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Article

A Villafranchian Hipparion-Bearing Mammal Fauna from Sésklo (E. Thessaly, Greece): Implications for the Question of Hipparion–*Equus* Sympatry in Europe

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Abstract: Recently collected fossil material in the Villafranchian locality of Sésklo, as well as a re-evaluation of a pre-existing, partly-published museum collection, allow the recognition of a lower faunal level in the locality, older than the main *Equus*-dominated fossil assemblage, dated in the Early Pleistocene (MNQ17). The lower level yielded, instead, an advanced hipparion, referred to the species *Plesiohipparion* cf. *shanxiense*, and a small number of associated taxa: an ostrich (*Struthio* cf. *chersonensis*), an unidentified proboscidean, the pig *Sus arvernensis*, two antelopes (*Gazella* cf. *bouvrainae* and *Gazellospira torticornis*), a large bovid (Bovini indet.), and a rhinoceros (*Stephanorhinus* sp.). The lower-level fauna is dated in the latest Pliocene (MN16) and indicates a rather open and dry palaeoenvironment. The faunal sequence in Sésklo shows that the hipparion did not co-occur with the stenonid horse, at least in this region. Previous reports on sympatry of these taxa may result from faunal mixing, requiring re-examination of the available samples.

Keywords: *Plesiohipparion*; Late Pliocene; Villafranchian; Greece; biostratigraphy; equid sympatry

1. Introduction

The fossiliferous locality of Sésklo is located 8 km west of the city of Vólos, the capital of the Prefecture of Magnesia (Thessaly, Greece) and 2 km north-east of the homonymous village (Figure 1a). The area is used as a clay pit operated by the cement industrial company “Hercules”, during the quarrying works of which, vertebrate fossils come occasionally to light. The first fossil finds known from the locality were unearthed in 1971 [1,2]. Thenceforth several fossil collections or excavations were carried out in the pit (Figure 2) producing a rich fossil vertebrate collection of Villafranchian age.

The Sésklo fauna is well known from several papers published during the last 40 years. It is a diverse fauna, comprising twenty-two mammalian taxa [2–10]. Most of the finds belong to the horse *Equus stenonis* Cocchi, 1867, but the family Bovidae constitutes the most diverse group within the assemblage. The fauna is biochronologically dated in the lower MN17 zone, as defined by Mein [11] (MNQ17 according to Guérin [12], or Saint-Vallier Faunal Unit, according to Italian authors, e.g., [13]), currently placed in the early part of the Early Pleistocene. Previous publications on the Sésklo fauna already mentioned the presence of fossils in at least four different findspots (A, B, Γ and Δ in Figure 2) within the quarry, deriving from different fieldwork expeditions [2,3,5]. Unfortunately, all material excavated or collected until 1982 was lumped together, forming a mixed sample that contained all specimens deriving from the locality, without any findspot indication.

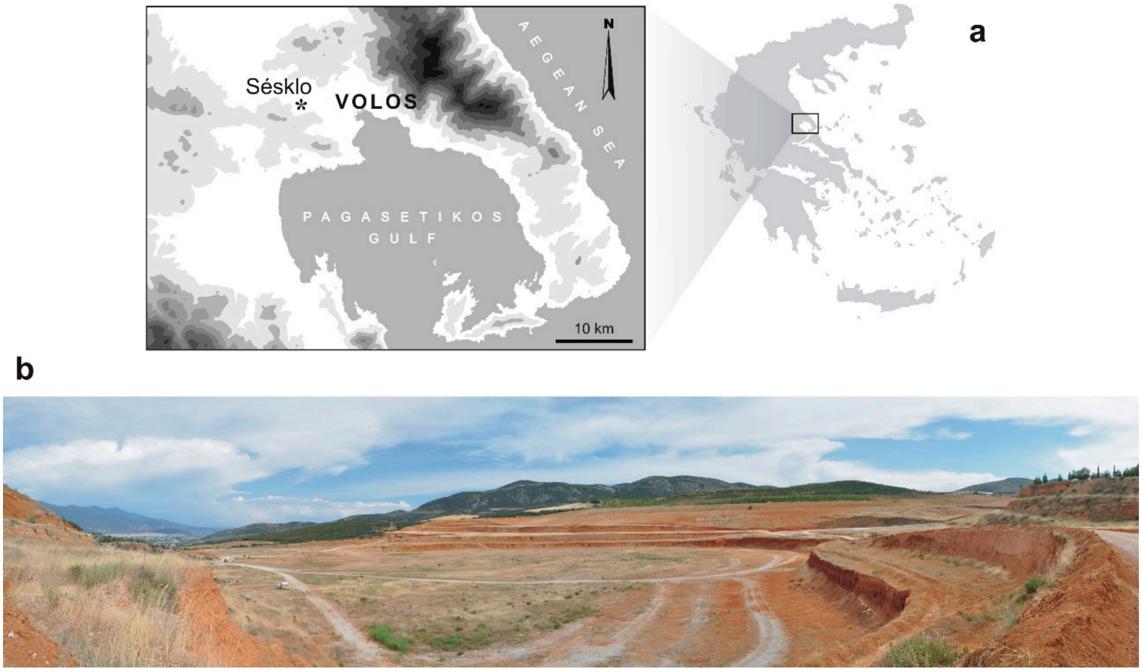

Figure 1. (**a**) Map of Greece, indicating the geographic location of the Sésklo locality (asterisk), west of the city of Vólos. Locality coordinates: 39.368° N, 22.851° E (WGS84 datum). Contour interval: 200 m. (**b**) Panoramic view of the clay pit seen from the North.

Differences in specimen fossilisation and morphology have shown, however, beyond doubt that a small part of the material derives from a different level. Athanassiou [5] excluded these specimens from the comprehensive study of the Sésklo fauna because of their different physical characters, as well as for the reason that most of them seemed to belong to a large-sized hipparion, not to a stenonid horse. Nonetheless, most of them were published at about the same time, together with selected material from the main fossil accumulation within the quarry (findspots B, or Δ, or both; Figure 2) as a mixed sample [3]. Their dark colour hinted to the similarly coloured clays at the base of the basin sedimentary sequence (Figures 2b and 3) as the most probable stratigraphic level of provenance. Indeed, one of the initially recorded findspots (Γ, see Figure 2) must have been situated in the dark clays. Much later, in the summer of 2005, during the ongoing works of the quarry, a new findspot was discovered, situated in the lower horizons of the red clayey layers that dominate the basin fill. The site was destroyed by the quarry machinery, but a few fragmentary specimens were delivered to the present author by the quarry supervisor A. Christophorides, who precisely mapped their location. This findspot was dubbed SE2 (Figure 2). The preparation of the fossil material during the following years showed, quite surprisingly, that SE2 also differs markedly from the main fossil accumulation because it exclusively yielded remains attributable to a hipparionine horse, instead of *Equus*. This discovery corroborated our previous assumption about the provenance of the dark-coloured sample, as both samples contain fossil remains of a very large-sized hipparion. The present paper is a comprehensive description of these two samples, which must have been very close stratigraphically and chronologically, and quite probably represent the same fauna. A preliminary version of the present paper was presented in the 15th Congress of the Regional Committee on Mediterranean Neogene Stratigraphy (RCMNS 2017) [14].

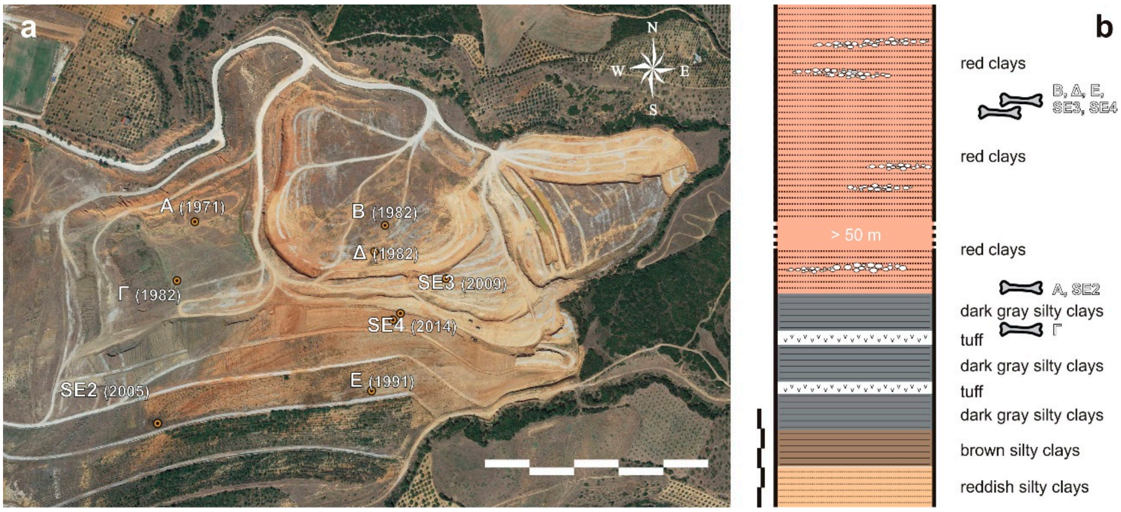

Figure 2. (**a**) Distribution of the fossiliferous sites/findspots within the Sésklo clay pit. The year of discovery of each one is indicated in parentheses. Graphical scale: 500 m. Satellite image source: Google. (**b**) Stratigraphic column of the Sésklo Basin sedimentary fill, based on Müller [15] and own data. The position of the fossiliferous sites is approximate. Graphical scale: 5 m.

