III, IV dex. (Σ-363); distal part of tibia, astragalus, calcaneum, os naviculare, os cuboideum, os cuneiforme mediale, os cuneiforme laterale sin. (Σ-1251); astragalus, calcaneum, os naviculare, os cuboideum, os cuneiforme mediale, os cuneiforme laterale, proximal parts of the ossa metatarsalia II, III, IV sin. (Σ-22); os naviculare, os cuboideum, os cuneiforme mediale, os cuneiforme laterale, ossa metatarsalia II, III, IV dex. (Σ-107, Σ-115); astragalus, calcaneum, os naviculare, os cuboideum, os cuneiforme mediale, os cuneiforme laterale dex. (Σ-625); astragalus sin. (Σ-188, Σ-228, Σ-250, Σ-312, Σ-611, Σ-612, Σ-613, Σ-614, Σ-1034); astragalus dex. (Σ-226, Σ-227, Σ-238, Σ-284, Σ-301, Σ-323, Σ-609, Σ-615, Σ-634, Σ-1030); astragalus, calcaneum sin. (Σ-502, Σ-601); astragalus, calcaneum dex. (Σ-608); calcaneum sin. (Σ-57, Σ-294, Σ-377, Σ-504, Σ-505, Σ-600, Σ-610, Σ-617, Σ-1046); calcaneum dex. (Σ-193, Σ-215, Σ-239, Σ-616, Σ-635); os naviculare sin. (Σ-236,

Σ-298, Σ-976); os naviculare, os cuboideum, os cuneiforme mediale, os cuneiforme laterale dex. (Σ-240); os cuneiforme mediale sin. (Σ-695); os cuneiforme laterale sin. (Σ-977); os cuneiforme laterale dex. (Σ-337); ossa metatarsalia II-IV sin. (Σ-109); os metatarsale III sin. (Σ-112, Σ-202); os metatarsale III dex. (Σ-126, Σ-177, Σ-192); proximal parts of ossa metatarsalia II-IV sin. (Σ-149, Σ-144, Σ-160); proximal parts of ossa metatarsalia II-IV dex. (Σ-47); proximal parts of ossa metatarsalia III-IV dex. (Σ-244); proximal part of os metatarsale III sin. (Σ-65, Σ-141, Σ-218, Σ-225, Σ-267, Σ-283, Σ-314, Σ-577); proximal part of os metatarsale III dex. (Σ-150, Σ-151, Σ-352, Σ-353, Σ-571, Σ-1252); distal part of os metatarsale III sin. (Σ-116, Σ-129, Σ-136, Σ-187, Σ-201, Σ-308, Σ-581, Σ-582, Σ-586, Σ-1045, Σ-1218, Σ-1256); distal part of os metatarsale III dex. (Σ-105, Σ-135, Σ-587, Σ-982); distal part of os metatarsale III (Σ-983, Σ-1257); distal part of os metatarsale III, phalanx proximalis, phalanx media, phalanx distalis, ossa sesamoidea phalangis proximalis, sin. (Σ-157); distal part of os metatarsale III, phalanx proximalis, phalanx media, dex. (Σ-981); os sesamoideum phalangis proximalis (Σ-182); phalanx proximalis sin. (Σ-602, Σ-1042); proximal part of phalanx proximalis (Σ-605, Σ-980, Σ-1043, Σ-1044, Σ-1262, Σ-1266, Σ-1280); phalanx proximalis, phalanx media dex. (Σ-326); phalanx media sin. (Σ-295, Σ-603); phalanx media, phalanx distalis dex. (Σ-620); phalanx distalis sin. (Σ-186, Σ-318, Σ-982); phalanx distalis dex. (Σ-321, Σ-1263); phalanx distalis (Σ-340, Σ-341, Σ-623, Σ-978).

MATERIAL CONSERVATION. — The material listed above belongs to the collections of the Museum of Geology and Palaeontology, National and Kapodistrian University of Athens, Greece.

LOCALITY. — Sésklo (Magnesia, Thessaly, Greece).

AGE. — Late Pliocene (lower MN17).

DESCRIPTION

Skull

The cranial morphology is known from three fairly well-preserved parts of skulls. At least two of them belong to aged individuals. The general aspect is that of a very large, relatively flat and elongated skull (Table 1; Fig. 3A). Its total length, from the prosthion to the supraoccipital crest, is estimated to 65 cm (combined measurement on Σ-203 and Σ-246), being one of the largest horse skulls. The neurocranium is relatively small. The temporal lines are very low and blunt. The frontal is broad. The nasals form a wide groove along their fairly plicate suture. The praemaxillaries and the nasal notch are very long, extending backwards to the area above P3 (combined observation

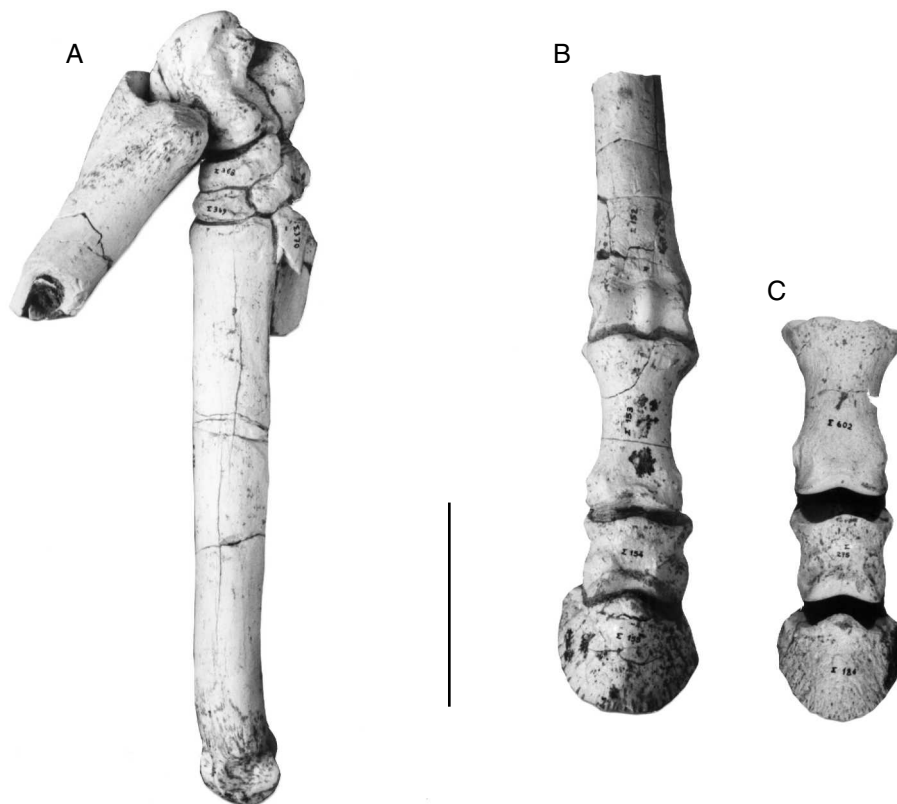


FIG. 6. — *Equus stenonis* Cocchi, 1867 from Sésklo; **A**, right tibia, calcaneum, astragalus, navicular, cuboid, cuneiforms and metatarsals II-IV (Σ -363); **B**, left distal metacarpal part, proximal, medial and distal phalanges (Σ -153); **C**, left posterior proximal (Σ -602), medial (Σ -295) and distal (Σ -186) phalanges. Scale bar: 100 mm.

on the available specimens). The upper cranial profile is slightly concave at the nasal region, while it is convex at the frontal region (above the orbits) and above the distal end of the nasal notch. The zygomatic arch is directed distally slightly towards the sagittal plane (it is not parallel to it).

Mandible

The mandible material consists of five small mandibular parts that belong to juvenile individuals and an almost complete (it only lacks the ascending rami) and well-preserved mandible (Σ -1026; already published by Symeonidis 1992: table I) of an adult individual. The latter has relatively big dimensions (Table 2) and it is very robust, especially in the symphysis region. The muzzle region is laterally compressed.

Upper dentition

The studied material contains an adequate number of upper tooththrows and isolated teeth of the permanent and deciduous dentition (Table 3; Fig. 4A-C). Specimens belonging to individuals of different ages, from relatively young to very aged, are available. The former are very hypsodont. The hypsodonty index (according to Eisenmann *et al.* 1988) for the almost unworn non-isolated teeth (premolars of the maxilla Σ -170) cannot be calculated, as the tooth length at the middle of the crown is not accurately measurable. However it can be estimated to 43-45 for the P3 and to 38 for the P4. The hypsodonty index for an isolated P2 is 80; for an M3 it is 48. The styles of the buccal side of both molars and premolars are narrow (especially the mesostyle); no groove is observed on them.

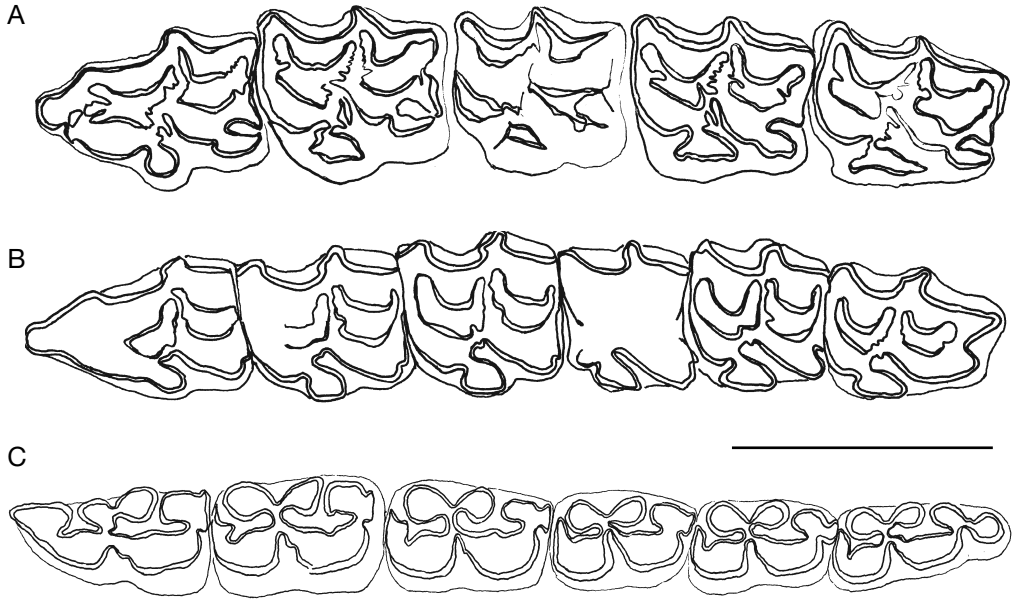


FIG. 7. — The occlusal surfaces of the *Equus stenonis* Cocchi, 1867 from Sésklo; **A**, the upper tooththrow of a young individual (Σ -170); **B**, the upper tooththrow of an aged individual (Σ -194); **C**, the lower tooththrow of an adult individual (Σ -1026). Scale bar: 50 mm.

The enamel plication is simple (Table 4; Fig. 7A, B). More intense enamel plication is, though, observed in the almost unworn teeth. A pli caballin is always present and well-developed in the unworn and moderately worn teeth (stages of wear 1-3), while it is absent in some worn ones. Its length is much greater in the fresh teeth (stage of wear 1). The number of plications (counted according to Eisenmann *et al.* 1988) is given in the Table 4. The low mean total number of the fosse-plications – four for the premolars and six for the molars – is typical for the species (Eisenmann 1980).

The generally short protocone is triangular, with straight or slightly convex lingual border, in the almost unworn teeth (it is elongated in the fresh M3 of Σ -946, as well as in the fairly worn molars of the Σ -1220), but it becomes more elliptical to round in the very worn ones. It generally resembles the morphology of Type 3 of Eisenmann *et al.* (1988: fig. 6A) or that of Type 7 in some cases (molars of Σ -1220). The protocone index is generally lower of 40 (except for the M1 and M2 of the maxilla Σ -1220 and the M2 of Σ -170), a

value that is considered by Gromova (1949a) as the upper limit for *Equus stenonis*. This is also the case for the mean values of the samples of Saint-Vallier, Senèze and La Puebla de Valverde, where, however, the maximal values reach as high as 48 (Eisenmann 1980: tables 56-58). The index of M1 is always higher than that of P4. The hypoconal groove is well-developed in the premolars and the M2 except for the worn ones. Occasionally (Σ -1029, Σ -1220) a hypoconal islet is formed instead. The postfossette is always closed.

The incisors are preserved in two specimens. One (Σ -203, Fig. 3B) belongs to a very old individual; all teeth, including the incisors, are almost totally worn out. On the contrary, the other (Σ -1208) belongs to a very young one; the incisors and the preserved canine are only slightly worn. The enamel islets on the incisor occlusal surface are much developed. Their form is very simple, without any plication. The presence of a canine indicates a male individual.

