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Reconsidering the Equids from the Early Pleistocene Fauna of Apollonia 1 (Mygdonia Basin, Greece)

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Abstract: The remains of equids are abundant in the Early Pleistocene faunas of Greece. "Apollonia-1" is one of the richest localities from the latest Villafranchian, providing eight skulls, mandibular remains and plenty of postcranial material during several field campaigns. This study focuses mainly on the skulls, mandibular remains and metapodials from the old and new collection described in detail. The specimens are compared with equids from several Greek and European fossiliferous localities dating from the late Villafranchian to the middle Galerian. The systematic position of *Equus apolloniensis* is also discussed. Based on its basicranial proportions, *E. apolloniensis* is considered a true *Equus*. A second species has also been identified recently, here referred to as *Equus* sp.; it is poorly represented, and it is even larger and more robust than *E. apolloniensis* based on a single metacarpal and third phalanges. The presence of two equid species in Apollonia 1 validates its Epivillafranchian (=latest Villafranchian) age.

Keywords: Mammalia; Perissodactyla; Equidae; *Equus apolloniensis*; Early Pleistocene; Greece

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1. Introduction

Since the beginning of the 1980s, little has been known about the Pleistocene faunas of Greece. The most important publications were those referred to the fauna of Megalopolis in the Peloponnese [1–5]. Sporadic articles describing or reporting the presence of some equid remains were also known from northern Greece (e.g., [6–13]). During the end of the 1970′s—beginning of the 1980s, new localities have been discovered, especially in northern Greece, and new material has been unearthed (e.g., [14–20]). In the following years, extensive fieldwork in the new sites provided rich mammal collections. Several articles have been published, studying these faunas, and providing significant paleontological and biochronological data for Greece and Eastern Mediterranean region (e.g., [21–43]).

The arrival of *Equus* in Eurasia through the Beringian land bridge is one of the most significant events at the beginning of the Pleistocene caused by global environmental changes from humid-warm to cool–dry conditions [44–48]. The *Equus* Datum is calibrated at 2.58 Ma in Europe and 2.55 Ma in China, while it is slightly younger in Sub Saharan Africa, 2.33 Ma. In the Mediterranean region, the *Equus* Datum is traced in the early Pleistocene (MNQ 16) localities of Montopoli (Italy) and El Rincon-1 (Spain). In Western and Central Europe, the *Equus* Datum is recognized in the French locality Roca-Neyra, where *Equus* and *Hipparion* co-existed [48,49]. The earliest evidence of *Equus* in Greece is traced in the locality Damatria in Rhodes Island and probably represents the first local appearance of the genus in this region ([50–53] and ref. therein). Recently, the two genera were also recognized in the locality Sésklo (Thessaly, Central Greece). The fauna from the lower levels of the section, dated to early Villafranchian (MNQ 16 (probably in its upper part), includes *Plesiohipparion* cf. *shanxiense*, while in the upper fauna (middle Villafranchian, MNQ 17), *Equus stenonis* is present [54]. However, the majority of *Equus* in Greece originates from the middle-late Villafranchian and Epivillafranchian.

Equids are usually the most common fossils in the Pleistocene faunal assemblages of Greece, often representing more than 50% of the palaeocenosis in terms of findings. One of the richest fossil equid collections in Greece comes from the fossiliferous sites of Mygdonia Basin, Northern Greece (Figure 1), framing a time interval from pre-Olduvai to early Middle Pleistocene [20]. Apollonia 1 is a key fossil site in this area as it revealed an extremely well-preserved fossil mammal assemblage of high diversity and abundance. The first collected material of equids from Apollonia 1 was studied earlier, and the new species *Equus apolloniensis* was erected [41]. The continued field campaigns in the locality provided more material, enriching the old collection. Thus, a revision of the old and the study of the new material is given in this article and provides more information for this taxon and its relationships with the European Pleistocene equids.