Figure 3. The lower part of the Sésklo Basin sedimentary fill, showing the transition from the lower dark-gray clays to the red clays that dominate the sequence. View from the North. The photograph was taken in October 1991. This part of the sequence is no longer visible in sections within the quarry, due to subsequent levelling.

Geological Setting

The locality of Sésklo is situated within a fluvial basin filled mainly with red-clay sediments (Figures 1b and 2b). 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. The clastic filling of the basin consists mainly of fine-grained clays, deposited in strata of various thicknesses and not well-defined contacts among them [15,16]. The whole series exhibits a general dip of 11° towards the east-south east, so the western part of the quarry is expected to expose older layers. No major unconformity is observed in the clastic series; the strata continuity is, though, interrupted by numerous faults of generally small slip. Intercalations or lenses of coarser material are often found among the clayey deposits, indicating high-energy episodes in a generally low-energy fluvial milieu (Figure 2b). Lithologically, the red clays are very uniform, as most of the series consists of red-coloured clayey layers. The lowermost layers of the basin differentiate, however, from the dominant red clay sedimentary fill in being very dark coloured (Figures 2b and 3). The colour is due to the high pyroclastic content of these layers, which according to Müller [15] and Mastoras [16] may have derived from a local volcanic centre. These layers, together with two intercalating tuff horizons, have not been visible or accessible for many years until today due to the quarry development, which otherwise has made it possible to access a sufficient part of the stratigraphic sequence and its faunal content.

2. Materials and Methods

The studied material comes from two sites within the clay pit of Sésklo. A part of it, bearing the designation 'Σ' before the specimen number, derives from an old collection carried out most probably in 1982, which presumably exploited a single accumulation of fossils (findspot Γ, Figure 2). This group of specimens is characterised by dark colour and intense mineralisation, pointing to the rich-in-pyroclastics dark-coloured clays at the base of the sequence as the layers of provenance. They are also distinctively heavier than the fossils deriving from the upper levels of Sésklo. Another part of the specimens was collected in 2005 during the quarrying operations in the findspot SE2 (WGS84 coordinates: 39.36568° N, 22.84676° E, altitude: 154 m; Figure 2) and are labelled as such. All studied material belongs to the collections of the Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece.

The studied specimens were measured with precision of 0.1 mm, when possible. The measurement methodology of the equid material follows Eisenmann et al. [17]. Inaccurate measurements, due to bad or incomplete preservation, are enclosed in parentheses. Measurements on incompletely preserved specimens may be given as 'greater-than', using the relevant sign (>).

To avoid ambiguities about the cited sources, citations to figures, plates, tables etc. of published papers are given in lowercase and abbreviated (e.g., pl. 1, fig.1), while citations to figures etc. of the present paper are given non- abbreviated, with a capital first letter (e.g., Figure 1, Table 1).

Abbreviations

L: length; W: width; DAP: craniocaudal diameter; DT: mediolateral diameter (p: of the proximal end; m: at the middle of the bone shaft; d: of the distal end; a: articular). The upper teeth are designated with capital letters (P: premolars; M: molars), while the lowers with lowercase letters (p: premolars; m: molars; d: deciduous).

3. Systematics

The studied material is referred to one avian and seven mammalian taxa, as follows:

3.1. Bird

Class: Aves Linnaeus, 1758.
Order: Struthioniformes Latham, 1790.
Family: Struthionidae Vigors, 1825.
Genus: *Struthio* Linnaeus, 1758.
Struthio cf. *chersonensis* (Brandt, 1873).

Material. SE2-1: distal part of left tarsometatarsus.

Description. The preserved distal part is less than the half of the original bone. The body of the bone is cylindrical in general shape, but forms a shallow and open median groove dorsally (Figure 4a). The bone's distal articular end is partly gnawed, thus no accurate measurements can be taken, except for the minimal DAP (craniocaudal diameter) of the trochlea, which measures 41.5 mm. The DT (mediolateral diameter) of the distal articular facet of the third metatarsal is more than 46 mm, while the DAP more than 50 mm. The second metatarsal distal end is tiny and rudimentary. That of the fourth one seems to have been well developed, but it is broken off distolaterally. It is directed slightly laterally with regard to the long axis of the bone.

Figure 4. Fossil specimens from the lower level of Sésklo: (**a**) *Struthio* cf. *chersonensis*, left tarsometatarsus, SE2-1, dorsal view; (**b**) *Gazellospira torticornis*, left metacarpal III–IV, SE2-7, dorsal view; (**c**) Bovini indet., left proximal metacarpal III–IV, Σ-1390, dorsal view; (**c′**) *idem*, proximal view; (**d**) Bovini indet., right distal tibia, SE2-6, dorsal view; (**e**) Bovini indet., left distal humerus, SE2-5, cranial view; (**e′**) *idem*, distal view; (**f**) *Gazella* cf. *bouvrainae*, right maxilla with P3–M3, SE2-21, occlusal view; (**g**) *Stephanorhinus* sp., right metacarpal IV, Σ-1052, palmar view; (**g′**) *idem*, medial view; (**g″**) *idem*, proximal view; (**h**) *Sus arvernensis*, left dentary with p4–m1, Σ-1391, occlusal view; (**h′**) *idem*, lingual view. Graphical scale in cm.

Remarks. According to the specimen's dimensions, the *Struthio* from Sésklo is much larger than the recent *Struthio camelus* Linnaeus, 1758, as well as larger compared to Late Miocene forms referable to *S. karatheodoris* Forsyth Major, 1888 [18,19]. The recent species has a minimal DAP of the third metatarsal distal trochlea (less than 34.7 mm) and DT of the same anatomical element (less than 38.7 mm) [18,19]. This means that the Sésklo specimen is about 20–25% larger than the largest specimens of the extant species. *S.* cf. *karatheodoris*, from the Late Miocene of Bulgaria, is closer to SE2-1 in mediolateral dimensions, but has a small minimal DAP of the third metatarsal distal trochlea. Thus, the trochlea of SE2-1 is less dorsoventrally compressed than that of *S.* cf. *karatheodoris*, e.g., in distal view, being closer in proportions to the recent species (see fig. 2B in [19]). A specimen that is metrically very close, if not equal, to the studied one, is the tarsometatarsus 5011 of *Struthio* sp. from the Odessa Catacombs [18,19], which is also chronologically close, dated to the MN15 or the beginning of MN16. Two other specimens from Çalta, Turkey (MN15), are also larger than the extant species [20] and dimensionally similar to SE2-1, but their fragmentary preservation (they lack both ends) does not allow any adequate metrical comparison with the latter. It is quite plausible that the Sésklo, Odessa and possibly Çalta specimens belong to a single species, which was present in Eastern Europe during the Ruscinian–Villafranchian time period. In a taxonomic revision of the Cenozoic birds, Mlíkovský [21] (pp. 60–62) considers all Late Neogene ostrich finds from the peri-Pontic region, including the finds from the Odessa Catacombs, as belonging to a single species, *Struthio chersonensis* (Brandt, 1873), so this is a quite probable species attribution for the Sésklo find.

3.2. Proboscidean

Class: Mammalia Linnaeus, 1758.
Order: Proboscidea Illiger, 1811.
Superfamily: Elephantoidea Gray, 1821.
Elephantoidea indet.

Material. SE2-15: proximal part of left humerus; SE2-18: proximal part of left radius and ulna. At least two additional specimens were not identified anatomically, because they are severely damaged, but must belong to a proboscidean judging from their very large size.

Description and Remarks. The available material is badly damaged by the quarry machinery. The preserved parts of the postcranial skeleton have the typical morphology of extant elephants, as described by Smuts et al. [22]. The humerus SE2-15 preserves the caudal part of the humeral head and the major tubercle. The latter is mediolaterally compressed and extends caudally and dorsally, being very prominent in caudal aspect. The diaphysis is preserved until the level of the deltoid tuberosity. The radius and ulna still remain articulated. The former is triangular in proximal view, and has a saddle-shaped proximal articulation with sharply-defined margins. The ulna lacks the olecranon. Its proximal surface for the articulation of the humerus is slightly concave. Measurements are given in Table 1.

Table 1. Dental and postcranial element measurements (in mm) of Elephantoidea indet., *Sus arvernensis*, *Gazella* cf. *bouvrainae*, *Gazellospira torticornis* and *Stephanorhinus* sp. from the lower level of Sésklo. The numbers in parentheses in the *Stephanorhinus* metrical parameters refer to the measurements defined by Guérin [23] (p. 113).