The deciduous dentition is known from a complete maxilla (Σ -383, Fig. 3C) and several isolated

molars (Σ -1211-1215, plausibly belonging to the same individual) of the same morphology. The deciduous molars are easily recognised by their relatively elongated occlusal surface, the thinner enamel and their small height. They have big dimensions; DM2-DM4 length measures 118 mm in Σ -383, which is slightly larger than a specimen from Saint-Vallier (about 115 mm) figured by Viret (1954: pl. 29-3), as well as than the specimens from Senèze (103-105 mm; Basel collection) and Gerakarou (103-114 mm; Koufos 1992). Concerning the enamel morphology, they do not differ from the permanent ones. The plications are few and the protocones short. A progressive lengthening of the protocone is observed from DM2 to DM4. The right DM1 is present in Σ -383, while the presence of the left one is indicated by its empty socket. This specimen bears the only indication for the presence of this tooth. The area in front of P2 is not preserved in most of the other available maxillae mentioned above, with the exception of some specimens that belong to aged individuals, which would not retain this tooth, if any, at that age. So the constant presence of the DM1 in the horse sample from Sésκλο cannot be confirmed.

Lower dentition

The existing lower dentition specimens are very few, compared to the rest of the equid material of the locality. The permanent dentition is only known from the complete mandible Σ -1026. There are also five deciduous dentition fragments. The permanent dentition belongs to a rather aged animal. The incisor occlusal surface is trapezoidal in shape (due to wear) and it lacks any enamel islets. There is no trace of a dm1. The cheek teeth morphology is clearly of stenonid type (Fig. 7C). The lobes of the double knot are almost parallel to the longitudinal axis of the tooth; their lingual border is always convex, as well as the labial borders of the protoconid and the hypoconid (except for the hypoconid of the p2, especially of the right one, which is almost straight). The ectoflexid is not very deep; it reaches the base of the isthmus in the

molars and it is a little shorter in the premolars. One should mention the small difference between molars and premolars concerning its depth. The linguaflexid is small and pointed; it has the same morphology in all cheek teeth. There is a well-developed pli caballinid in all premolars, while it is absent or vestigial in molars. No protostylid is observed. The total length of the toothrow is 191 mm. The total length of the premolars and the molars is 102 mm and 89 mm respectively. The hypsodonty of the lower teeth is not well-known. An almost unworn m1 in the juvenile mandible Σ -441 is 63 mm high, corresponding to a hypsodonty index of about 50 or lower. The lower cheek dimensions are given in Table 5.

The deciduous molars do not essentially differ in the enamel morphology compared to the permanent ones. However, the ectoflexid is much deeper, penetrating the isthmus of the double knot (it reaches the linguaflexid in dm4). The deciduous molars are also more elongated (Table 5). The total length of the deciduous toothrow (dm2-dm4) equals about 110-111 mm (combined measurement on the specimens Σ -1027 and Σ -1130 that presumably belong to the same individual), which is a little higher or comparable to the lengths measured in Senèze (102.5-110.5; Prat 1980) and Gerakarou (108 mm; Koufos 1992) and a little lower than the lengths given by Viret (1954) for Saint-Vallier (111-116 mm). A pli caballinid and a protostylid are observed in all teeth. A dm1 of small size is present in one specimen. It is not known if this tooth was present in the rest of the juvenile mandibles, as the area in front of dm2 is not preserved in anyone of them.

Postcranial material

The postcranial skeleton is known from a great number of limb bones, as well as from several vertebrae and some rib fragments. The limb bones are very long.

The humerus and radius (Tables 6; 7) are represented in the material by numerous parts (there is no complete bone). Their morphology is typically equid, showing no special anatomical charac-

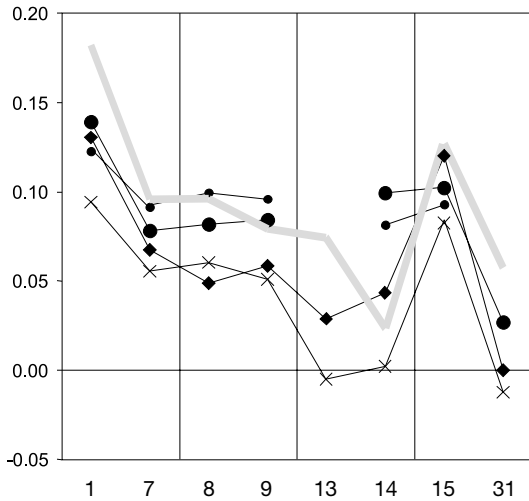


FIG. 8. — Logarithmic ratio diagram comparing the cranium measurements of horse samples from Sésκλο and other localities; —●—, Saint-Vallier, n = 1, Eisenmann (1980); —◆—, Senèze, n = 1-3, Basel collection; —●—, La Puebla de Valverde, n = 1-2, Eisenmann (1980); —x—, Gerakarou, n = 2-10, Koufos (1992); —■—, Sésκλο, n = 1-4. Standard: *Equus hemionus* Pallas, 1775, Eisenmann (1980).

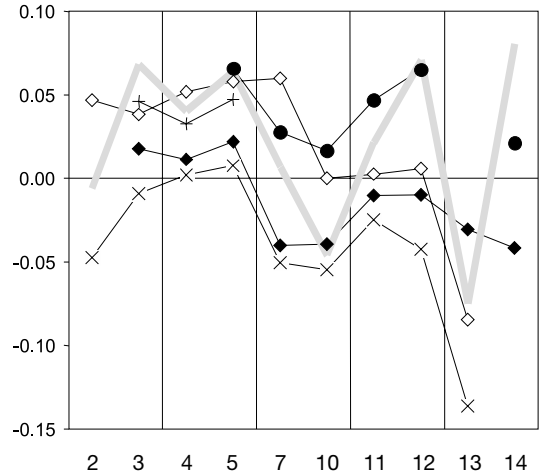


FIG. 9. — Logarithmic ratio diagram comparing the mandibular measurements of horse samples from Sésκλο and other localities; —●—, Saint-Vallier, n = 2-4, Viret (1954); —◆—, Senèze, n = 1-5, Basel collection; —x—, Gerakarou, n = 1-10, Koufos (1992); —+—, Dafneró, n = 1-2, Koufos & Kostopoulos (1993); —◇—, Vólax, n = 1, Koufos & Vlachou (1997); —■—, Sésκλο, n = 1. Standard: sample from Valdarno, n = 1-7, Basel collection.

ters. The proximal part of the humerus is hardly known, as it is represented by only three badly preserved specimens. The distal part has large dimensions that equal those measured on specimens from Saint-Vallier (Basel collection) and those given by Viret (1954: 146) and Prat (1980: table 24) for the same locality. The specimens from Vólax (Koufos & Vlachou 1997) have also comparable dimensions (but somewhat more compressed trochlea). The specimens from Gerakarou (Koufos 1992) are distinctly smaller. The proximal and distal parts of the radius are almost equally represented in the material. Most of the specimens are very well-preserved; the proximal part of the ulna in natural position is also preserved on two of them; in one case it is fused to the radius.

The carpal bones are rather few: there are only three isolated bones, a magnum, a trapezoid (both belonging to the same individual) and a lunatum, as well as one complete carpus of a juvenile individual (Σ -477). The DAP and DT of the proximal articular surface of the magnum measure 39.4 and about 47 mm respectively.

The same measures for the distal articulation are 35.3 and 45.0 mm. The trapezoid is broken and it cannot be measured. The lunatum is relatively small; its maximal height (measured on the anterior surface) is 28.2 mm and its maximal width (DT) on the proximal articular surface is 32.5 mm. Their dimensions and morphology are very similar to those of specimens from Saint-Vallier and Senèze (Basel collection).

The metacarpal III (Table 8; Fig. 5F, K, L) is one of the best-represented bones in the sample, making it statistically more interesting. There are 45 specimens of adult individuals, but only four of them are complete. Three more specimens are juvenile. They are relatively robust, although they are not generally so stout as the metacarpals from western European localities. The lateral metacarpals are fused to the third metacarpal in some specimens (six of the totally 23 proximal parts). The distal part has moderately developed keel and sharp supra-articular fossae, which is in accordance with the morphology of *Equus*

stenonis (Gromova 1949a; De Giuli 1972). The mean distal supra-articular breadth is slightly higher than the mean distal articular breadth. The morphology of the small articular facets for the carpals and the lateral metacarpals is very variable and the borders among them are often not very clear (dull). This indicates that the corresponding measurements (8 and 9) have no statistical importance, as they are considerably variable.

The femur (Table 9) is the most uncommon long bone of the studied material. The tibia (Table 10; Fig. 4D) is on the contrary represented by numerous specimens, almost exclusively of the distal part of the bone (the fragile proximal part is anyway rare as a fossil). No complete femur or tibia is found in the material. Both bones present typical equid morphology.

The calcaneum and the astragalus (Tables 11; 12; Fig. 5A-E) are the most common tarsals; each is represented by 15-20 fairly well-preserved specimens. The calcaneum possesses a moderately developed epiphysse (caput). In general it is much less robust than the caballoid calcaneum.

The astragalus shows characters that have been considered diagnostic for *Equus stenonis* (Gromova 1949a; Prat 1980) and clearly distinguish them from the typical caballoid morphology of the bone: a) the articulation for the calcaneum is accomplished by three surfaces, instead of four; b) the lateral keel of the trochlea is distally less developed; c) in all specimens the medial keel of the trochlea turns out distally to a tubercle that is rarely observed in the modern species; d) the tubercle at the proximal end of the medial keel of the trochlea is moderately developed; e) the articular surfaces for the navicular and the cuboid form a very high edge between them. De Giuli (1972) states that the characters of the articular surfaces are not diagnostic. However, all studied specimens show high morphological similarity. The general appearance of the bone is rather narrow. The maximal height is comparable to the maximal breadth (the mean ratio of these two measurements is 0.96, ranging from 0.91 to 1.05).

The rest of the tarsal bones are found mainly in articulation with the adjacent tarsals and metatarsals (Σ -240, Σ -363, Σ -625 and Σ -1251). There are also some isolated ones. In one case (Σ -240), the cuboid and the lateral cuneiform are fused together.

The metatarsals III (Table 13; Figs 5G-J; 6A) are morphologically similar to the metacarpals (they have long diaphyses, moderately developed keel, sharp supra-articular fossae), with some differences, such as the more circular cross section at their proximal part and the flexion of the distal part towards the rear (a major criterion for the discrimination of distal metapodial fragments). They are also absolutely longer; the ratio of the mean maximal height of the third metacarpal to that of the third metatarsal is 86.4%. The supra-articular tuberosities are well-developed; the distal supra-articular breadth is generally higher than the distal articular breadth. No fusion between the third and the lateral metatarsals is observed.

The proximal phalanges (Table 14; Fig. 6B, C) are characterised by the very sharp *trigonum phalangis* (the so-called "V-scar"), which is not very much developed towards the distal part of the bone. This has been considered as a primitive character that distinguishes the stenonid from the caballoid horses (Sondaar 1968; De Giuli 1972; Forsten 1975); however, Forsten (pers. comm.) recently doubted this distinction. The anterior proximal phalanges are in general higher, stouter and they have more symmetrical proximal articulation. The posterior ones are laterally more concave, having larger proximal articulation and more slender shaft, while the distal supra-articular tuberosities have a higher position on the bone.

The medial phalanges (Table 15; Fig. 6B, C) are short and robust, especially the anterior ones. The posterior ones are longer and narrower distally, having a more trapezoid aspect. A metrical comparison to other known specimens does not show any significant differences in the total height. In the measurements of breadth the material from Sésklo is clearly smaller than Saint-Vallier but generally larger than Senèze.