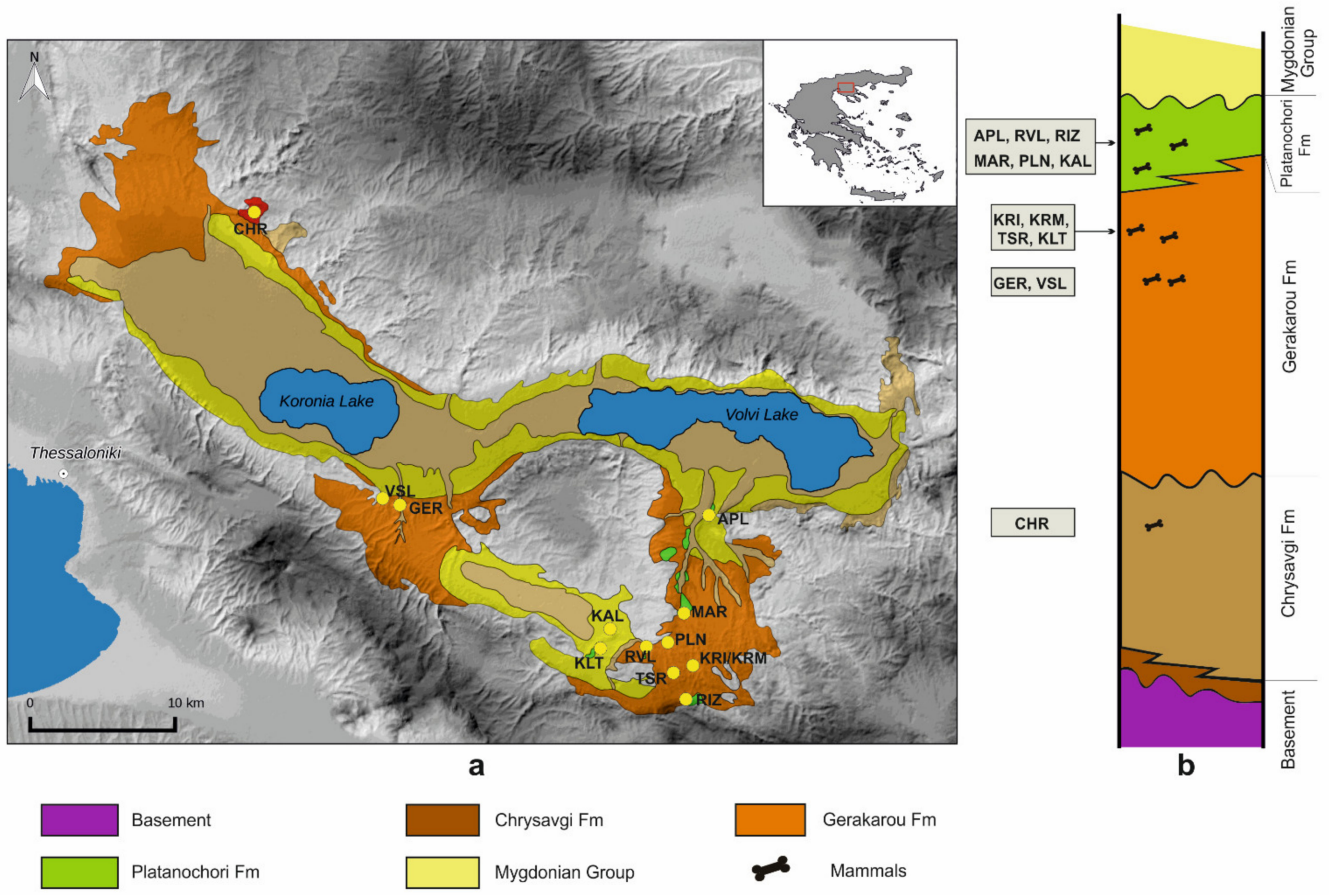


Figure 1. (**a**) Geological map of the Neogene and Quaternary lithostratigraphic units of the Mygdonia Basin (map and data from [55]; modified by [31]); (**b**) simplified composite stratigraphic column of the Mygdonia Basin indicating the position of the fossiliferous localities.

2. Geological Setting

The fossiliferous site Apollonia 1 is situated near the village Nea Apollonia, about 45 km northeast of Thessaloniki city within the Neogene–Quaternary deposits of Mygdonia Basin (Figure 1), a tectonic depression formed during the early Middle Miocene [20]. The Neogene/Quaternary deposits of the basin were divided into two main groups, the Premygdonian and the Mygdonian group [56]. Three successive formations have been distinguished in the Premygdonian group: Chrysavgi Fm, Gerakarou Fm and Platanochori Fm [55]. Apollonia 1 is situated within the Platanochori Formation; it mainly consists of sands, sandstones, conglomerates, silty-sands, silts, clays, marls, and marly limestones deposited in fluvial, fluviolacustrine environment [18,55]. Five other localities have been found in the same Formation: Kalamoto-1, Ravin of Voulgarakis, Riza-1, Marathoussa and Platanochori-1. The study of these faunal assemblages suggests an Epivillafranchian

(=latest Villafranchian) age [18,31,36]. Apollonia 1 was discovered during the summer of 1991 [20], and after subsequent excavations until 1996, a great number of fossil mammals were unearthed. Another series of the field campaign was developed from 2012 to 2014, which further enriched the collection ([32,57], present study).