Elephantoidea indet.	**DAPpa**	**DTpa**				
Humerus (SE2-15)	—	>180				
Radius (SE2-18)	(49)	(93)				
Ulna (SE2-18)	—	187				
Sus arvernensis	**Lp4**	**Wp4**	**Lm1**	**Wm1**	**Lm2**	**Wm2**
Lower dentition (Σ-1391)	15.0	11.4	14.0	13.0	20.5	16.2
Gazella* cf. *bouvrainae	**LP3**	**WP3**	**LP4**	**WP4**	**LM1**	**WM1**
Upper dentition	9.1	10.0	9.9	11.0	12.8	13.2
(SE2-21)	**LM2**	**WM2**	**LM3**	**WM3**	**LM1–M3**	
	16.2	13.4	16.7	11.6	43.0	
Gazellospira torticornis	**DAPm**	**DTm**	**DAPda**	**DTda**		
Mc III–IV (SE2-7)	21.8	23.2	25.6	39.9		
***Stephanorhinus* sp.**	**DAPp (3)**	**DTp (2)**	**DAPm (5)**	**DTm (4)**		
Mc IV (Σ-1052)	43.3	46.0	21.7	41.2		

L: length; W: width; DAP: craniocaudal diameter; DT: mediolateral diameter (p: of the proximal end; m: at the middle of the bone shaft; d: of the distal end; a: articular). The upper teeth are designated with capital letters (P: premolars; M: molars), while the lowers with lowercase letters (p: premolars; m: molars).

The proboscidean finds belong to a small-sized taxon. Among the existing Proboscidea during the Plio-Pleistocene of Europe, the specimens from Sésklo SE2 are dimensionally consistent with an attribution to *Anancus arvernensis* (Croizet and Jobert, 1828), a species already known from Sésklo [2,5,24]. However, the material from SE2 is totally inadequate for a specific or even a generic attribution.

3.3. Suid

Order: Artiodactyla Owen, 1848.
Family: Suidae Gray, 1821.
Genus: *Sus* Linnaeus, 1758.
Sus arvernensis (Croizet and Jobert, 1828).

Synonymy. 1992 *Sus* cf. *strozzii* Forsyth Major, 1881—Symeonidis, p. 13; pl. IV, figs. 4 and 4a. 2005 *Sus minor*—Kostopoulos and Athanassiou, p. 181. 2016 *Dasychoerus arvernensis* (Croizet and Jobert, 1828)—Pickford and Obada, p. 133.

Material. Σ-1391: left dentary fragment bearing the p4, m1 and m2.

Description and Remarks. The suid from Sésklo (Figure 4h,h′) belongs to an aged individual, as all preserved teeth are heavily worn. This is particularly true for m1, which is worn down to the very bottom of the crown. As a result of the excessive dental wear, no cuspid characters are preserved in the occlusal surfaces. The dental dimensions are given in Table 1. The specimen is relatively small (see a relevant comment in [25], p. 181), being metrically smaller than the common Early Pleistocene species *Sus strozzii* Meneghini, 1862, the Pliocene *Propotamochoerus provincialis* (Gervais, 1859) and the early Middle Pleistocene (and more recent as well) *Sus scrofa* Linnaeus, 1758 (Figure 5).

Small Ruscinian and Villafranchian suids were originally described from Southern France, under the species names *Aper arvernensis* Croizet and Jobert, 1828 and *Sus minor* Depéret, 1890 (initially regarded as a small-sized "race" of *Sus provincialis* Gervais, 1859). There is general concession among authors that these two species are synonyms, but there was a long debate over which one could be considered valid (see, e.g., [26–30] for accounts of the different opinions). Under current usage the former is valid, following the principle of priority [31]. Berdondini [28] proposed the grouping of these samples, together with *Sus strozzii* and the recent *S. verrucosus* and *S. celebensis*, under the subgenus name *Dasychoerus* Gray, 1873, in accordance to their apparent morphological similarities and their assumed close phylogenetic relationships. This taxonomic view has been accepted by authors of more recent studies (e.g., [31–33]) who furthermore raised *Dasychoerus* to the generic rank, but was subsequently challenged in a new phylogenetic analysis which re-classified the species *arvernensis* and *strozzii* under the genus *Sus* [34]. Since there is no general agreement on the genus-level taxonomy of these species, the customarily used genus name *Sus* is applied here.

The studied specimen was formerly published by Symeonidis [3] as 'specimen 85Σ'; the author referred it to *Sus strozzii*, without any description and discussion on its taxonomic attribution. As is evident from Figure 5, the dental dimensions of Σ-1391 are distinctly smaller than the corresponding metrical ranges of *S. strozzii*. In fact, Σ-1391 fits well within the metrical ranges of *Sus arvernensis* samples from European localities, such as Villafranca d'Asti (Italy), Roussillon (France) and Alcoy (Spain) [26–28,35]. The m2 from the Northern Greek locality of Miliá is also metrically very close to Sésklo (Figure 5b; [30]). The small dimensions of the studied specimen allow an attribution to *S. arvernensis*, despite the advanced wear of its teeth that precludes any morphological comparisons.

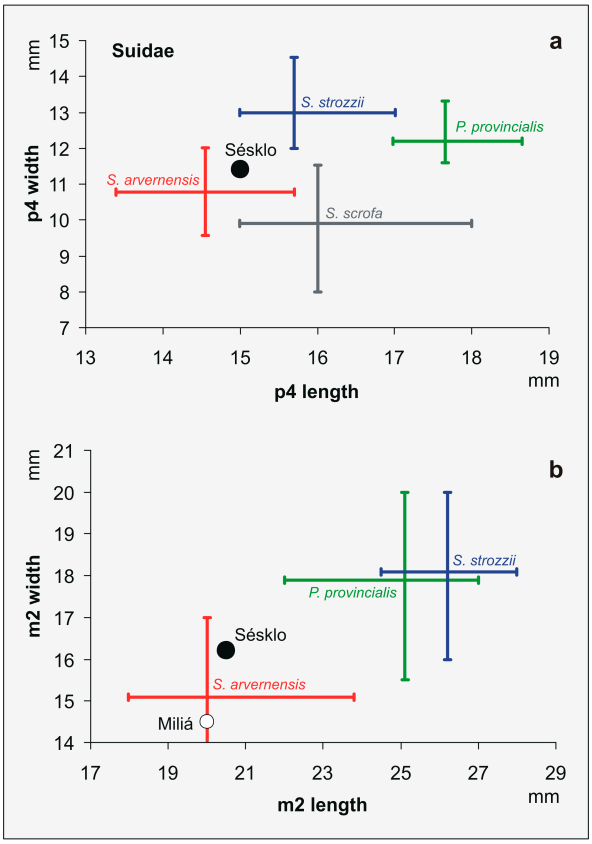

Figure 5. Comparison of the dental dimensions (in mm) of the *Sus arvernensis* dentary part Σ-1391 from Sésklo to the published metrical ranges of the fourth premolar (**a**) and the second molar (**b**) of *Sus arvernensis*, *Sus strozzii*, *Propotamochoerus provincialis* and *Sus scrofa*. The m2 from Miliá plots metrically close to the Sésklo specimen. Original data on species ranges and the Miliá specimen taken from [30–32,36].

3.4. Gazelle

Order: Artiodactyla Owen, 1848.
Family: Bovidae Gray, 1821.
Subfamily: Antilopinae Baird, 1857.
Genus: *Gazella* de Blainville, 1816.
Gazella cf. *bouvrainae* Kostopoulos, 1996.

Material. SE2-21: right maxillary fragment with P3–M3; Σ-1019: left m3.

Description. The upper dentition of SE2-21 is almost completely preserved, lacking the P2 (Figure 4f). All available teeth are broad and characterised by prominent labial styles. The enamel surface is smooth labially, but finely wrinkled lingually. The premolar section seems to be long, though it cannot be measured because of the lack of P2. The P3 and P4 are simple, not bilobe, with well-rounded lingual walls. The paracone rib is prominent labially, situated close to the parastyle and eventually almost merged with it at the base of the crown. The molars have a mesiodistally shorter and broader mesial lobe with more pointed lingual wall, with regard to the distal one. The paracone and metacone ribs are very weak in M1 and M2, but prominent in M3. All molars lack an entostyle lingually between the lobes, as well as any enamel islets in their occlusal surface. Measurements are given in Table 1.

The left m3 Σ-1019 preserves a small part of the dentary on its labial side. It is only slightly worn (the talonid is practically unworn) and hypsodont. The labial conids have angular labial walls. There is no mesostylid. The lingual conids are linguolabially narrow with prominent ribs along their lingual walls. The lingual stylids are well marked, particularly in the upper part of the crown. Mesially, there is a strongly developed goat fold. The talonid is very narrow and pointed distally, in occlusal aspect. The tooth's dimensions are: maximal length = 24.6 mm, alveolar width = 9.2 mm, height = 31.1 mm.