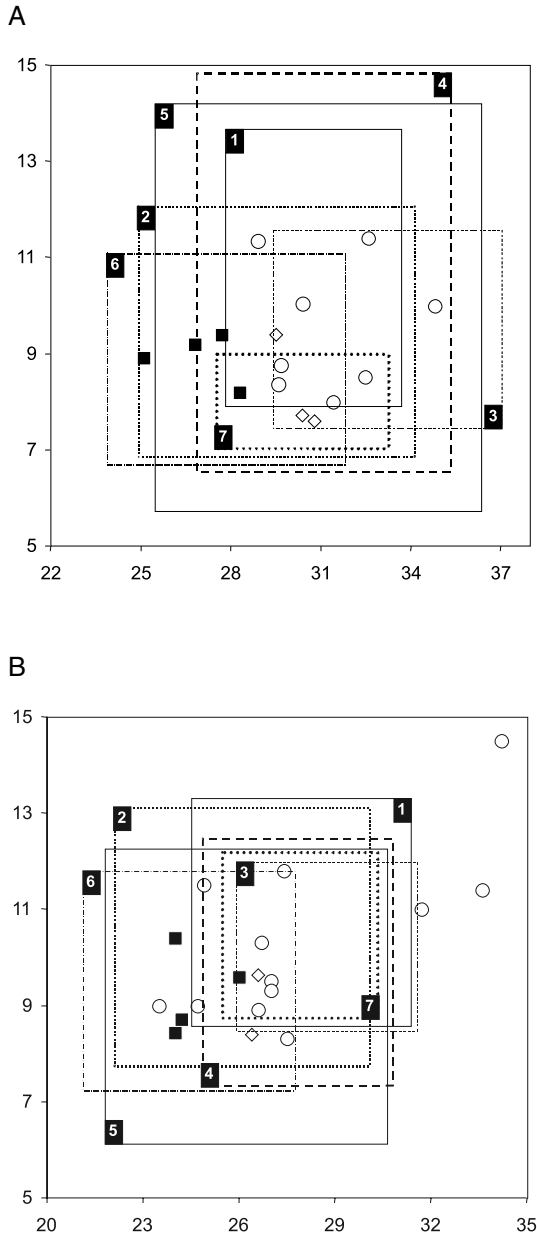


FIG. 10. — Scatter-diagrams of premolar (A) and molar (B) occlusal length (x-coordinate) to protocone length (y-coordinate) of several horse samples; ■ Valdarno, Basel collection; ◇, Vólax, Koufos & Vlachou (1997); O, Sésklo. The numbered squares represent the measurement ranges from Saint-Vallier (1), Senèze (2), La Puebla de Valverde (3), Chilhac (4), Venta Micena (5), Libakos & Gerakarou (6) and Dafneró (7), according to Eisenmann (1980), Boeuf (1983, 1986), Marin (1987), Steensma (1988), Koufos (1992) and Koufos & Kostopoulos (1993), respectively.

The distal phalanges (Table 16; Fig. 6B, C) are rather wide, generally wider and more robust compared to other *E. stenorhis* specimens, except for those from Saint-Vallier and Chilhac (also Senèze for the posterior ones). The posterior ones are narrower, more pointed anteriorly and generally smaller than the anterior ones. The proximal, medial and distal phalanges were discriminated to anterior and posterior according to the criteria given by Prat (1957), Förster (1960), Eisenmann & De Giuli (1974) and Dive & Eisenmann (1991).

DISCUSSION

The metrical data show that the equid from Sésklo is a large sized *Equus*. The cranial morphology shows many of the typical characters of *E. stenorhis* (generally long snout, deep nasal notch, etc.), as described by Viret (1954), Azzaroli (1965, 1966, 1982, 1990), De Giuli (1972), Prat (1968, 1980) and Koufos (1992). A small difference is observed in the shape of the zygomatic arches, which are slightly inclined distally towards the sagittal plane. The studied material resembles the type skull (IGF-562; Azzaroli 1966: tav. XLIII) and those from Senèze (skull Se-336 of the Basel collection; see also Eisenmann 1980: pl. XI-1) and La Puebla de Valverde (Eisenmann 1980: pl. X-3) in this character. However, some authors (Azzaroli 1965; De Giuli 1972) mention as a specific character of *E. stenorhis* the fact that the zygomatic arch is directed parallel to the sagittal plane (see also Viret 1954: pl. 27). Anyway, the observed difference is not big; also the fact that the only specimen, in which the zygomatic arch is preserved (Σ -246), is fairly compressed and distorted makes this difference less important. The taxonomical importance of this character may be limited, as some intermediate conditions, like the skull Se-553 of the Basel collection (which is juvenile, however, and restored to some extent) or the GER-8 from Gerakarou, also exist. All other cranial characters are common with those of the known representatives of the species.

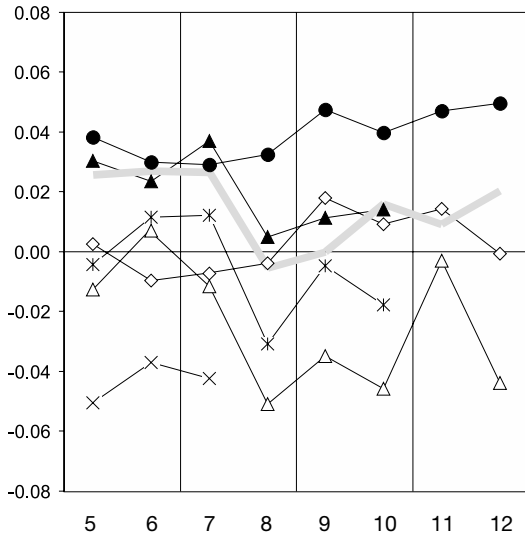


FIG. 11. — Logarithmic ratio diagram comparing radius measurements of horse samples from Sésklo and other localities; —●—, Saint-Vallier, n = 2-4, Basel collection; —▲—, Chilhac, n = 3-4, Boeuf (1983, 1986); *—, Venta Micena, n = 2-7, Marin (1987); —△—, Libakos, n = 4-8, Steensma (1988); —×—, Gerakarou, n = 2, Koufos (1992); —◇—, Vólax, n = 1-3, Koufos & Vlachou (1997); —■—, Sésklo, n = 7-9. Standard: sample from Valdarno, n = 4-6, Basel collection.

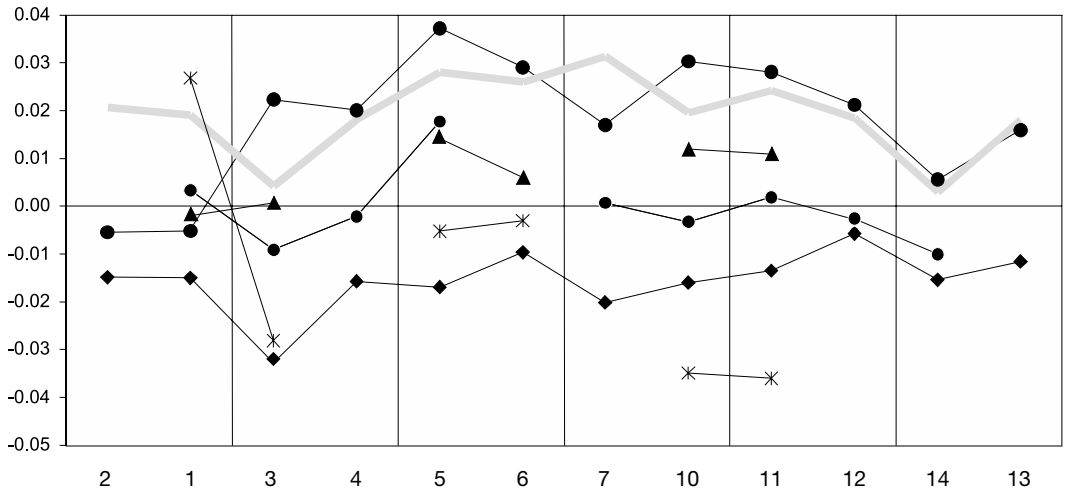
The observed size difference from the other *E. stenonis* populations is rather small (Fig. 8). The studied skulls are among the largest, ranging about the size of the large specimens from Saint-Vallier and La Puebla de Valverde. The biggest differences are observed in the measurements 1 (muzzle length), 13 (palatal breadth) and 31 (cheek length), indicating the very big dimensions of the Sésklo equid skull. On the contrary, a low value was measured for the minimal muzzle breadth (measurement 14), although the maximal muzzle breadth (measurement 15) is the highest. This could be partly explained by a minor distortion of the specimen Σ-203 (the only specimen on which 14 could be measured), as well as by the very old ontogenetical age of the individual to which it belonged. Regarding the measurements of the upper toothrow (7, 8 and 9), where the metrical variation of the several populations is smaller, the horse of Sésklo is placed among the largest samples from Saint-Vallier and La

Puebla de Valverde. Regarding the overall morphology, the studied sample best resembles that of Gerakarou, which is considerably smaller and stratigraphically younger, and that of Senèze (Basel Collection).

Comparing the mandible Σ-1026 to other known specimens of the same species (Fig. 9), it appears to have a rather short and robust snout (relatively low values in the measurements 2 and 13, high value in 14). Considerable difference is observed in the minimal breadth of the symphysis (measurement 14), where the specimen from Sésklo has the highest value (44 mm). Viret (1954: 139) reports an even higher value (48 mm) for the mandible mounted on the skeleton from Senèze in the Muséum of Lyon (however, this mandible does not belong to the skeleton and its stratigraphical provenance is doubtful; Eisenmann 1981: 170). De Giuli (1972) also measures 47 mm on a specimen from Olivola. It seems that there is high individual variation in this variable, considering that the measurable specimens from all localities are very few. The relative narrowness of the muzzle in the area of i3 (measurement 7) is due to a deformation of the specimen at the anterior part of the muzzle.

The upper teeth are typical for *Equus stenonis*, having very few enamel plications and short protocone. The low mean total number of the fossette plications – four for the premolars and six for the molars – is comparable (although generally lower) to the numbers given for other localities, such as Saint-Vallier (8 and 6 respectively; Eisenmann 1980), Senèze (5-6 and 4-5; Eisenmann 1980), La Puebla de Valverde (8-9 and 6-7; Eisenmann 1980), Libakos (5 and 5; Steensma 1988), Dafneró (6 and 6; Koufos & Kostopoulos 1993), Gerakarou (6 and 3; Koufos 1992), Vólax (5 and 6; Koufos & Vlachou 1997). A comparison of the protocone length in relation to the occlusal length of the cheek teeth (Fig. 10) shows a considerable variability in these measurements, mainly because they depend on the wear stage of the teeth. In the case of P3/4 (Fig. 10A) the studied teeth are included in the range of the samples from Venta Micena and Chilhac, while

A



B

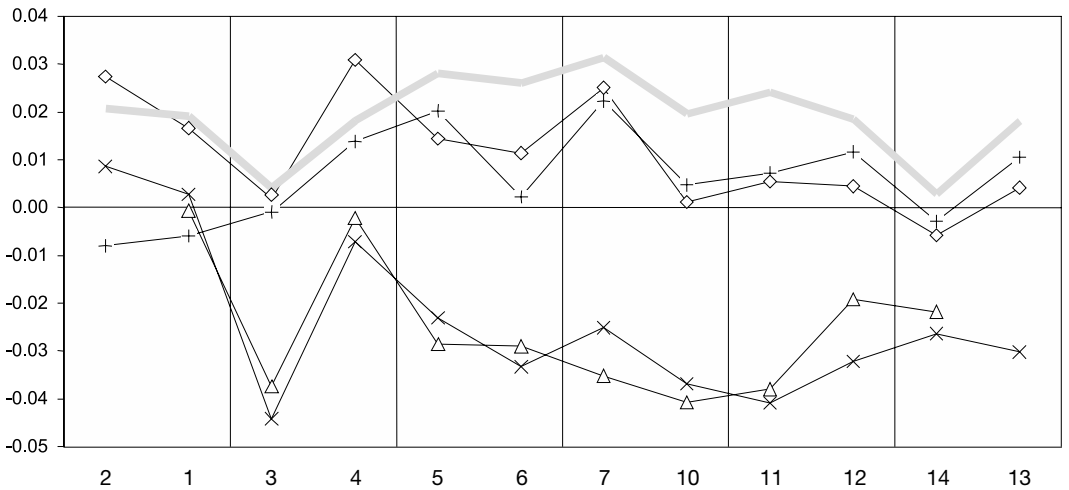


FIG. 12. — Logarithmic ratio diagrams comparing the metacarpal III measurements of the horse sample from Sésklo to those from to West European (A) and Greek (B) localities; —●—, Saint-Vallier, n = 3-5, Basel collection; —◆—, Senèze, n = 4-6, Basel collection; —●—, La Puebla de Valverde, n = 31-59, Eisenmann (1979); —▲—, Chilhac, n = 5-9, Boeuf (1983, 1986); —*—, Venta Micena, n = 13-23, Marin (1987); —△—, Libakos, n = 4-25, Steensma (1988); —*—, Gerakarou, n = 5-14, Koufos (1992); —+—, Dafneró, n = 3-5, Koufos & Kostopoulos (1993); —◇—, Vólax, n = 1-4, Koufos & Vlachou (1997); —■—, Sésklo, n = 4-25. Standard: sample from Valdarno, n = 3, Basel collection.

the ranges of Saint-Vallier, Senèze and La Puebla de Valverde samples also include most of them. Other samples from Greece, as Libakos and Gerakarou, have generally smaller premolars, while the samples from Dafneró and Vólax, two

localities of comparable age to that of Sésklo, have relatively shorter protocones (in part because of the generally advanced stage of wear; Koufos pers. comm.). In the case of M1/2 (Fig. 10B), the studied sample shows a wider dis-

persion; however, the aberrant points represent slightly worn molars. The molar samples from Senèze, Chilhac, Dafneró and Venta Micena correspond fairly well to the studied material.