Remarks. The most common European species of the genus *Gazella* during the Villafranchian is *G. borbonica* Depéret, 1884, which is well known from rich samples, particularly from south-west Europe [37–40]. This species is, though, less frequently found in south-east Europe, where two additional species are present as well: *G. bouvrainae* Kostopoulos, 1996 and *G. aegaea* Athanassiou, 2002 [4,5,8,41]. All three are already known from the old collections of Sésklo [4,5,8]. The studied specimens' morphology and size are consistent with an attribution to the genus *Gazella*. The cusp morphology is very similar to that of the *Gazella* samples from the upper levels of the Sésklo Basin (MNQ17) and other contemporary localities of Greece and Western Europe [4,5,42,43]. Metrically, it appears to be distinctly larger with regard to the *G. borbonica* samples from Villafranchian localities of Europe (Figure 6). Indeed, SE2-21 has a longer tooth row than any sample referred to *G. borbonica*, in which, e.g., the molar section is 34.7–40 mm long [44]. Thus, an attribution of the find to this species is unlikely. The somewhat older *G. emilii* Bouvrain, 1998, from the Ruscinian (MN15) of Çalta, Turkey, is also smaller [45]. Nevertheless, the studied specimens are quite comparable to the *Gazella* material already known from Sésklo (Figure 6; [5]), which is mostly not attributable to species, because of the great gazelline taxonomic diversity observed in this locality and the usual lack of association with the taxonomically diagnostic skulls and horn cores. Compared to the *G. bouvrainae* samples from Greek localities, including Sésklo, SE2-21 has very similar dimensions, being always within their range (Figure 6). Moreover, *G. bouvrainae*-type material has a molar section length of 41.8–44.2 mm [4], which also includes SE2-21. It is possible, then, that the studied specimen belongs to the species *G. bouvrainae*. Unfortunately, the dental morphology and dimensions of the third species found in Sésklo, *G. aegaea*, remain unknown, so no comparisons can be made with it. The m3 Σ-1019 is morphologically consistent with an attribution to a *Gazella* species, but it is rather large, and somewhat larger than the maximal dimensions of the type material of *G. bouvrainae*: the maximal length of the Gerakaroú m3s is 23.5 mm [41] (p. 581). Note, however, that the Gerakaroú fauna is more recent. In conclusion, the *Gazella* find from Sésklo SE2 is larger than the contemporaneous West European species *G. borbonica*, very similar to *G. bouvrainae* and can be quite probably identified with the latter.

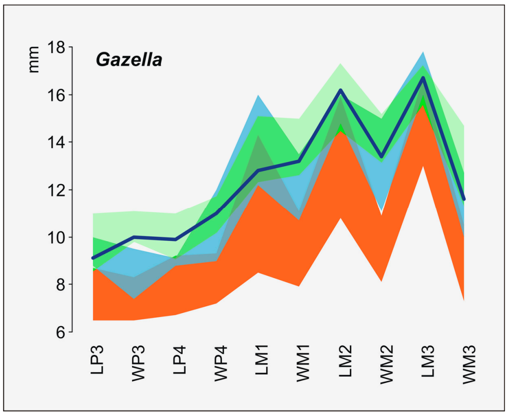

Figure 6. Comparison of the dental dimensions (in mm) of *Gazella* cf. *bouvrainae* from Sésklo SE2 (upper tooth row SE2-21, blue line) to the dimensional ranges of the large sample of *Gazella borbonica* from La Puebla de Valverde, Spain (orange area, original data according to [44]), which essentially also include the ranges of El Rincón, Spain [37] and Saint-Vallier, France ([42] and personal data). The measurement range of upper teeth from the Sésklo old collections referred to *Gazella* sp. (sky blue area, data according to [5]) and the type material of *G. bouvrainae* from Gerakaroú, Greece (green area, data according to [41]), are also plotted.

3.5. *Spiral-Horned Antelope*

Order: Artiodactyla Owen, 1848.
Family: Bovidae Gray, 1821.
Subfamily: Antilopinae Baird, 1857.
Genus: *Gazellospira* Pilgrim and Schaub, 1939.
Gazellospira torticornis (Aymard, 1854).

Synonymy. 1992 *Gazellospira torticornis* (Aymard) *pro parte*—Symeonidis, p. 11, pl. V, VI. 1992 *Gazella borbonica* (Depéret, 1816) *pro parte*—Symeonidis, p. 12. 1998 *Gazellospira torticornis* (Aymard, 1854)—Athanassiou, pp. 135–155; pl. Z, figs. 3 and 4; pl. H, fig. 1. 2005 *Gazellospira torticornis* (Aymard, 1854)—Athanassiou.

Material. SE2-7: distal part of a left metacarpal III–IV.

Description and Remarks. This partial metacarpal (Figure 4b) is characterised by a dorsopalmar compression in the distal part of its shaft and, more importantly, by a concave palmar side, which forms a groove along most of the palmar face of the specimen. The latter character diverges from the typical bovid morphology, approaching the cervid one, and is distinctive of *Gazellospira* [46]. The dorsal side bears a very narrow and shallow longitudinal canal, which is visible only distally, because of the complete fusion of the third and fourth metacarpals. The distal articular end has very prominent keels, which become thinner and sharper palmarly. The articulations of the third and fourth metacarpals are almost equally large. The specimen's dimensions are given in Table 1. It is metrically similar to the largest metacarpals III–IV already known from the upper level of Sésklo [9] and falls within the metrical range given by Duvernois and Guérin [47] (p. 353).

3.6. *Large Bovid*

Order: Artiodactyla Owen, 1848.
Family: Bovidae Gray, 1821.
Subfamily: Bovinae Gray, 1821.
Tribe: Bovini Gray, 1821.
Bovini indet.

Material. SE2-5: distal part of left humerus; Σ-1390: proximal part of left metacarpal III–IV; SE2-6: distal part of right tibia.

Description and Remarks. Three large-sized specimens are characterised by bovid morphology (according to the distinctive features defined by Heintz [48]), and high robustness. Measurements are given in Table 2. The humerus lacks the medial epicondylus. The trochlea has a deep medial groove and sharply margined lateral condyle (Figure 4e,e'). The lateral epicondylus forms a sharp crest along its lateral margin. The metacarpal (Figure 4c,c') and the tibia (Figure 4d) are stout, having considerably strong bodies with regard to their proximal and distal ends (Table 2).

Table 2. Dimensions (in mm) of postcranial elements from the lower level of Sésklo referred to Bovini indet.

Humerus	**DAPm**	**DTm**	**DAPd**	**min DAPda** [1]	**DTd**	**DTda**
SE2-5	40.0	34.5	(75)	38.5	75.5	70.5
Metacarpal III–IV	**DAPp**	**DTp**	**DAPm**	**DTm**		
Σ-1390	41.0	62.0	40.4	42.4		
Tibia	**DAPm**	**DTm**	**DAPd**	**DTd**		
SE2-6	33.5	43.8	54.1	73.3		

[1] Minimal DAP of the trochlea.

Since the bovid taxonomy is based primarily on cranial morphology, the scanty available postcranial material is not very informative taxonomically. The specimens' large size and robust proportions indicate that they quite probably belong to a bovine taxon. In the biochronological (pre-MN17) and biogeographic context of the lower level of Sésklo, the candidate bovid genera of that size are *Leptobos* Rütimeyer, 1878, *Alephis* Gromolard, 1980, and *Grevenobos* Crégut-Bonnoure and Tsoukala, 2017. Compared to the known dimensional ranges of *Leptobos* species, the studied specimens fall metrically within the ranges of the large-sized species, such as *L. merlai* De Giuli, 1986 and *L. etruscus* (Falconer, 1859), while they are generally larger than *L. elatus* (Croizet and Pomel, 1853) and *L. furtivus* Duvernois and Guérin, 1989 (see [47], p. 364, [49], pp. 81, 98, 110, [50], pp. 185–186). All specimens are also metrically similar to the *Alephis* material from France and Spain, described by Michaux et al. and Montoya et al. [35,51], as well as to the postcranial material from Miliá, Greece, referred to *Grevenobos antiquus* Crégut-Bonnoure and Tsoukala, 2017 [52]. Hoping that more diagnostic material will emerge in the future, the available fossils are currently referred to as Bovini indet.

3.7. Rhinoceros

Order: Perissodactyla Owen, 1848.
Family: Rhinocerotidae Gray, 1821.
Genus: *Stephanorhinus* Kretzoi, 1942.
Stephanorhinus sp.

Material. Σ-1052: proximal part of right metacarpal IV.

Description and Remarks. The specimen is mentioned by Symeonidis [3] as "specimen 77Σ: metacarpal" in his specimen list for "*Dicerorhinus* cf. *etruscus*", without description. It preserves the proximal two-thirds of the original bone (Figure 4g,g′). The body of the bone curves laterally and its cross section is almost triangular, the medial side being flat and the lateral forming an edge. The proximal end bears a large triangular articular facet for the unciform and two medial ones for the third metacarpal (Figure 4g′,g″); the anterior is elliptic in shape and directed craniocaudally, while the posterior is sub-circular, situated at the caudal edge of the proximal articulation. The specimen's dimensions in mm, taken according Guérin [23], are given in Table 1.

The morphology of the Sésklo specimen is very similar to that of *Stephanorhinus megarhinus* (Christol, 1834) from Montpellier [23] (p. 513), but it is metrically smaller, comparable to *S. jeanvireti* (Guérin, 1972) [23] (p. 514). The single available rhinocerotid find is certainly insufficient for a specific attribution. The family is scarcely represented in Sésklo; it is also known by a few, mainly autopodial specimens from the upper level of the locality referred to *Stephanorhinus* sp. as well [5] (pp. 270–273). It is yet unknown if the finds are attributable to a single species in both levels.