The main morphological characters of the lower permanent teeth (shape of the double knot and the ectoflexid) are quite similar to those typical of *Equus stenonis* (Viret 1954; De Giuli 1972; Eisenmann 1981). A metrical comparison of the tooththrow length (Fig. 9) shows that the one available specimen Σ -1026 resembles the specimens from Dafneró, as well as those from Vólax and Saint-Vallier.

The radius specimens are of large size, comparable to those from Saint-Vallier and Chilhac (Fig. 11). The latter has values practically equal to the sample of Sésklo, while Saint-Vallier shows relatively higher distal epiphysis values. The specimens of Líbakos and Gerakaróú are clearly of smaller size.

The third metacarpals from Sésklo, although relatively robust, are more slender compared to those of Valdarno, Saint-Vallier, Chilhac and Dafneró, while they are more robust than those of the chronologically younger populations of Venta Micena, Líbakos and Gerakaróú. The relative robustness of the compared samples can be graphically seen in the ratio diagrams for the third metacarpal (Fig. 12), where it is represented by the inclination of the lines connecting the points of the measurements 1 and 3. Similar to the sample from Sésklo are the samples from La Puebla de Valverde, Senèze and Vólax, as the corresponding lines in the diagram are parallel. Vólax sample is also metrically equal to Sésklo, while the other two samples have smaller dimensions. In the same ratio diagrams of Fig. 12, Sésklo shows very high values for most of the measurements, especially those of the height, suggesting a considerably big animal (some higher values are, however, reported from Olivola; De Giuli 1972). Also the epiphyseal measurements are high and close to those of Saint-Vallier (some maximal values are even higher than the maximal of Saint-Vallier). Morphologically, the studied sample has affini-

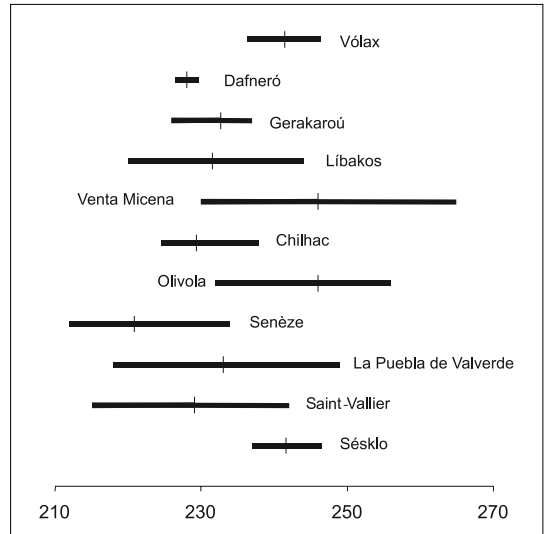


Fig. 13. — Comparison of the third metacarpal maximal length of several horse samples. The metrical variation and the mean (cross) are given for each sample. Data from the Basel collection and according to De Giuli (1972), Eisenmann (1979), Prat (1980), Boeuf (1983, 1986), Marin (1987), Steensma (1988), Koufos (1992), Koufos & Kostopoulos (1993) and Koufos & Vlachou (1997).

ties to those from Vólax, La Puebla de Valverde and Senèze, as their lines in the diagram are almost parallel. Dafneró is also similar in many measurements, but the metacarpals from this locality are shorter. A comparison of the metacarpal length (measurement 1) from several localities (Fig. 13) shows that the samples from Sésklo and Vólax are smaller in this dimension only comparatively to Olivola and Venta Micena. Another graphical comparison (of the maximal length to the minimal diaphyseal breadth and distal articular breadth; Fig. 14A, B, respectively) shows a close metrical similarity of Sésklo to the samples from Olivola, La Puebla de Valverde, Dafneró and Vólax.

The distal parts of tibia make a fairly good statistical sample ($n = 23-27$). Plotted in a scatter-diagram (Fig. 15) they have an intermediate position between the more robust specimens from Saint-Vallier and those from Senèze, Chilhac and Venta Micena. (However, Viret 1954 and Prat 1980 report ranges from Saint-

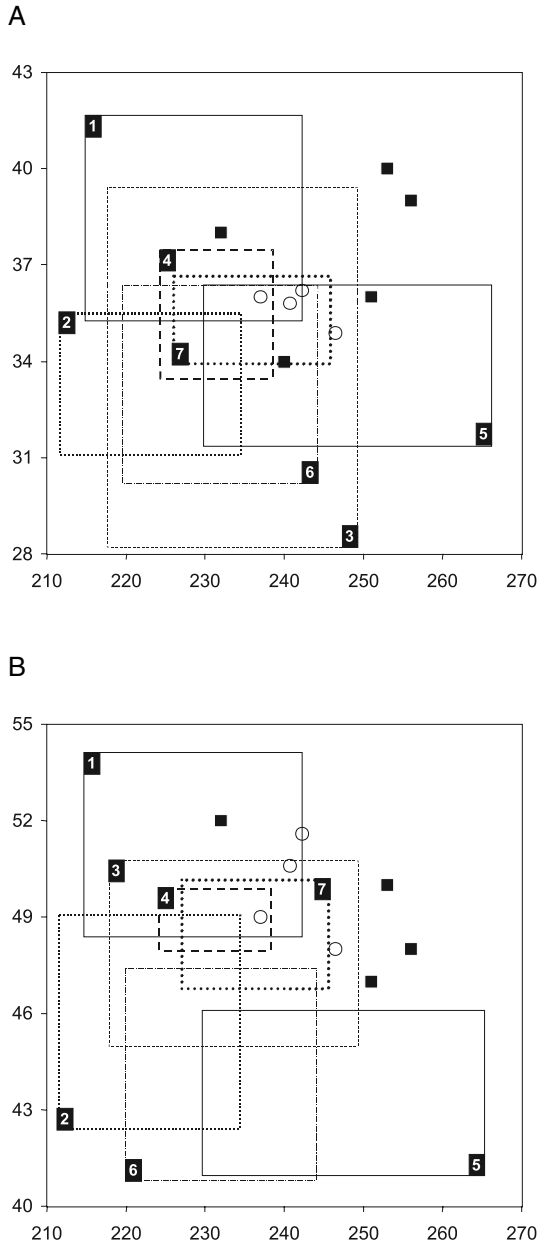


FIG. 14. — Scatter-diagrams of the third metacarpal measurement 1 (x-coordinate) to the measurements 3 (A) and 11 (B) (y-coordinate) of several horse samples; ■, Olivola, De Giuli (1972); O, Sésκλο. The numbered squares represent the measurement ranges from Saint-Vallier (1), Senèze (2), La Puebla de Valverde (3), Chilhac (4), Venta Micena (5), Líbakos & Gerakaróu (6) and Dafneró & Vólax (7), according to Eisenmann (1979), Prat (1980), Boeuf (1983, 1986), Marin (1987), Steensma (1988), Koufos (1992), Koufos & Kostopoulos (1993) and Koufos & Vlachou (1997), respectively.

Vallier that almost overlap with the ranges of the Sésκλο sample). Vólax and especially Gerakaróu and Líbakos present lower values.

A graphical comparison of the calcanea (Fig. 16) shows two size groups, Líbakos and Gerakaróu being clearly smaller in dimensions. The Sésκλο calcanea have practically the same height as those from Saint-Vallier (measurements 1 and 2), but they are smaller in all other dimensions, indicating reduced robustness. A marked morphological similarity is observed between Sésκλο and Gerakaróu (the corresponding lines in the diagram are almost parallel). The big differences in the measurements 4 and 5 indicate different epiphyse morphology for Olivola and Líbakos, but these measurements are more variable than the other ones.

Another ratio diagram (Fig. 17) comparing known *Equus stenonis* astragalus samples shows that those from Sésκλο are relatively large, comparable in dimensions to the specimens from Saint-Vallier, Dafneró and Vólax. They differ from the Saint-Vallier specimens mainly in the dimensions of the articular facet for the navicular. A morphological similarity to the sample from Saint-Vallier, as well as to the much smaller specimens from Gerakaróu (as in the case of calcaneum), is observed.

Comparing the third metatarsals from Sésκλο to the other known samples, they appear to be more slender than those from most western European localities (Saint-Vallier, Chilhac), while they are more robust than the stratigraphically younger samples from Greece (Líbakos, Gerakaróu). The inclination of the lines connecting the points of the measurements 1 and 3 in the ratio diagrams (Fig. 18) depicts graphically the slenderness of the metatarsals from Sésκλο in relation to the other samples. Senèze and Vólax have similar proportions, though they are a little more robust. In the same ratio diagrams of Fig. 18, one can observe the generally big dimensions of the metatarsals from Sésκλο, especially in the measurements of height (1 and 2). The same is observed in Fig. 19, where the range of the measurement 1 from Sésκλο is absolutely com-

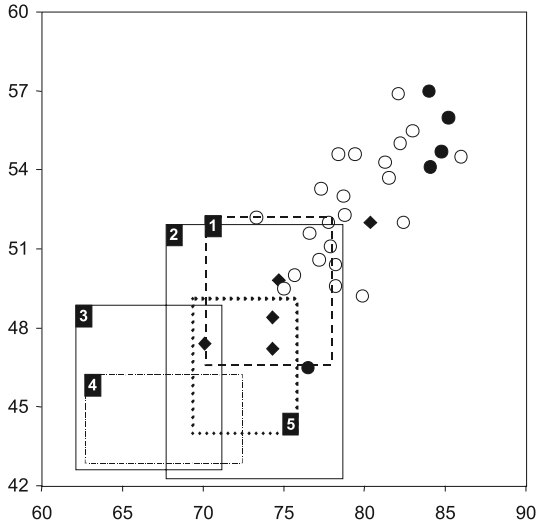


FIG. 15. — Scatter-diagram of the tibia measurements 7 (x-coordinate) and 8 (y-coordinate) of horse samples from several localities; ●, Saint-Vallier, Basel collection; ◆, Senèze, Basel collection; ○, Sésklo. The numbered squares represent the measurement ranges from Chilhac (1), Venta Micena (2), Libakos (3), Gerakarou (4) and Vólax (5) according to Boeuf (1983, 1986), Marin (1987), Steensma (1988), Koufos (1992) and Koufos & Vlachou (1997), respectively.

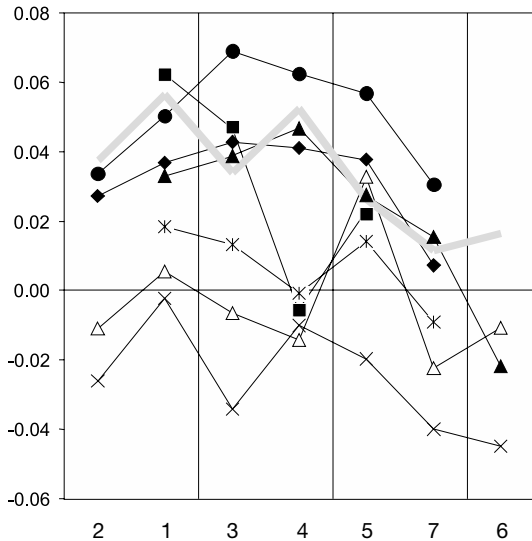


FIG. 16. — Logarithmic ratio diagram comparing the calcaneum measurements of horse samples from Sésklo and other localities; ●, Saint-Vallier, n = 10-15, Basel collection; ◆, Senèze, n = 3, Basel collection; ■, Olivola, n = 3-5, De Giuli (1972); ◆, Chilhac, n = 5-6, Boeuf (1983, 1986); *-, Venta Micena, n = 8-10, Marin (1987); -△-, Libakos, n = 5-10, Steensma (1988); -x-, Gerakarou, n = 2, Koufos (1992); —, Sésklo, n = 2-10. Standard: sample from Valdarno, n = 3-6, Basel collection.

parable to that of Olivola. In the measurements of breadth (3, 5, 7, 10, 11; Fig. 18) they are smaller than the very robust metapodials from Saint-Vallier, being comparable to the samples from Chilhac, La Puebla de Valverde, Dafneró and Vólax. Considering the general proportions, as expressed by the shape of the curves in Fig. 18, the studied material shows no strict morphological resemblance to any of the compared samples; as in the case of the third metacarpals, one can observe a similarity with Senèze, mainly in the measurements 1-7, but here it is not so well-expressed. Saint-Vallier, La Puebla de Valverde and Vólax are also similar in the measurements 5-14, 7-14 and 10-14 respectively. A comparison of the maximal length to the minimal diaphyseal breadth and distal articular breadth (Fig. 20) shows (as in the case of the metacarpals) metrical similarities to the samples from Olivola, Dafneró and Vólax, while La Puebla de Valverde is also close. The proximal phalanges appear to be quite similar to other known *Equus stenonis* samples. The ratio diagrams (Fig. 21) show the big dimensions of the studied material, especially in the measurements of height, and the relatively low measurements of breadth. This indicates a rather slender bone. The same is observed in the scatter-diagrams of Fig. 22, where the phalanges from Sésklo are placed between the robust ones from Saint-Vallier and the very slender ones from Venta Micena. The ratio diagrams (Fig. 21) do not indicate any morphological similarity among the samples (but in most cases the available samples are poor).

Summarising the description and comparison, the *Equus stenonis* sample from Sésklo belongs to a big horse with cranial and dental characters of stenonid type and very long limb bones. The morphology of the cranial and postcranial material resembles the dimensionally smaller samples from Senèze and Gerakarou. Among the large sized samples, those from La Puebla de Valverde, Saint-Vallier, Olivola and Vólax are closer to the dimensions and proportions of the bone samples from Sésklo. The more or less contemporaneous sam-

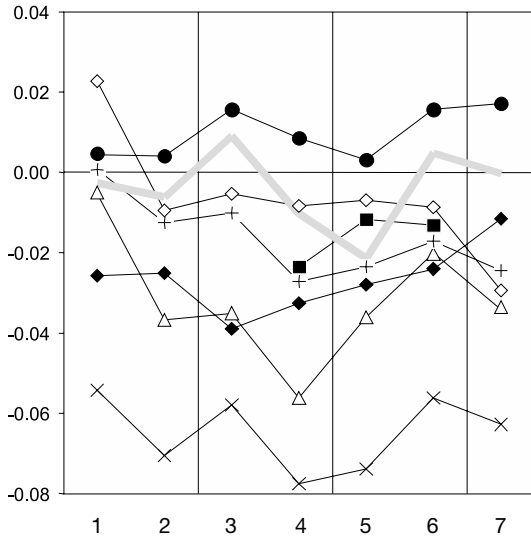


FIG. 17. — Logarithmic ratio diagram comparing the astragalus measurements of horse samples from Sésκλο and other localities; —●—, Saint-Vallier, n = 18-26, Basel collection; —◆—, Senèze, n = 4-5, Basel collection; —■—, Olivola, n = 7-11, De Giuli (1972); —▲—, Chilhac, n = 7, Boeuf (1983, 1986); —*—, Venta Micena, n = 41-47, Marin (1987); —△—, Libakos, n = 6-9, Steensma (1988); —x—, Gerakaróu, n = 6-8, Koufos (1992); —+—, Dafneró, n = 5-6, Koufos & Kostopoulos (1993); —◇—, Vólax, n = 1-2, Koufos & Vlachou (1997); —□—, Sésκλο, n = 9-16. Standard: sample from Valdarno, n = 7-8, Basel collection.

ples from Dafneró and Vólax do not show any significant dimensional or proportional difference from the studied sample. They only have shorter proximal phalanges, while the metapodials from Dafneró are also shorter and slightly stouter. However, it is not expected that these differences have any taxonomical importance, as they can be due to sampling bias (the samples are relatively small) or to small geological age differences.

The long metapodials indicate that the Sésκλο horse presumably had a shoulder height comparable to that of the Olivola or Venta Micena horses. However, the exact skeletal size is not known, as most of the long bones (except for the metapodials) are only preserved as parts and their total lengths are unknown. A general aspect of the skeletal proportions is given in Fig. 23, where the lengths of some available bones are compared. The Sésκλο curve resembles partly those of Saint-Vallier and Gerakaróu, as

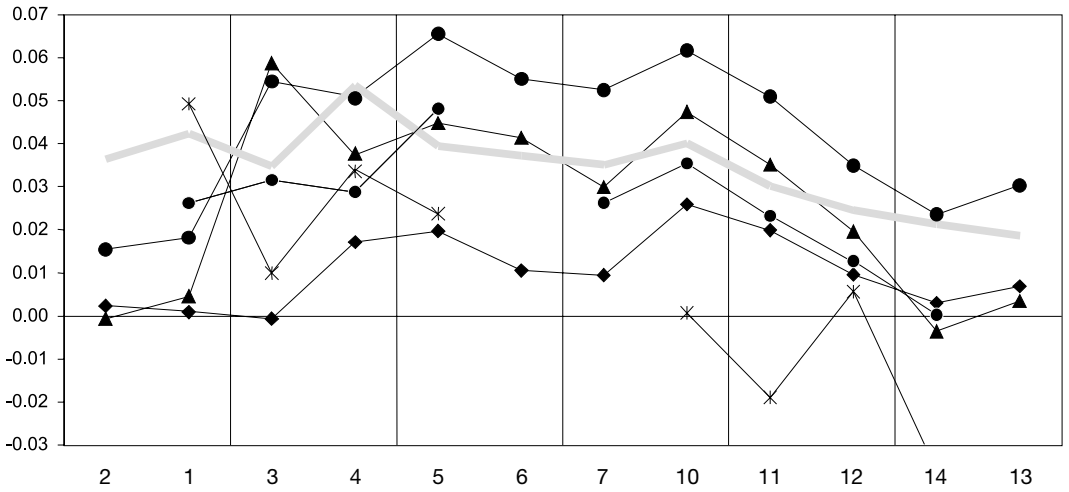
well as Chilhac in the long bone proportions of the rear foot.

BIOCHRONOLOGY-PALAEOECOLOGY

The genus *Equus* first appeared in the Eurasia during the late Pliocene (about 2.5 My. ago; Lindsay *et al.* 1980; Bonadonna & Alberdi 1987; Azzaroli 1990) or even earlier, according to some indications from eastern Europe (Forsten 1992), and dispersed throughout the continent, developing diverse stenorid forms. The stenorid dominance came to an end when the caballoid horses dispersed again through the Beringia, presumably as a result of the global climatic deterioration during the middle Pleistocene (Forsten 1996). The first stenorid immigrants were large sized horses that gradually showed a general tendency of size reduction during the late Pliocene and early Pleistocene (Forsten 1999), possibly responding to climatic shifts. This change is particularly evident in the Greek faunas, where the big and fairly stout *Equus stenonis* of the late Pliocene localities (Sésκλο, Dafneró, Vólax) was replaced by the small and slender form of the terminal Pliocene-early Pleistocene from Libakos, Gerakaróu and other less rich localities. The rest of the fauna from Sésκλο, which has a “Middle Villafranchian” character, also supports a late Pliocene age. The simultaneous presence of *Anancus arvernensis* and *Mammuthus meridionalis* indicates an MN17 age (Mein 1990). *Gazella borbonica* appears in the Ruscinian and survives until the lower MN17 (MNQ17 according to Guérin 1990, or Saint-Vallier Faunal Unit according to the Italian authors). The canid *Nyctereutes megamastoides* is another primitive element that disappears in Europe after the “Wolf Dispersal Event” at the beginning of the MNQ19 and the Olivola Faunal Unit (Azzaroli *et al.* 1988; Guérin 1990). The available biochronological data show a lower MN17 (MNQ17 or Saint-Vallier Faunal Unit) age for the fauna of Sésκλο.

The biometrical study and the proportions of the *Equus* long bones can give good information about the animal’s locomotion and its palaeo-environment. Eisenmann (1984) and Eisenmann

A



B

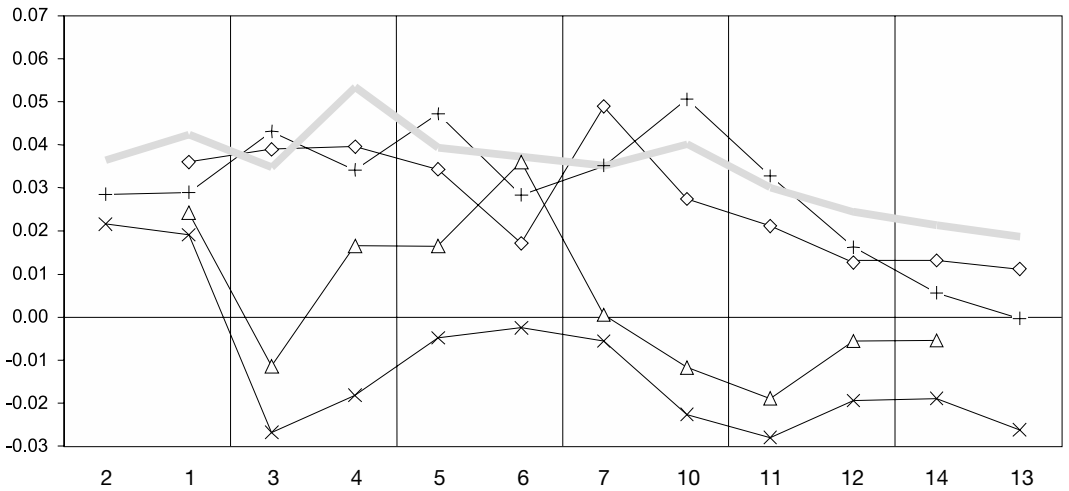


FIG. 18. — Logarithmic ratio diagram comparing the metatarsal III measurements of the horse sample from Sésklo to those from West European (A) and Greek (B) localities; ●, Saint-Vallier, n = 8-14, Basel collection; ◆, Senèze, n = 6-7, Basel collection; ▲, Chilhac, n = 2-3, Basel collection; ●, La Puebla de Valverde, n = 42-82, Eisenmann (1979); *, Venta Micena, n = 24-36, Marin (1987); △, Libakos, n = 24-41, Steensma (1988); ×, Gerakarou, n = 8-17, Koufos (1992); +, Dafneró, n = 2-4, Koufos & Kostopoulos (1993); ◇, Vólax, n = 1-7, Koufos & Vlachou (1997); —, Sésklo, n = 5-26. Standard: sample from Valdarno, n = 11-17, Basel collection.

& Guérin (1984), based on observations on extant populations, relate the robustness of the long bones to the humidity and the hardness of the substratum. According to these authors, the robust bones indicate humid environment, the

slender ones dry environment, while the hardness of the substratum is better related to the dimensions of the distal phalanges: supposing that the compared animals are of similar body mass, the wide phalanges indicate soft substratum, while

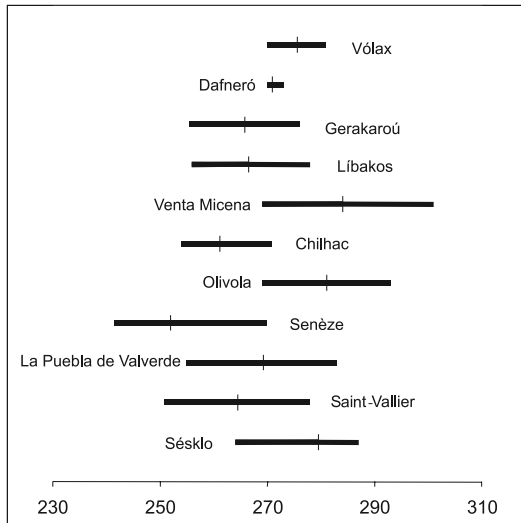


FIG. 19. — Comparison of the third metatarsal maximal length of several horse samples. The metrical variation and the mean (cross) are given for each sample. Data from the Basel collection and according to De Giuli (1972), Eisenmann (1979), Prat (1980), Boeuf (1983, 1986), Marin (1987), Steensma (1988), Koufos (1992), Koufos & Kostopoulos (1993) and Koufos & Vlachou (1997).

the narrow ones hard or rocky. Moreover, the shape of the mandibular symphysis could be related to the animal's diet. According to the interpretation of Eisenmann (1998), the symphyseal morphology of the mandible from Sésklo, which is considerably wide and robust, possibly indicates open environmental conditions and diet of abrasive food. This fits well with the hypsodonty, the relative shortness of the ectoflexid in the lower cheek teeth (Gromova 1952) and the low number of plications in the upper cheek teeth (Gromova 1949b, 1952). The long bones from Sésklo are relatively more robust compared to most southern Europe samples, but they are more slender compared to central or western European samples (Figs 12; 18; 21). This may indicate a moderate or rather dry palaeoenvironment, according to the mentioned criteria of Eisenmann (1984) and Eisenmann & Guérin (1984). The distal phalanx is rather narrower, compared to the phalanges of similar sized stenorid horses, indicating a fairly hard substratum. Although there are no data on the length of