3.8. Hipparionine Horse

Order: Perissodactyla Owen, 1848.
Suborder: Hippomorpha Wood, 1937.
Family: Equidae Gray, 1821.
Tribe: Hipparionini Quinn, 1955.
Genus: *Plesiohipparion* Qiu, Huang and Guo, 1987.
Plesiohipparion cf. *shanxiense* Bernor, Sun and Chen, 2015.

Synonymy. 1992 *Equus (Hippotigris) stenonis* Cocchi, 1867 *pro parte*—Symeonidis, pp. 4–5; pl. III, figs. 2, 2a, 3, 3a, 4 and 4a; pl. IV, figs. 2 and 2a.

Material. SE2-3: left dentary fragment with p2 and part of p3; SE2-8: left dentary fragment with p3–m1 and parts of p2 and m2; SE2-4: left m3; SE2-2: part of mandible with left d2–d3 and right d2–d4; Σ-1037: distal part of right humerus; Σ-1047, Σ-1048, Σ-1049: distal part of left radius; SE2-22: distal part of right metacarpal III; Σ-1040: epiphysis of left tibia (juvenile); Σ-632: left third tarsal (lateral cuneiform); Σ-571, Σ-1039: proximal parts of left metatarsal III; Σ-633: diaphysis of metatarsal III; Σ-1036: right calcaneus; Σ-630: right calcaneus part; Σ-382, Σ-618, Σ-1035: left astragalus; Σ-629, Σ-1033, Σ-1038: right astragalus; Σ-1002: left proximal phalanx III; Σ-1001, Σ-1004: right proximal phalanx III; Σ-631: right distal phalanx III.

Description of the Dentition. The dentition is known from three mandibular specimens, a juvenile, an adult and a senile (SE2-2, SE2-8 and SE2-3, respectively), as well as an isolated m3. The preserved permanent teeth are characterised by a U-shaped linguaflexid, and angular metaconid and metastylid, a configuration that is usually known as a "caballine" double knot (e.g., [17,53,54]), or "houfenoid" double knot (specifically for hipparions; e.g., [55]). This feature also allows the distinction of these hipparion cheek teeth from the *Equus* ones from the upper level of Sésklo, which are characterised by a stenonid double knot (i.e., V-shaped linguaflexid, and round metaconid and metastylid) [5,6]. The enamel is not intensely plicate; in occlusal aspect, it exhibits, though, minor very fine and open folding. The postflexid is symmetrical. The labial wall of the labial conids is only slightly convex, almost straight. The ectoflexid is broad and short, and does not penetrate the isthmus. It is a simple arc in m1, but its distal wall forms a bifid pli caballinid in the premolars (incipient in p3, well developed in p4). The p2 and the partly preserved p3 of the senile specimen SE2-3, are much worn and their occlusal morphology is not observable, except for the symmetrical postflexid in p2. Measurements are given in Table 3.

Table 3. Dental dimensions (in mm) of *Plesiohipparion* cf. *shanxiense* from the lower level of Sésklo (site SE2). The measurements are occlusal, excluding cement, except for Ld2–d4, which is alveolar (measurement methodology according to [17]).

	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm3	Wm3
SE2-8	—	—	28.9	13.7	27.2	13.6	24.7	12.2	—	—
SE2-4	—	—	—	—	—	—	—	—	27.1	11.2
SE2-3 (senile)	27.8	13.6	—	—	—	—	—	—	—	—
	Ld2–d4	**Ld2**	**Wd2**	**Ld3**	**Wd3**	**Ld4**	**Wd4**			
SE2-2 left	—	35.8	11.1	30.9	9.8	—	—			
SE2-2 right	103.5	35.8	10.5	30.3	9.6	33.2	9.4			

d: deciduous tooth.

The deciduous teeth have the characteristic elongated shape of the equid lower deciduous cheek teeth series. There is no d1. Their most prominent feature is the houfenoid morphology of the metaconid–metastylid complex ("double knot"), and the almost straight enamel along the labial wall, as in the permanent dentition. The preflexid and the postflexid are sagittally elongate; the latter is symmetrical. The isthmus of the double knot is very narrow and it is not penetrated by the ectoflexid. There is a pli caballinid in the labial wall of all teeth; it is bifid in d3. A protostylid is visible in the labial wall of d3 and d4, but it is not yet worn. Measurements are given in Table 3.

Description of the Limb Bones. Some of the available limb bones, such as the humerus, radius and tibia, do not differ from the typical recent equid morphology. However, the available autopodial bones are distinctively different from those of *Equus*, except for the calcaneus, which does not differ significantly. The single calcaneus from Sésklo referred to *Plesiohipparion* (Σ-1036) is somewhat more massive than the *Equus stenonis* ones from the upper level of the same locality, and its head (calcaneal tuberosity) is more spherical, without a transverse constriction at its proximal end, as is the case with *Equus*. The Sésklo *Plesiohipparion* astragali differ from *Equus* in having higher height/width ratio, and higher neck (*collum tali*) (Figure 7c–e,c′–e′). This is apparently related to the advanced reduction of the lateral metatarsals in *Equus*, which caused the widening of the central one, and of the tarsal bones articulated to it as well. This is also observed in the studied metapodials: The distal third-metacarpal part SE2-22 is noticeably dorsopalmarly deeper and mediolaterally narrower (i.e., it is more circular, not elliptical, in cross section) than the *Equus* ones from the same locality (Figure 7h,h′,i,i′); moreover, it bears longitudinal grooves medially and laterally on its palmar face to accommodate the second and fourth metacarpals, respectively. The third metatarsals (Figure 7f,g) also appear to be narrower and deeper dorsopedally; at least one (Σ-571) is, though, mediolaterally compressed. The proximal phalanges are the most evidently diverging morphologically from those of *Equus* (Figure 7j–m,j′–m′): As in the case of metapodials, they are more cylindrical in cross section, being less dorsovolarly compressed. Moreover, in dorsal or volar aspect, their distal end is narrower with regard to the proximal one. Their *trigonum phalangis* ('V-scar') is much shorter, confined to the proximal half of the bone, and less sharply defined than in *Equus*, having the form of a thick and blunt V-shaped ridge markedly projecting volarly (Figure 7j′–m′). Measurements of the limb bones are given in Table 4.

Table 4. Postcranial element dimensions (in mm) of *Plesiohipparion* cf. *shanxiense* from the lower level of Sésklo. The measurement numbers refer to the measurements defined by Eisenmann et al. [17]: Radius: **3**, minimal breadth; **4**, depth of the diaphysis at the level of **3**; **8**, distal articular breadth; **9**, distal articular depth; **10**, distal maximal breadth; **11**, breadth of the radial condyle; **12**, breadth of the ulnar condyle. Metacarpal III: **1**, maximal length; **3**, minimal breadth; **4**, depth of the diaphysis at the level of **3**; **10**, distal maximal supra-articular breadth; **11**, distal articular breadth; **12**, depth of the distal articular keel; **13**, minimal depth of the distal lateral condyle; **14**, depth of the distal medial condyle. Metatarsal III: **3**, minimal breadth; **4**, depth of the diaphysis at the level of **3**; **5**, proximal articular breadth; **6**, proximal articular depth; **7**, maximal diameter of the articular face t for the third tarsal. Calcaneus: **1**, maximal length; **2**, length of the proximal part; **3**, minimal breadth; **4**, proximal maximal breadth; **5**, proximal maximal depth; **6**, distal maximal breadth; **7**, distal maximal depth. Astragalus: **1**, maximal length; **2**, maximal diameter of the medial condyle; **3**, breadth of the trochlea (at the apex of each condyle); **4**, maximal breadth; **5**, distal articular breadth; **6**, distal articular depth; **7**, maximal medial depth. Proximal phalanx III: **1**, maximal length; **2**, dorsal length; **3**, minimal breadth; **4**, proximal breadth; **5**, proximal depth; **6**, distal maximal breadth; **7**, distal articular breadth; **8**, distal articular depth; **9**, minimal length of the trigonum phalangis. Distal phalanx III: **3**, maximal breadth; **5**, articular depth; **6**, maximal height.