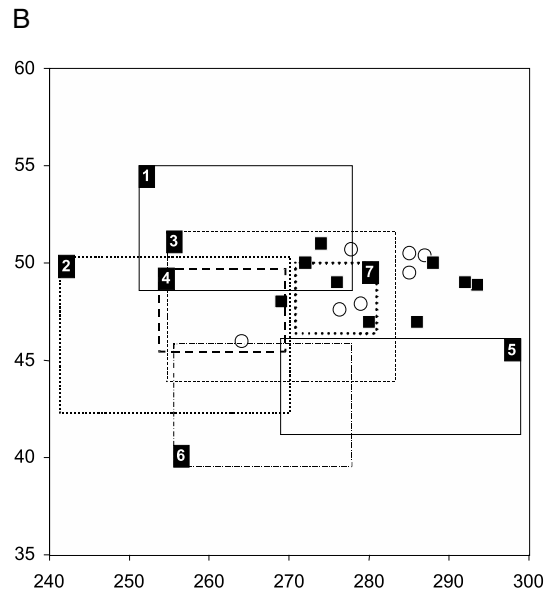
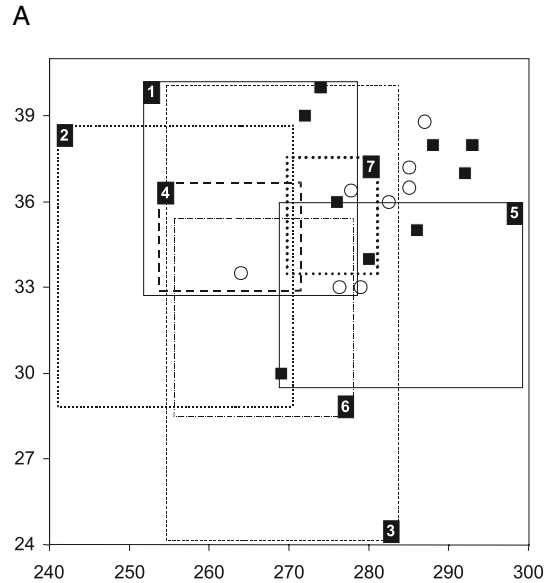


FIG. 20. — Scatter-diagrams of the third metatarsal measurement 1 (x-coordinate) to the measurements 3 (A) and 11 (B) (y-coordinate) of several horse samples; ■, Olivola, De Giuli (1972); ○, Sésklo. The numbered squares represent the measurement ranges from Saint-Vallier (1), Senéze (2), La Puebla de Valverde (3), Chilhac (4), Venta Micena (5), Libakos & Gerakaróú (6) and Dafneró & Vólax (7), according to Eisenmann (1979), Prat (1980), Boeuf (1983, 1986), Marin (1987), Steensma (1988), Koufos (1992), Koufos & Kostopoulos (1993) and Koufos & Vlachou (1997), respectively.

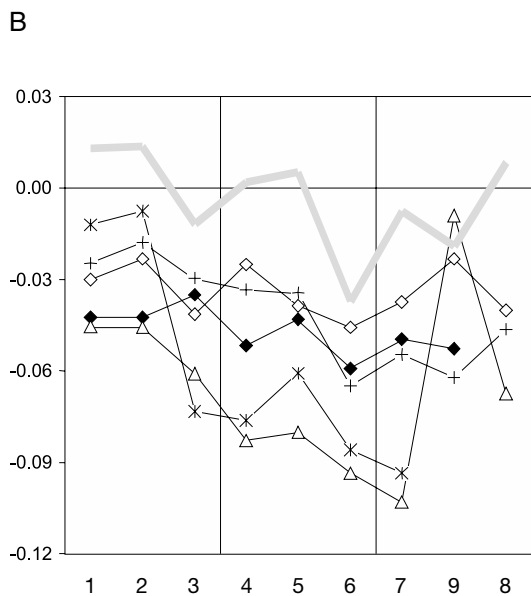
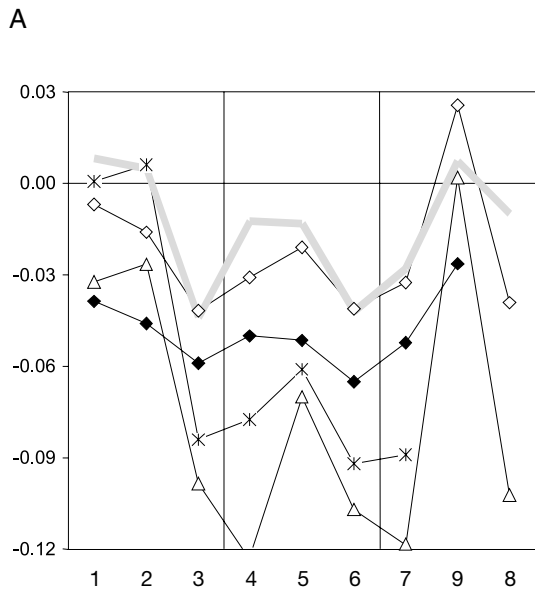


FIG. 21. — Logarithmic ratio diagrams comparing the anterior (A) and the posterior (B) proximal phalanx measurements of horse samples from Sésklo and other localities; ◆, Senèze, n = 4-8, Basel collection; *, Venta Micena, n = 6-8, Marin (1987); —△—, Libakos, n = 1-3, Steensma (1988); —+—, Dafneró, n = 2-3, Koufos & Kostopoulos (1993); —◇—, Vólax, n = 1, Koufos & Vlachou (1997); —, Sésklo, n = 3-5. Standard: sample from Saint-Vallier, n = 15-17, Prat (1980).

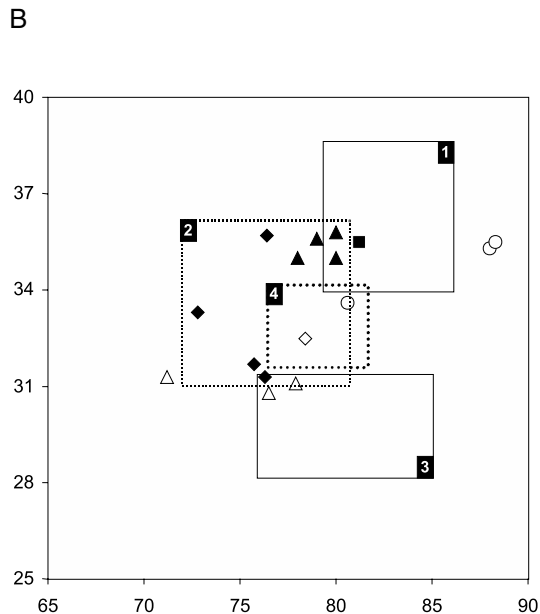
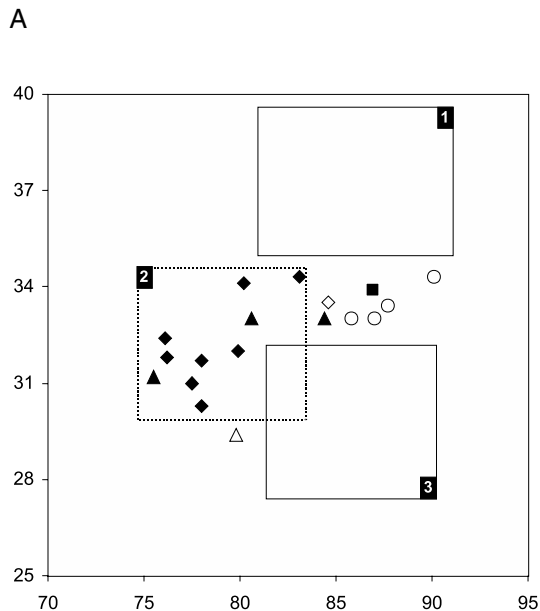


FIG. 22. — Scatter-diagrams of the anterior (A) and the posterior (B) proximal phalanx measurements 1 (x-coordinate) and 3 (y-coordinate) of several horse samples; ◆, Senèze, Basel collection; ■, Valdarno, Basel collection; ▲, Chilhac, Boeuf (1983, 1986); △, Libakos, Steensma (1988); ◇, Vólax, Koufos & Vlachou (1997); O, Sésklo. The numbered squares represent the measurement ranges from Saint-Vallier (1), Senèze (2), Venta Micena (3) and Dafneró (4), according to Prat (1980), Marin (1987) and Koufos & Kostopoulos (1993), respectively.

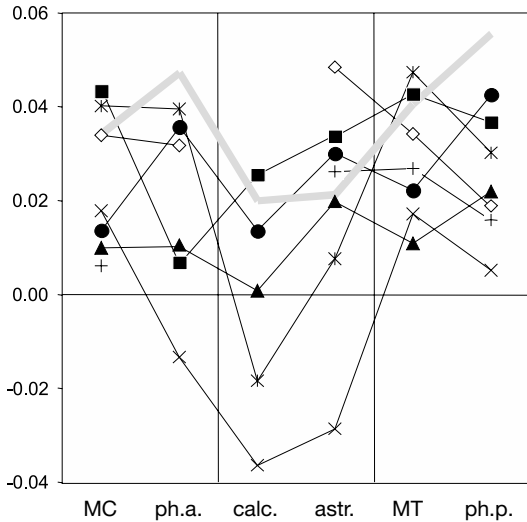


FIG. 23. — Logarithmic ratio diagram comparing the height of several bones of horse samples from Sésklo (—) and other localities; data from Saint-Vallier (—●—), Olivola (—■—), Chilhac (—▲—), Venta Micena (—*—), Gerakarou (—x—), Dafneró (—+—) and Vólax (—◇—) according to Prat (1980, in part), De Giuli (1972), Boeuf (1983, 1986), Marin (1987), Koufos (1992), Koufos & Kostopoulos (1993) and Koufos & Vlachou (1997), respectively. Standard: sample from Senèze, Basel collection. Abbreviations: **MC**, metacarpal III; **ph.a.**, anterior proximal phalanx; **calc.**, calcaneum; **astr.**, astragalus; **MT**, metatarsal III; **ph.p.**, posterior proximal phalanx.

proximal long bones, the very long metapodials and phalanges allow the assumption that the Sésklo horse was a very good runner, well adapted to an open environment. The dominance of antelopes (*Gazella* Blainville, 1816 and *Gazellospira* Pilgrim & Schaub, 1939), as well as the rarity of forest dwellers (deer, suids, etc.), is another indication of open and rather dry environment.

Acknowledgements

Special thanks are ought to Prof. N. Symeonidis (University of Athens, Greece) for assigning this study to me, Dr B. Engesser (Director of the Osteological Department, Natural History Museum of Basel, Switzerland) for permitting the study of the Museum collections, as well as to Ass. Prof. G. Theodorou (University of Athens, Greece) and Prof. G. Koufos (University of Thessaloniki, Greece) for useful conversations. The author is also grateful to the revisers of this

study, Dr V. Eisenmann (National Natural History Museum, Paris, France) and Dr A. Forsten (Finnish Museum of Natural History, University of Helsinki, Finland) for their very useful comments and corrections on the manuscript.

REFERENCES

- AIRAGHI C. 1928. — Mammiferi pliocenici dell'isola di Coe (Dodecaneso). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano* LXVII: 125-135.
- ATHANASSIOU A. 1996. — *Contribution to the Study of the Fossil Mammals of Thessaly*. Ph.D. thesis, University of Athens, Athens, Greece, 393 p. (in Greek).
- AZZAROLI A. 1965. — The two villafranchian horses of the Upper Valdarno. *Palaeontographia Italica* LIX: 1-12.
- AZZAROLI A. 1966. — Pleistocene and living horses of the Old World. An essay of a classification based on skull characters. *Palaeontographia Italica* LXI: 1-15.
- AZZAROLI A. 1982. — On Villafranchian palaeartic Equids and their allies. *Palaeontographia Italica* LXXII: 74-97.
- AZZAROLI A. 1990. — The genus *Equus* in Europe, in LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 339-356.
- AZZAROLI A., DE GIULI C., FICCARELLI G. & TORRE D. 1988. — Late Pliocene to early Mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 66: 77-100.
- BOEUF O. 1983. — *Le site Villafranchien de Chilhac (Haute-Loire, France). Étude paléontologique et biochronologique*. Thèse, Université de Paris VII, Paris, France, 253 p.
- BOEUF O. 1986. — L'Équidé du site Villafranchien de Chilhac (Haute-Loire, France): *Equus stenonis guthi* nov. subsp. *Annales de Paléontologie* 72: 29-67.
- BONADONNA F. P. & ALBERDI M. T. 1987. — *Equus stenonis* Cocchi as a biostratigraphical marker in the Neogene-Quaternary of the Western Mediterranean Basin: consequence on Gallerian-Villafranchian chronostratigraphy. *Quaternary Science Reviews* 6: 55-66.
- CALOI L. 1997. — New forms of *Equus* in the Western Europe and palaeoenvironmental changes. *Geobios* 30: 262-284.
- CALOI L. & PALOMBO M. R. 1987. — Osservazioni sugli Equidi Italiani del Pleistocene Medio inferiore. *Geologica Romana* XXVI: 187-221.
- DE GIULI C. 1972. — On the type form of *Equus stenonis* Cocchi. *Palaeontographia Italica* LXVIII: 35-49.