Radius	**3**	**4**	**8**	**9**	**10**	**11**	**12**		
Σ-1047	—	—	62.3	38.0	69.6	25.3	14.2		
Σ-1048	39.0	30.0	59.8	38.4	70.6	—	12.5		
Σ-1049	—	—	64.4	39.4	75.9	28.7	12.1		
Metacarpal III	**3**	**4**	**10**	**11**	**12**	**13**	**14**		
SE2-22	33.8	27.6	42.9	43.4	38.3	30.6	32.0		
Metatarsal III	**3**	**4**	**5**	**6**	**7**				
Σ-571	27.7	31.4	45.3	37.8	43.0				
Σ-633	29.0	29.3	—	—	—				
Σ-1039	30.4	32.2	47.5	37.5	43.6				
Calcaneus	**1**	**2**	**3**	**4**	**5**	**6**	**7**		
Σ-1036	124.8	85.0	20.8	35.2	54.7	49.0	43.7		
Σ-630	—	—	—	—	—	52.3	—		
Astragalus	**1**	**2**	**3**	**4**	**5**	**6**	**7**		
Σ-382	60.5	59.2	30.1	54.0	48.0	—	—		
Σ-618	64.8	65.7	29.3	58.6	50.0	37.0	51.6		
Σ-629	68.1	65.3	30.8	58.5	48.9	39.5	52.6		
Σ-1033	66.0	62.8	30.6	56.5	45.0	37.5	50.6		
Σ-1035	—	68.8	33.8	—	—	—	—		
Σ-1038	64.9	63.3	29.9	56.0	46.1	37.9	52.0		
Proximal Phalanx III	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Σ-1001	80.0	73.0	31.3	45.9	37.5	38.5	38.3	23.5	36.3
Σ-1002	81.6	74.2	29.7	43.8	37.0	36.7	36.6	23.1	37.4
Σ-1004	78.0	70.1	28.9	45.6	38.0	36.9	35.0	21.7	33.8
Distal Phalanx III	**3**	**5**	**6**						
Σ-631	58.0	27.0	36.5						

Figure 7. Fossil specimens of *Plesiohipparion* cf. *shanxiense* from the lower level of Sésklo, partly compared to specimens of *Equus stenonis* from the upper level of the same locality: (**a**) *P.* cf. *shanxiense*, left dentary fragment with p3–m1 and parts of p2 and m2, SE2-8, occlusal view; (**b**) *P.* cf. *shanxiense*, part of mandible with left d2–d3 and right d2–d4, SE2-2, right lateral view; (**b′**) *idem*, occlusal view; (**c**) *P.* cf. *shanxiense*, right astragalus, Σ-629, dorsal view; (**c′**) *idem*, pedal view; (**d**) *P.* cf. *shanxiense*, right astragalus, Σ-1038, dorsal view; (**d′**) *idem*, pedal view; (**e**) *E. stenonis*, right astragalus, Σ-615, dorsal view; (**e′**) *idem*, pedal view; (**f**) *P.* cf. *shanxiense*, left proximal metatarsal III, Σ-571, dorsal view; (**g**) *P.* cf. *shanxiense*, left proximal metatarsal III, Σ-1039, dorsal view; (**h**) *P.* cf. *shanxiense*, right distal metacarpal III, SE2-22, dorsal view; (**h′**) *idem*, palmar view; (**i**) *E. stenonis*, left metacarpals II–IV, Σ-113, dorsal view; (**i′**) *idem*, palmar view; (**j**) *P.* cf. *shanxiense*, right proximal phalanx III, Σ-1004, dorsal view; (**j′**) *idem*, volar view; (**k**) *P.* cf. *shanxiense*, left proximal phalanx III, Σ-1002, dorsal view; (**k′**) *idem*, volar view; (**l**) *P.* cf. *shanxiense*, right proximal phalanx III, Σ-1001, dorsal view; (**l′**) *idem*, volar view; (**m**) *Equus stenonis*, anterior left proximal phalanx III, Σ-353, dorsal view; (**m′**) *idem*, palmar view. Graphical scale in cm.

Remarks. A very diverse and abundant group during the Late Miocene, the hipparionine equids declined rapidly during the Pliocene in Eurasia, until their final extinction and replacement by *Equus* at the end of this epoch [56,57]. Nevertheless, the tridactyl equid remains found in Ruscinian and Villafranchian faunas still retain a considerable morphologic and taxonomic diversity. Two groups are identified, one characterised by V-shaped linguaflexids in the lower dentition (known as the hipparionine group), and another by U-shaped linguaflexids (known as the caballoid or houfenoid group). The available material is, though, scarce in most localities, so the detailed morphology of these populations is usually not well known, and their classification is ambiguous in many cases. The hipparionine finds from Sésklo certainly belong to one of the last hipparions of Europe, as evidenced by their large size and robustness, and their houfenoid dentition, as well as by their stratigraphic proximity to the middle Villafranchian (MNQ17) fauna of the locality.

Several species have been named in the Ruscinian and lower Villafranchian of Eurasia. One of the most typical Ruscinian species is the *Hipparion crassum* Gervais, 1859, characterised by hipparionine dentition and short and robust metapodials. Its metapodials are, indeed, much shorter and proportionally more robust than those from Sésklo: the third metacarpal total length is about 150 mm [58] (pl. XII), while that of the studied material seems to have been about 26 cm (rough estimation based on the bone morphology). The remarkably short metapodials are actually the most important character of this species [59] and clearly preclude an attribution of the Sésklo material to this taxon (see also Figure 8a). Moreover, the lower cheek teeth of *H. crassum* possess a hipparionine double knot (with rounded metaconid and metastylid), quite unlike the houfenoid double knot of the Sésklo mandibular specimens.

In contrast to *H. crassum* there are also species evolved during the Ruscinian with quite slender limb bones. *Hipparion longipes* Gromova, 1952 was originally described from the Late Miocene of Pavlodar, Kazakhstan, but fossils attributable to this species have been also described from younger localities, such as Çalta, Turkey, and Megalo Emvolon, Greece (both dated to late Ruscinian, MN15) [64]. It is a large-sized species, characterised by very long but slender metapodials, unlike the Sésklo ones. It is, though, metrically close to Sésklo in short-bone dimensions, like those of the astragalus (Figure 9a,b). Another long-limbed Ruscinian species, *Hipparion fissurae* Crusafont and Sondaar, 1971, named on the material from Layna in Spain (MN15), is quite distinct from the Sésklo hipparion in having very long and slender metapodials as well [61,69] (see also Figure 8). Moreover, its lower cheek teeth are smaller and have quite rounded double knots (see fig. 6 in [61]), unlike the Sésklo hipparion. A less slender species, the Asiatic *Hipparion tchicoicum* Ivanjev, 1966, has large metapodials, similar in dimensions and proportions to the Sésklo ones (somewhat more slender, however), but its dentition is quite different, characterised by hipparionine pattern, penetrating ectoflexids in premolars, and smaller size [65,70].

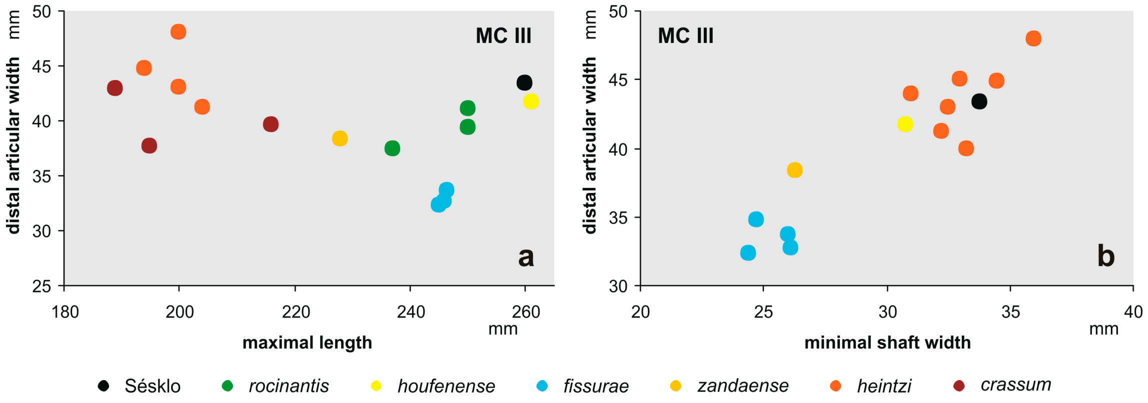

Figure 8. *Cont.*

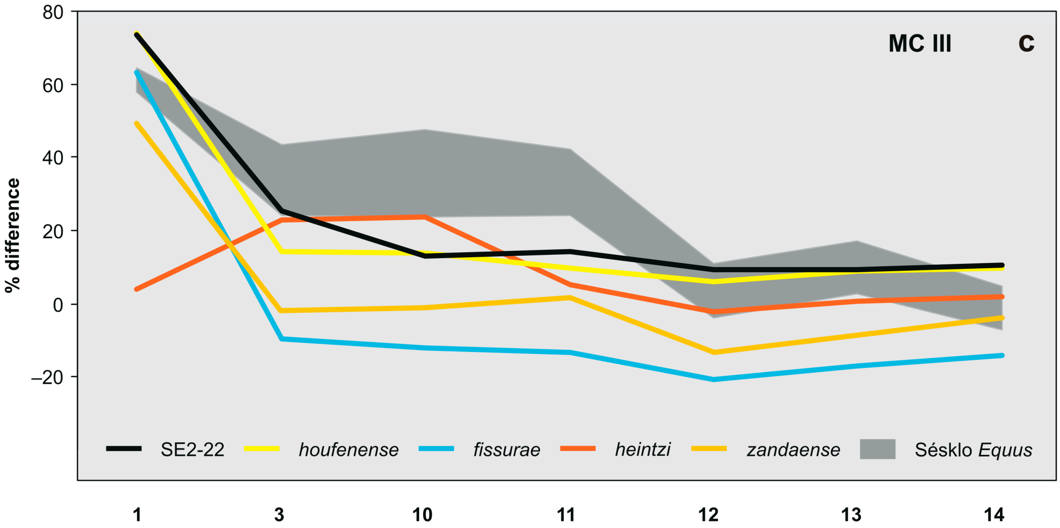

Figure 8. Metrical comparison (in mm and as % differences) of the metacarpal III among Plio-Pleistocene hipparionine samples from Eurasian localities, based on published data [60–68]: (**a**) scatter plot of the maximal length to the distal articular width; (**b**) scatter plot of the minimal shaft width to the distal articular width; (**c**) ratio diagram of seven metrical parameters. The specimen plotted as *Pl. houfenense* (**a**–**c**) is not securely referred to this species [62]. An arbitrary standard sample was used for the ratio diagram (**c**). The measurement **1** (maximal length) of SE2-22 (**a**,**c**) is estimated. The numbered measurements in (**c**) refer to those defined by Eisenmann et al. [17] and are explained in the Table 4 caption. The metrical range of the *Equus stenonis* sample from Sésklo [5,6] is also plotted in (**c**).