- DERMITZAKIS M. D., EISENMANN V. & GALOUKAS S. F. 1991. — The presence of Pleistocene mammals in Lesbos Island (E. Aegean). *Bulletin of the Geological Society of Greece* XXV: 405-421.
- DESIO A. 1931. — Le isole Italiane dell'Esgeo. *Memorie Descrittive della Carta Geologica d'Italia* XXIV: 1-534.
- DIVE J. & EISENMANN V. 1991. — Identification and discrimination of the first phalanges from Pleistocene and modern *Equus*, wild and domestic, in MEADOW R. H. & UERPMANN H. P. (eds), *Equids in the Ancient World*. Vol. II. *Beihfte zum Tübinger Atlas des Vorderen Orients* (B) 19 (2): 280-330.
- EISENMANN V. 1979. — Les métapodes d'*Equus sensu lato* (Mammalia, Perissodactyla). *Geobios* 12: 863-886.
- EISENMANN V. 1980. — Les chevaux (*Equus sensu lato*) fossiles et actuels: crânes et dents jugales supérieures. *Cahiers de Paléontologie*, 186 p.
- EISENMANN V. 1981. — Étude des dents jugales inférieures des *Equus* (Mammalia, Perissodactyla) actuels et fossils. *Palaeovertebrata* 10: 127-226.
- EISENMANN V. 1984. — Sur quelques caractères adaptatifs du squelette d'*Equus* (Mammalia, Perissodactyla) et leurs implications paléo-écologiques. *Bulletin du Muséum national d'Histoire naturelle* 4^e série, C, 6: 185-195.
- EISENMANN V. 1998. — Folivores et tondeurs d'herbe: forme de la symphyse mandibulaire des Equidés et des Tapiridés (Perissodactyla, Mammalia). *Geobios* 31: 113-123.
- EISENMANN V. 1999. — *Equus granatensis* of Venta Micena and evidence for primitive non-stenonid horses in the Lower Pleistocene. *Proceedings of the International Conference of Human Palaeontology "The Hominids and their Environment during the Lower and Middle Pleistocene of Eurasia"*, Orce 1995: 175-189.
- EISENMANN V. in press. — The primitive horses of the Vatera formation (Lesbos, Greece). *Annales géologiques des Pays helléniques*.
- EISENMANN V., ALBERDI M. T., DE GIULI C. & STAESCHE U. 1988. — Methodology, in WOODBURN M. & SONDAAR P. (eds), *Studying fossil horses*. E. J. Brill, Leiden, The Netherlands: 1-71.
- EISENMANN V. & DE GIULI C. 1974. — Caractères distinctifs des premières phalanges antérieures et postérieures chez certains Equidés actuels et fossils. *Bulletin de la Société géologique de France* 7^e série, XVI: 352-361.
- EISENMANN V. & GUÉRIN C. 1984. — Morphologie fonctionnelle et environnement chez les Périssodactyles. *Geobios* M. S. 8: 69-74.
- FORSTEN A. 1975. — Adaptive evolution of the equid foot. *Zeitschrift für Säugetierkunde* 40: 304-308.
- FORSTEN A. 1992. — Early *Equus* dispersal and taxonomy: conflicting opinions. *Courier Forschungsinstitut Senckenberg* 153: 171-176.
- FORSTEN A. 1996. — Climate and evolution of *Equus* (Perissodactyla, Equidae) in the Plio-Pleistocene of Eurasia. *Acta Zoologica Cracoviensia* 39: 161-166.
- FORSTEN A. 1998. — *Equus* species as stratigraphic markers. Reality or wishful thinking? *Quaternary Science Reviews* 17: 1097-1100.
- FORSTEN A. 1999. — A review of *Equus stenonis* Cocchi (Perissodactyla, Equidae) and related forms. *Quaternary Science Reviews* 18: 1373-1408.
- FÖRSTER U. 1960. — *Die Pferdephalangen aus dem keltischen Oppidum von Manching*. Inaugural-Dissertation, Tierärztliche Fakultät der Ludwig-Maximilians-Universität, München, Germany, 35 p.
- GROMOVA V. 1949a. — Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1: Obzor i opisani form. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 17 (1): 1-373.
- GROMOVA V. 1949b. — Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 2: Evoljutsija i klassifikatsija roda. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 17 (2): 1-162.
- GROMOVA V. 1952. — Gippariony (rod *Hipparion*) po materialam Taraklii, Pavlodara i drugim. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 36: 1-475.
- GROVES C. P. 1986. — The taxonomy, distribution and adaptations of recent Equids, in MEADOW R. H. & UERPMANN H. P. (eds), *Equids in the Ancient World*. *Beihfte zum Tübinger Atlas des Vorderen Orients* (A) 19 (1): 11-65.
- GUÉRIN C. 1990. — Biozones or Mammal Units? Methods and limits in Biochronology, in LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 119-130.
- KOSTOPOULOS D. S. & ATHANASSIOU A. S. 1997. — Les gazelles du Pliocène moyen-terminale de la Grèce continentale. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 205: 413-430.
- KOUFOS G. D. 1992. — Early Pleistocene Equids from Mygdonia basin (Macedonia, Greece). *Palaeontographia Italica* LXXIX: 167-199.
- KOUFOS G. D. & KOSTOPOULOS D. S. 1993. — A stenonoid horse (Equidae, Mammalia) from the Villafranchian of Western Macedonia (Greece). *Bulletin of the Geological Society of Greece* XXVIII: 131-143.
- KOUFOS G. D. & VLACHOU TH. 1997. — *Equus stenonis* from the Middle Villafranchian locality of Volax (Macedonia, Greece). *Geodiversitas* 19: 641-657.
- LINDSAY E. H., OPDYKE N. D. & JOHNSON N. M. 1980. — Pliocene dispersal of the horse *Equus* and late Cenozoic mammalian dispersal events. *Nature* 287: 135-138.
- MARIN M. 1987. — *Equus stenonis granatensis* en el Pleistoceno inferior de Venta Micena (Granada, España). *Paleontologia i Evolució* Mem. Esp. 1: 255-282.

- MASTORAS D. 1985. — *Geologische Bearbeitung des Neogen-Gebietes um Sesklon (Thessalien, Griechenland)*. Diplomarbeit, Christian-Albrechts-Universität, Kiel, Germany, 75 p.
- MEIN P. 1990. — Updating of MN zones, in LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 73-90.
- MÜLLER M. 1983. — *Zum Neogen in Ost-Thessalien (Griechenland)*. Dissertation, Universität des Saarlandes, Saarbrücken, Germany, 181 p.
- PARASKEVAIDIS I. 1953. — *Canis und Equus aus Attika. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 96: 453-496.
- PRAT F. 1957. — Sur la discrimination des phalanges antérieures et postérieures d'Équidés. *Procès verbaux de la Société linnéenne de Bordeaux* XCVII: 22-25.
- PRAT F. 1964. — Contribution à la classification des Équidés villafranchiens. *Procès verbaux de la Société linnéenne de Bordeaux* CI: 14-32.
- PRAT F. 1968. — *Recherches sur les Équidés pléistocènes en France*. Thèse de doctorat, Faculté des Sciences de l'Université de Bordeaux, Bordeaux, France, 692 p.
- PRAT F. 1980. — Les Équidés villafranchiens en France, genre *Equus*. *Cahiers du Quaternaire* 2: 1-290.
- SONDAAR P. Y. 1968. — The osteology of the manus of fossil and recent Equidae. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen* XXV: 1-76.
- STEENSMA K. J. 1988. — *Plio-/Pleistozäne Großsäugetiere (Mammalia) aus dem Becken von Kastoria / Grevena, südlich von Neapolis – NW Griechenland*. Dissertation, Technische Universität Clausthal, Clausthal, Germany, 315 p.
- SYMEONIDIS N. 1992. — Lower Pleistocene (Villafranchian) fossil Mammals from the Sesklo basin (Volos). *Annales géologiques des Pays helléniques* XXXV: 1-21 (in Greek).
- SYMEONIDIS N. K. & TATARIS A. 1983. — The first results of the geological and palaeontological study of the Sesklo basin and its broader environment. *Annales géologiques des Pays helléniques* XXXI: 146-190 (in Greek and German).
- VAN DER MEULEN A. J. & VAN KOLFSCHOTEN T. 1988. — Review of the Late Turolian to Early Biharian mammal faunas from Greece and Turkey. *Memorie della Società Geologica Italiana* XXXI: 201-211.
- VIRET J. 1954. — Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* IV: 1-200.

*Submitted on 31 July 2000;
accepted on 5 December 2000.*

ANNEXES

TABLE 1. — Cranial measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, muzzle length (from the prosthion to the middle of the line connecting the anterior borders of the P2); **7**, premolar length (P2-P4, alveolar, on the vestibular side); **8**, molar length (alveolar, on the vestibular side); **9**, upper cheek teeth length (P2-M3, alveolar); **13**, palatal breadth (at the level of P4-M1); **14**, minimal muzzle breadth; **15**, muzzle breadth, between the posterior borders of the I3; **31**, cheek length (from the back of the narial opening to the most anterior point of the orbit).

	1	7	8	9	13	14	15	31
Σ-194	-	103.0	85.6	187.0	-	-	-	-
Σ-199	-	102.5	88.0	189.5	-	-	-	-
Σ-203	160	92.0	84.5	175.1	84	(43)	70.5	-
Σ-246	-	-	-	-	-	-	-	(180)
Σ-1208	-	-	-	-	-	-	74.5	-
Σ-1220	-	-	89.5	-	-	-	-	-

TABLE 2. — Mandibular measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, length (from the point between the i1 to the back of the condyle); **2**, muzzle length (from the point between the i1 to the middle of the line connecting the anterior borders of the p2); **3**, premolar length (p2-p4, alveolar, on the vestibular side); **4**, molar length (m1-m3, alveolar, on the vestibular side); **5**, cheek teeth length (p2-m3, alveolar); **6**, distance between the back of the alveole of m3 and the posterior edge of the ascending ramus; **7**, muzzle breadth (between the posterior alveolar borders of the i3); **8**, height of the mandible at the condyle; **9**, height of the ascending ramus (at the bottom of the depression between the condyle and the coronoide process); **10**, height of the jaw posterior to the m3; **11**, height of the jaw between p4 and m1; **12**, height of the jaw in front of p2; **13**, length of the symphysis; **14**, minimal breadth of the symphysis.

	1	2	3	4	5	6	7
Σ-1026	-	138.0	102.0	89.0	191.0	-	62.0
	8	9	10	11	12	13	14
Σ-1026	-	-	99.0	83.0	74.0	93.0	44.0

TABLE 3. — Upper cheek teeth measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **2**, tooth length (on the occlusal surface, cement excluded); **3**, protocone length (on the occlusal surface); **4**, tooth breadth (on the occlusal surface, cement excluded).

	Stage of wear	P2			P3			P4		
		2	3	4	2	3	4	2	3	4
Σ-170	1	47.0	7.7	29.0	36.3	10.7	29.7	-	-	-
Σ-194	4	42.7	-	(25.5)	32.5	8.5	29.0	29.5	8.3	31
Σ-196	?	43.7	7.6	28.8	-	-	-	-	-	-
Σ-197	?	-	-	-	-	-	-	34.8	10.0	31.0
Σ-199	4	42.0	-	26.5	31.4	8.0	29.5	29.6	8.7	31.2
Σ-946	1-2	-	-	-	-	-	-	-	11.4	28
Σ-1029	1	-	-	-	-	11.8	-	-	-	-
Σ-1203	3	-	-	-	-	-	-	-	-	-
Σ-1220	3-4	-	-	-	32.6	11.4	29	28.8	(11.3)	30
		2	M1 3	4	2	M2 3	4	2	M3 3	4
Σ-170	1	33.6	11.4	27.0	34.2	14.5	26.2	-	-	-
Σ-194	4	23.5	9.0	28.9	27.0	9.3	29.3	32.4	10.7	26.0
Σ-196	?	-	-	-	-	-	-	-	-	-
Σ-197	?	30.3	10.0	31.6	-	-	-	-	-	-
Σ-199	4	24.7	9.0	29.0	27	9.5	29.1	34.0	10.8	26.3
Σ-946	1-2	27.5	8.3	27.0	28.5	-	-	27.0	11.7	21.3
Σ-1029	1	31.7	11.0	28.3	-	-	-	-	-	-
Σ-1203	3	26.6	8.9	28.5	26.7	10.3	28.0	-	-	-
Σ-1220	3-4	24.9	11.5	28.9	27.4	11.8	28.8	32.5	12.5	25.4
		2	DM2 3	4	2	DM3 3	4	2	DM4 3	4
Σ-383		48.3	5.6	24.0	34.0	8.2	25	36.2	9.9	22.4
Σ-1211 - Σ-1215		-	5.6	23.6	35.6	7.4	24.1	35.8	10.3	22.3

TABLE 4. — Number of plications on the upper cheek teeth of *Equus stenonis* Cocchi, 1867 from Sésklo.