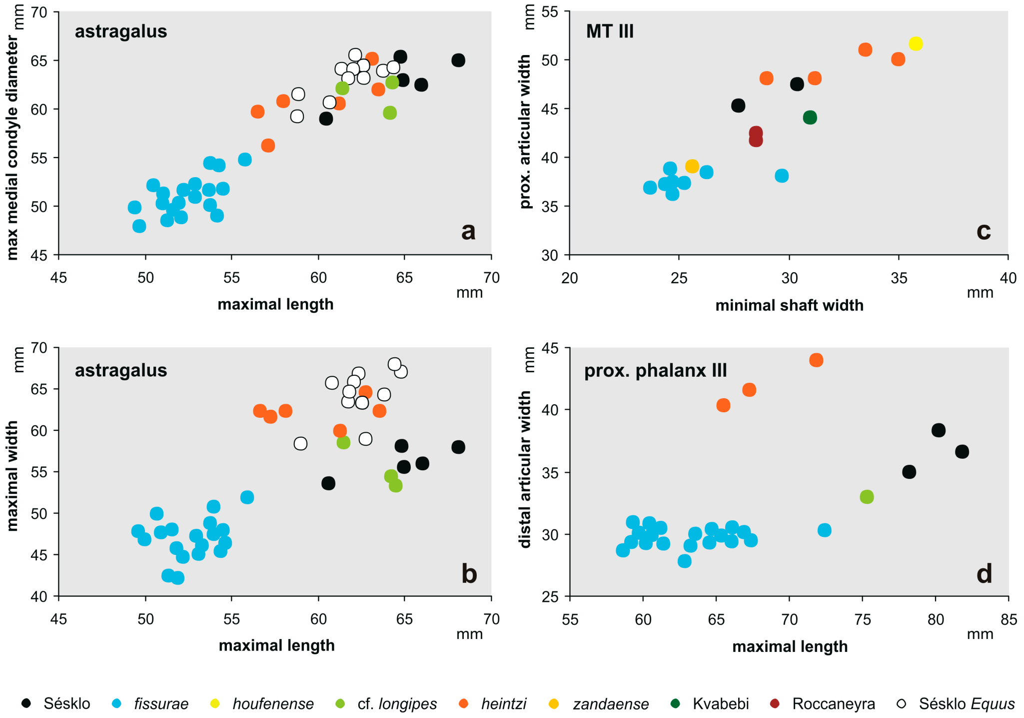

Figure 9. Metrical comparison (in mm) of the astragalus (**a**,**b**), metatarsal III (**c**) and proximal phalanx III (**d**) among Plio-Pleistocene hipparionine samples from Eurasian localities, based on published data [61–64,68,71]. The *Equus stenonis* astragalus sample from the upper fossiliferous level of Sésklo [5,6] is also plotted (**a**,**b**).

Some geochronologically later European samples, dated to the Villafranchian age, represent larger than the Ruscinian ones and robustly built hipparions. The very poorly known *Hipparion moriturum* Kretzoi, 1954 from Kislang, Hungary, seems to be similar in dimensions to the studied postcranial material, though rather more robust, with a metatarsal III length of 277 mm and a distal articular width of 43.1 mm [72] (p. 325). This species has, however, intensely plicate enamel, unlike the Sésklo material [73]. The locality is dated to the middle Villafranchian (MN17) based on the alleged co-occurrence of *Hipparion* and *Equus*. A similar species, also very poorly known, is *Hipparion malustenense* Radulesco and Samson, 1967, which was named on a single metatarsal III and scarce dental material from Mălușteni, Romania [74]. Later authors have, though, questioned the conspecificity of the referred material, as well as the hipparionine attribution of certain specimens, suggesting that they may belong to *Equus* [71]. The metatarsal is somewhat smaller than the Sésklo specimens in articular breadths, but it is distinctively shorter in total length [71,74], approaching the proportions seen in *H. crassum*. Forsten [65] actually believed that both *H. malustenense* and *H. moriturum* may belong to *H. crassum*.

The large size of the hipparion from Sésklo, its robust skeletal elements, as well as its houfenoid lower dentition, differentiate it from the Ruscinian species mentioned above. Its morphological features occur in the latest hipparionines and are considered derived [17,54]. In fact, these are typical characters of the "*Plesiohipparion*" group, *sensu* Bernor et al. [72], and the *Plesiohipparion* taxon (in genus or subgenus rank), according to Forsten [75] and Zouhri and Bensalmia [76], which is characterised by large size and advanced dentition with houfenoid lower cheek teeth. *Plesiohipparion* belongs to a suprageneric group of Palaearctic taxa unified by the houfenoid lower dentition that also includes the Asian *Proboscidipparion* Sefve, 1927 and the African *Eurygnathohippus* van Hoepen, 1930. The latter is clearly distinguished from the studied material because of the presence of ectostylids in its lower cheek teeth, which is a distinctive character of these African hipparions. The main apomorphic feature of *Proboscidipparion*, its greatly retracted nasals, is not observable in the Sésklo sample, as it lacks cranial specimens. The type species of this genus, *Pr. sinense*, which is also large and geochronologically close to Sésklo, has, though, quite larger metapodials [77] (p. 184), indicating a more robust animal that stood higher than the Sésklo hipparion.

Plesiohipparion is typified by the south-west European species *H. rocinantis* Hernandez-Pacheco, 1921 (usually synonymised with *H. crusafonti* Villalta, 1952 since Pirlot [67]) from the lower Villafranchian (MN16) of Spain (Villarroya, La Puebla de Almoradier, Las Higueruelas). It is large sized, though somewhat smaller than the Sésklo hipparion, and its dental occlusal morphology is quite similar to the latter [67] (pp. 57, 105), (see fig. 20G,H in [78]), except for the absence of protostylids in the Sésklo sample. Pirlot [67] and von Koenigswald [73] reported metapodial measurements from Villarroya (metacarpals III: 237–250 mm long, with a distal diameter of 37.5–41.1 mm; metatarsals III: 269–278 mm long, with a proximal diameter of 42.9–45.4 mm), which are also somewhat smaller than the Sésklo specimens (Figure 8). The samples from Roccaneyra (France) and Kvabebi (Georgia), which are possibly identifiable as *P. rocinantis*, are somewhat smaller than the Sésklo one in articular dimensions as well (Figure 9c; [71]); the Sésklo metatarsals must have been, though, considerably longer, judging from the estimated metacarpal length of 26 cm. Other species referred to *Plesiohipparion* include smaller-sized species, such as *Pl. zandaense* (Li and Li, 1990), as well as the large-sized *Pl. houfenense* (Teilhard de Chardin and Young, 1931) and *Pl. huangheense* Qiu, Huang and Guo, 1987. The latter two exhibit only very slight differences from each other and both appear to be closely related to *Pl. rocinantis* (Forsten [75] actually believed that they are conspecific to it; see also [76]). *Pl. houfenense* has a lower dentition, which is quite similar dimensionally and metrically to that from Sésklo (see fig. 151 in [79]). A geographically adjacent form from Gülyazı, Turkey, was described as "*Plesiohipparion*" aff. *huangheense* by Bernor and Lipscomb [80], and despite its rather bad preservation, it looks dentally very similar to the Sésklo specimens, except for the presence of protostylids in its teeth. However, this dental structure tends to be reduced or lost in the more recent *Plesiohipparion* finds [80], while a certain degree of individual variation in this feature is also possible. Another sample from China, recently described as a new species, *Plesiohipparion shanxiense* Bernor, Sun and Chen, 2015, is dentally identical to the studied sample, both in morphology (including the aforementioned absence of protostylids) and dimensions [62]. A metatarsal referred by Bernor et al. [62] to this species is extremely large, about 20% larger in width dimensions than the Sésklo specimens (plots outside of the diagram area in the relevant scatter plot of Figure 9c), but it is unrelated to the holotype, as it comes from another locality. The scanty material available and the contemporary presence of the also very large-sized *Proboscidipparion sinense* in the Pleistocene of China may make certain postcranial element attributions less secure.

In the graphical comparisons of Figure 8, the Sésklo metacarpal SE2-22 plots closely to the samples of *Pl. rocinantis* and *Pl. houfenense*, while it also has the same proportions to the latter species (Figure 8c) (note, however that this single specimen is not securely referred to *Pl. houfenense* [62], while the measurement 1 of SE2-22 is estimated). The metacarpals of *H. fissurae* and *Pl. zandaense* have also similar proportions, except that they are smaller (the former is also more slender). The scatter plots of Figure 9a,b show the large size of the hipparionine astragali from Sésklo, also with regard to the *Equus stenonis* ones from the upper fossiliferous level of the same locality, which are lower and broader (see also Figure 7c–e). The same is true for the astragali of the short-legged *Pr. heintzi* from Çalta, Turkey. The proximal metatarsals III from Sésklo are among the largest specimens with regard to their articular width, but their diaphyses appear to be more slender compared to certain specimens referred to *Pr. heintzi* from Çalta and a specimen referred with reservation to *Pl. houfenense*. The proximal phalanges III are comparatively long, close to a specimen of *H.* cf. *longipes* from Çalta, and much more slender than *Pr. heintzi* from the same Turkish locality.