	Stage of wear	P2	P3	P4	M1	M2	M3
Σ-170	1	2-3-2-2/2	3-3-?-?/2	-	1-5-3-2/2	1-3-1-1/2	-
Σ-194	4	0-0-1-1/0	0-0-1-0/0	1-2-1-0/1	0-0-0-0/0	0-0-1-0/0	0-1-1-1/1
Σ-197	?	-	1-2-1-1/1	1-2-1-1/1	-	-	-
Σ-199	4	0-0-1-1/0	0-0-1-0/0	1-2-1-0/1	0-0-0-0/0	0-0-1-0/0	0-2-1-1/1
Σ-946	1-2	-	-	?-?-3-1/2	1-5-2-1/1	1-5-4-1/2	2-2-1-2/1
Σ-1029	1	-	?-?-1-1/2	-	1-5-2-1/2	-	-
Σ-1203	3	-	-	-	0-0-2-1/1	1-4-3-1/1	-
Σ-1220	3-4	-	0-4-1-0/1	1-3-1-0/1	0-1-1-0/0	0-1-2-1/0	0-3-1-3/0

TABLE 5. — Lower cheek teeth measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; 2, tooth length (on the occlusal surface, cement excluded); 3, prefixid length; 4, double knot length; 5, postflexid length; 6, tooth breadth (on the occlusal surface, cement excluded).

	2	3	p2			p3			p4						
			4	5	6	2	3	4	5	6	2	3	4	5	6
Σ-1026	37.5	8.1	15.1	15.3	16.7	31.9	9.6	19.1	14.8	(17.1)	30.9	9.7	(18.7)	14.0	-
	2	3	m1			m2			m3						
			4	5	6	2	3	4	5	6	2	3	4	5	6
Σ-1026	27.3	7.1	16.1	10.9	15.9	28.0	8.8	15.8	11.5	15.1	31.5	9.1	14.9	12.5	14.5
Σ-441	34.4	9.8	14.9	13.3	11.4	-	-	-	-	-	-	-	-	-	-
	2	3	dm2			dm3			dm4						
			4	5	6	2	3	4	5	6	2	3	4	5	6
Σ-441	-	-	-	-	-	-	-	-	-	-	(34.5)	10.3	17.7	11.1	-
Σ-1027	40.8	-	16.5	13.4	13.6	33.4	10.2	18.3	10.5	14.1	-	-	-	-	-
Σ-1130	-	-	-	-	-	33.1	10.4	18.1	11.0	13.9	35.1	10.1	18.4	10.9	14.1
Σ-1226	39.5	11.7	17.9	13.8	13.6	-	-	-	-	-	-	-	-	-	-
	2	3	d3/4												
			4	5	6										
Σ-951	32.5	11.6	17.6	13.1	13.7										
Σ-1125	33.4	10.4	15.5	12.8	12.3										

TABLE 6. — Humerus measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; 3, minimal diaphyseal breadth; 4, diaphyseal DAP, at the level of 3; 5, proximal maximal breadth; 6, proximal maximal DAP; 7, maximal breadth of the trochlea; 8, distal maximal DAP; 9, maximal height of the trochlea; 10, minimal height of the trochlea; 11, height of the trochlea at the sagittal crest (near the condyle).

	3	4	5	6	7	8	9	10	11
n	6	5	1	2	10	9	11	9	10
min	37.0	46.0	94.0	110.0	70.6	76.7	51.8	36.6	45.3
\bar{x}	38.6	47.8	94.0	112.2	80.1	80.9	54.7	38.9	47.8
max	41.0	49.2	94.0	114.3	85.0	85.5	58.5	41.8	50.0

TABLE 7. — Radius measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; 3, minimal diaphyseal breadth; 4, diaphyseal DAP, at the level of 3; 5, maximal breadth of the proximal articulation; 6, maximal DAP of the proximal articulation; 7, proximal maximal breadth; 8, maximal breadth of the distal articulation; 9, maximal DAP of the distal articulation; 10, distal maximal breadth; 11, breadth of the radial condyle; 12, breadth of the ulnar condyle.

	3	4	5	6	7	8	9	10	11	12
n	2	2	9	8	9	7	7	7	8	8
min	43.8	30.0	76.0	37.0	83.8	63.6	36.2	75.5	24.0	15.0
\bar{x}	45.4	31.0	79.8	39.2	88.2	65.7	37.7	79.4	25.2	17.7
max	47.0	32.0	86.0	40.5	96.5	69.5	40.0	83.8	28.0	19.6

TABLE 8. — Metacarpal III measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, maximal length; **2**, medial length; **3**, minimal diaphyseal breadth; **4**, diaphyseal DAP, at the level of 3; **5**, maximal breadth of the proximal articulation; **6**, maximal DAP of the proximal articulation; **7**, maximal diameter of the articular facet for the magnum; **8**, maximal diameter of the anterior articular facet for the unciform; **9**, maximal diameter of the articular facet for the trapezoid; **10**, distal maximal supra-articular breadth; **11**, maximal breadth of the distal articulation; **12**, diameter of the keel; **13**, minimal DAP of the lateral condyle; **14**, maximal DAP of the medial condyle.

	1	2	3	4	5	6	7
n	4	4	17	17	20	22	18
min	237.0	227.5	33.5	24.9	50.5	31.7	42.0
\bar{x}	241.6	231.3	35.9	27.9	53.7	35.0	44.7
max	246.5	235.6	38.7	30.2	57.9	37.7	47.0
s	3.9	3.4	1.5	1.3	2.0	1.7	1.7
V	1.6	1.4	4.2	4.7	3.6	4.8	3.7
	8	9	10	11	12	13	14
n	16	15	24	22	25	25	25
min	15.0	7.5	47.0	47.1	33.6	27.5	28.8
\bar{x}	16.6	8.5	51.0	50.6	37.0	29.0	30.8
max	18.3	9.7	56.0	54.0	38.9	30.5	32.8
s	0.8	0.7	1.9	1.7	1.3	0.8	0.9
V	4.9	8.1	3.8	3.3	3.4	2.8	2.9

TABLE 9. — Femur measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **5**, proximal maximal breadth; **6**, proximal maximal DAP; **7**, distal maximal breadth; **10**, diameter of the caput femoris.

	5	6	7	10
n	1	1	1	2
\bar{x}	123.5	92.5	98.5	57.2

TABLE 10. — Tibia measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **3**, minimal diaphyseal breadth; **4**, diaphyseal DAP, at the level of 3; **7**, distal maximal breadth; **8**, distal maximal DAP.

	3	4	7	8
n	12	12	23	27
min	44.3	29.6	73.3	49.0
\bar{x}	48.0	32.1	79.1	52.3
max	50.2	34.8	86.0	56.9
s	1.5	1.3	2.9	2.3
V	3.2	4.1	3.7	4.3

TABLE 11. — Calcaneum measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, maximal length; **2**, length of the proximal part; **3**, minimal breadth; **4**, proximal maximal breadth; **5**, proximal maximal DAP; **6**, distal maximal breadth; **7**, distal maximal DAP.

	1	2	3	4	5	6	7
n	4	2	10	5	7	8	8
min	118.6	79.9	21.4	35.9	48.8	51.0	51.7
\bar{x}	121.4	80.5	22.4	37.1	51.2	53.0	54.2
max	124.0	81.0	23.4	38.5	54.0	56.5	58.3
s	2.6	0.8	0.8	1.1	1.8	1.9	2.2
V	2.1	1.0	3.5	3.0	3.5	3.5	4.0

TABLE 12. — Astragalus measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, maximal height; **2**, maximal diameter of the medial condyle; **3**, breadth of the trochlea (at the apex of each condyle); **4**, maximal breadth; **5**, maximal breadth of the distal articulation; **6**, maximal DAP of the distal articulation; **7**, medial maximal DAP.

	1	2	3	4	5	6	7
n	12	12	13	11	10	16	9
min	58.8	59.5	28.5	59.0	47.8	34.0	49.3
\bar{x}	62.0	63.7	30.7	65.1	51.7	36.4	53.2
max	64.6	66.3	33.5	68.9	55.6	39.7	56.1
s	1.9	2.0	1.3	3.3	2.5	1.6	2.1
V	3.0	3.1	4.3	5.0	4.9	4.5	4.0

TABLE 13. — Metatarsal III measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, maximal length; **2**, medial length; **3**, minimal diaphyseal breadth; **4**, diaphyseal DAP, at the level of 3; **5**, maximal breadth of the proximal articulation; **6**, maximal DAP of the proximal articulation; **7**, maximal diameter of the articular facet for the large cuneiform; **8**, maximal diameter of the articular facet for the cuboid; **9**, maximal diameter of the articular facet for the small cuneiform; **10**, distal maximal supra-articular breadth; **11**, maximal breadth of the distal articulation; **12**, diameter of the keel; **13**, minimal DAP of the lateral condyle; **14**, maximal DAP of the medial condyle.

	1	2	3	4	5	6	7
n	8	5	19	18	23	26	21
min	264.0	256.0	30.6	29.2	45.2	35.5	42.0
\bar{x}	279.6	266.9	35.3	34.0	50.4	40.1	46.0
max	287.0	277.3	38.8	37.7	53.9	45.2	48.9
s	7.4	7.6	2.2	2.0	2.1	2.1	1.9
V	2.6	2.8	6.4	5.8	4.2	5.3	4.2
	8	9	10	11	12	13	14
n	15	12	20	16	19	18	15
min	9.0	6.5	45.4	46.0	35.2	26.2	29.7
\bar{x}	12.3	8.3	50.2	48.7	37.3	28.1	31.5
max	14.5	10.5	53.6	50.7	40.1	30.2	37.9
s	1.7	1.0	2.2	1.5	1.2	1.0	2.0
V	13.8	11.6	4.3	3.0	3.2	3.6	6.2

TABLE 14. — Proximal phalanx measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, maximal length; **2**, anterior length; **3**, minimal diaphyseal breadth; **4**, proximal maximal breadth; **5**, proximal maximal DAP; **6**, distal maximal breadth (at the tuberosities); **7**, maximal breadth of the distal articulation; **8**, maximal DAP of the distal articulation; **9**, minimal length of the trigonum phalangis.

Anterior proximal phalanx	1	2	3	4	5	6	7	8	9
n	4	4	5	3	4	5	5	5	5
min	85.8	77.6	33.0	55.8	37.0	44.2	43.9	25.0	44.2
\bar{x}	87.7	78.6	33.3	56.6	38.1	46.1	45.5	26.1	46.8
max	90.1	79.6	34.3	57.2	39.5	47.4	46.1	26.6	48.8
Posterior proximal phalanx	1	2	3	4	5	6	7	8	9
n	3	3	3	3	3	3	3	3	3
min	80.6	72.2	33.6	55.4	39.5	43.4	43.3	25.6	37.5
\bar{x}	85.6	76.9	34.8	59.3	41.1	45.0	45.1	26.5	42.1
max	88.3	80.0	35.5	61.4	43.0	46.5	46.5	27.0	45.0

TABLE 15. — Medial phalanx measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, maximal length; **2**, anterior length; **3**, minimal diaphyseal breadth; **4**, proximal maximal breadth; **5**, proximal maximal DAP; **6**, maximal breadth of the distal articulation.

Anterior median phalanx	1	2	3	4	5	6
n	4	2	4	3	4	4
min	46.7	33.6	44.3	50.0	33.3	47.4
\bar{x}	47.4	34.8	44.7	52.3	34.6	49.2
max	48.0	35.9	45.0	53.9	35.7	51.0
Posterior median phalanx	1	2	3	4	5	6
n	3	3	3	3	4	3
min	48.6	35.5	40.8	51.5	33.0	44.0
\bar{x}	49.9	36.6	42.3	52.1	35.5	45.1
max	50.8	37.7	43.4	53.0	36.8	46.0

TABLE 16. — Distal phalanx measurements of *Equus stenonis* Cocchi, 1867 from Sésklo; **1**, length (from the posterior edge of the articular surface to the anterior tip of the phalanx); **2**, anterior length; **3**, maximal breadth; **4**, maximal breadth of the articulation; **5**, maximal DAP of the articulation; **6**, maximal height.

Anterior distal phalanx	1	2	3	4	5	6
n	3	4	3	2	3	4
min	58.0	49.5	63.2	50.7	30.5	42.3
\bar{x}	59.2	52.6	67.8	50.9	30.8	43.3
max	60.5	55.4	70.6	51.0	31.0	44.0
Posterior distal phalanx	1	2	3	4	5	6
n	1	1	3	3	2	3
min	56.3	53.3	57.0	45.0	27.7	37.1
\bar{x}	56.3	53.3	60.8	45.5	29.1	40.1
max	56.3	53.3	63.0	46.2	30.5	42.0