Summarising the comparisons, the still incompletely known hipparion from Sésklo apparently belongs to a species of the genus *Plesiohipparion*. Based on the currently available dental and postcranial material, it is provisionally referred to *Pl. shanxiense*, because of its large size and its perfect morphological and metrical match with the holotype of this species [62]. Specimens from China and Turkey referred to *Pl. huangheense*, as well as samples of *Pl. houfenense*, are also quite similar. It is interesting that these late Eurasian species currently classified under the generic name *Plesiohipparion*, do not exhibit among them significant morphological differences in their dentition, while their metrical ones could possibly be attributed to temporal and/or geographical variation across their vast biogeographic distribution. This was apparently the reason why Forsten [75] considered the species-level taxonomic diversity of *Plesiohipparion* as a possible result of oversplitting, suggesting a single valid species name (*Pl. rocinantis*) for all these samples across Eurasia [75,76]. More recent research has shown, however, the existence of a considerable variation in postcranial morphology, which points to a certain taxonomic diversity within the genus *Plesiohipparion* (e.g., [68]). The true extent of this diversity remains to be investigated in future research. Discoveries of new material with associated craniodental and postcranial elements are certainly needed in order to improve our knowledge on these late hipparion populations.

4. Biostratigraphy–Palaeoecology

The chronology of the Sésklo Basin is based on its fossil fauna. Radiometric dates are not available, mainly because the potentially datable tuff horizons are buried and not accessible, while a magnetostratigraphic sampling hasn't yet produced any results. Although the available faunal material from the lower level of Sésklo is not abundant, it offers some clues on the geological age of this horizon. The genus *Struthio* is known from several Neogene localities and it is considered to exist at least till the late Pliocene (MN16) in the peri-Pontic region [21]. *Sus arvernensis* is a Pliocene species, predominantly Ruscinian (MN14–MN15), that is also widespread in the early Villafranchian (MN16) before evolving to the typical Villafranchian species *S. strozzii* [30,32]. *Gazella bouvrainae* is currently known only from localities dated to MN17 (MNQ17–MNQ18) [4]. The large antelope *Gazellospira torticornis* is also typically a middle Villafranchian (MN17) species, but it has been also found in older (MN16) and more recent (MNQ19) localities [47,81], particularly in Eastern Europe.

The affinities of the hipparionine horse from Sésklo to the large-sized *Plesiohipparion* species point to a late MN16 or even MN17 age [75] (although the MN17 dating quite probably results from the alleged co-existence with *Equus* in many localities). The absence of protostylids in the Sésklo sample, if not subject to individual variation, is also a character indicating a later age, as Bernor and Lipscomb [80] observed a reduction of this structure within the *Plesiohipparion* species succession. Furthermore, the absence of *Equus* in the lower level of Sésklo, while by far the commonest taxon in the upper level of the same locality, points to a pre-2.5 Ma age [57]. In conclusion, the fauna of the lower level of Sésklo is better placed biochronologically to MN16, possibly in its upper part, because of the large and advanced *Plesiohipparion* and the stratigraphic proximity of the MNQ17 fauna of the basin. This dating also means that the biochronologic range of the gazelle *G. bouvrainae* extends quite probably back to MN16.

Based on its upper level faunal composition, the Sésklo palaeoenvironment has been reconstructed as open and rather dry, first, because of the prevalence of horses in number of individuals, and second, because of the high taxonomic diversity of antelopes [5]. In a more recent dental mesowear and microwear study, Rivals and Athanassiou [82] found that the grazers and the mixed-feeders dominate the fauna, indicating again a predominantly open and dry environment, with patches of open woodland or thickets. The lower-level fauna evokes a similar picture, as a considerable part of its components—*Struthio*, Bovini, *Stephanorhinus*, *Plesiohipparion*—indicates an open environment. It should be pointed out that the single available *Plesiohipparion* metacarpal is estimated to have been longer than the corresponding *Equus* ones from the same locality, implying a more cursorial animal. Other components of the fauna—*Gazella*, *Gazellospira*—were certainly inhabitants of rather open and dry environments, like the recent middle-sized antelopes, whereas the only potentially forest/woodland dweller is *Sus arvernensis*. Overall, the faunal compositions at Sésklo do not show any significant difference in the environment between the two levels.

5. Discussion

Fossil material excavated in the past without proper records about its exact stratigraphic provenance often results in mixing of specimens from different stratigraphic levels, time averaging in biochronological studies, and false associations among heterochronous taxa. This was apparently the case with the Sésklo fauna, where two fossil faunas deriving from distinct stratigraphic levels were lumped together as a single sample. The physical characters of certain specimens collected probably in 1982, that point to the lower layers of the local sedimentary sequence, as well as new material collected from the stratigraphically adjacent findspot SE2, document the existence of an older hipparion-dominated fauna in the Sésklo quarry, quite distinct from the later *Equus*-dominated one. The two site-clusters that yielded the two faunas are well separated from each other (Figure 2). The lower level comprises the sites A, Γ and SE2, while the upper the sites the B, Δ, E, SE3 and SE4. The site A is the only one that has not yielded any equid specimens: all its finds belong to the proboscidean *Anancus arvernensis* (Croizet and Jobert, 1828), presumably to a single individual [2,5,24]. Although the *Anancus* from Sésklo has been considered of MNQ17 age in accordance to the rest of the upper-level fauna [5], it is better placed in MN16, based on the present biostratigraphic data (see also Athanassiou [24], p. 29). This is still within the biochronologic distribution of the species. The lower and the upper site-clusters have a horizontal distance of about 400 m from each other, which, given the general 11° dip of the layers, means a stratigraphic difference of about 70 m. In a fluvial environment, which is generally characterised by fast sediment deposition with regard to other continental sedimentary basins (e.g., lacustrine) this difference may indicate a chronologic divergence of tens to a few hunderds of thousand years between the two levels [83], which is consistent with their dating in MN16 and MNQ17, respectively. The faunal lists of the two levels according to the currently available data are given in Table 5.

Table 5. Updated faunal list of the two fossiliferous levels in Sésklo, based on published sources [2–8], the present study, and currently available unpublished data.

Lower Level (MN16)	**Upper Level (MNQ17)**
Aves	Rodentia
Struthio cf. *chersonensis*	cf. *Hystrix*
Proboscidea	Carnivora
Anancus arvernensis	*Ursus etruscus*
Artiodactyla	*Nyctereutes megamastoides*
Sus arvernensis	*Vulpes alopecoides*
Gazella cf. *bouvrainae*	*Pliocrocuta perrieri*
Gazellospira torticornis	*Homotherium crenatidens*
Bovini indet.	Proboscidea
Perissodactyla	*Mammuthus meridionalis*
Stephanorhinus sp.	Perissodactyla
Plesiohipparion cf. *shanxiense*	*Equus stenonis*
	Stephanorhinus sp.
	Artiodactyla
	Croizetoceros ramosus
	cf. *Dama rhenana*
	Eucladoceros sp.
	Palaeotragus (Mitilanotherium) inexspectatus
	Gazella borbonica
	Gazella bouvrainae
	Gazella aegaea
	Gazellospira torticornis
	Gallogoral meneghinii sickenbergii
	Euthyceros thessalicus
	Antilopinae indet.
	Bovidae indet.

Plesiohipparion–Equus Sympatry

A common question referring to the biogeography and biochronology of the early Villafranchian equid taxa is whether *Equus stenonis* coexisted with a late hipparionine species [71]. In Asia, hipparionine species, most notably *Proboscidipparion sinense* Sefve, 1927, have survived well into the Villafranchian and reportedly co-occurred with *Equus* [84]. The two taxa have been also frequently reported in the past to coexist in several European localities, but in general these claims are not based on sound stratigraphic evidence [71]. A true association requires the co-occurrence of both taxa in the same fossil accumulation, or, at least, in the same stratigraphic level within the same locality. This is still to be demonstrated at least in western Eurasia, although Eisenmann [71] accepts this association for the French locality of Roccaneyra. The fossil record in Sésklo, as currently documented, shows that the local hipparionine population did not occur sympatrically with stenonid horses, implying an equid faunal turnover with the arrival of *Equus* in Europe at about 2.5 Ma. This may have been also the case in several other Villafranchian localities, where the available material comes from old, not well stratigraphically-controlled collections. It would be intriguing to investigate this subject, particularly in localities geographically adjacent to Sésklo (e.g., Gülyazı, Turkey), where an hipparion dentally very similar to that from Sésklo, allegedly co-occurs with *Equus* [72] (p. 325). Due to its close stratigraphic proximity with *Equus stenonis*, the *Plesiohipparion* from Sésklo must represent one of the last European populations of hipparionine horses in Europe, just before their final extinction.

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