The Apollonia fauna was originally correlated with the latest Villafranchian, although the poor collection and limited determinations; the fauna is unique among other known localities from Mygdonia Basin [20]. The enrichment of the collection and its study provided more information for the fauna's biochronology, which is currently suggested as Epivillafranchian [58,59]. The collection includes more than 1000 specimens. The determination of the Apollonia 1 material allows the recognition of the following taxa: *Erinaceus europaeus*, Leporidae indet., *Lagurodon arankae*, *Canis etruscus*, *Canis apolloniensis*, *Lycaon lycaonoides*, *Vulpes praeglacialis*, *Ursus etruscus*, *Meles dimitrius*, *Pachycrocuta brevirostris*, *Homotherium latidens*, *Lynx issiodorensis*, *Megantereon cultridens*, *Mammuthus meridionalis vestinus*, *Stephanorhinus* sp., *Equus apolloniensis*, *Equus* sp., "*Arvernoceros verestchagini*", *Praemegaceros pliotarandoides*, *Pontoceros ambiguous mediterraneus*, *Bison* cf. *degiuli*, *Soergelia brigittae*, *Praeovibos mediterraneus*, *Hemitragus orientalis*, cf. *Ovis* sp. ([24,25,32,38,40,41], pers. obs.). The equids predominate in the fauna, and the studied sample includes remains of the whole skeleton; in the present article, we focus on the cranial and mandibular remains and metapodials.

3. Materials and Methods

The equid sample from Apollonia 1 is quite rich, including several cranial remains (some of them are well preserved) and plenty metapodials. It is stored in the Museum of Geology-Palaeontology-Palaeoanthropology of the Aristotle University of Thessaloniki (LGPUT). Equid collections from late Villafranchian to middle Galerian, used as comparative material, have been studied in the following museums and institutes: Italy: Museo di Storia Naturale dell'Univerisità degli Studi di Firenze (Montopoli, Upper Valdarno, Olivola, Matassino, Casa Frata, Pirro Nord). France: Claude Bernard University Lyon 1 (Senèze, Saint-Vallier); Musée des Confluences in Lyon (Senèze, Saint-Vallier); University of Bordeaux (Saint-Vallier); Musée de Paléontologie Christian Guth, Chilhac (Chilhac-2, 3); Musée National de Préhistoire, Les Eyzies-de-Tayac-Sireuil (Ceyssaguet). Switzerland: Naturhistorisches Museum Basel (Senèze, Saint-Vallier, Upper Valdarno). Germany: Senckenberg Research Station of Quaternary Palaeontology in Weimar (Süssenborn). Greece: Museum of Geology-Palaeontology-Palaeoanthropology of the Aristotle University of Thessaloniki (Gerakarou 1, Libakos, Dafnero-1,3, Volax, Krimini-1,2,3, Tsiotra Vryssi, Vassiloudi, Platanochori 1); Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens (Sésklo, Alykes, Volos). Data from literature on German equids from Untermassfeld and Mosbach were taken from [60–62], on Spanish equids from La Puebla de Valverde from [63] and Venta Micena from [64] and on Italian equids from Selvella-Gioiella from [65].

The discussion on the taxonomy of the slender stenonoid equids from Greece is beyond the scope of this study. Slender equids, from the late Villafranchian Greek localities, Gerakarou 1 and Libakos attributed to *E. mygdoniensis* and *E. altidens,* respectively [22,66,67], are similar in size and proportions, and they highly represent the same taxon. However, the material is still under study and will be presented later (Gkeme et al. in prep.). To avoid any confusion, the slender equid from Libakos will be referred to as *Equus*.

Simpson's logarithmic ratio diagrams [68] are used to compare the studied material, which is restricted to the most important and abundant skeletal elements, i.e., the cranium and the metapodials. *Equus grevyi* was used as a reference (measurements taken from [69]). Principal component analysis (PCA) was acquired using PAST 4.05 [70]. Missing values in PCA were treated by applying Iterative Imputation. Statistical differences among metapodials metrics of different species were tested using one-way PERMANOVA in PAST 4.05. Results of this test were considered significant at A95.

Measurements and the dental terminology follow [71–73]; upper- and lower-case letters denote upper and lower teeth, respectively. Specimens belonging to juvenile individuals were excluded from this analysis.

4. Systematic Palaeontology

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758
Equus apolloniensis Koufos, Kostopoulos and Sylvestrou, 1997
Holotype: Cranium LGPUT-APL-148, described and figured by [41] (pl. 1, Figures 1 and 2).



Figure 2. *Equus apolloniensis*, APL-148; (**a**–**d**) cranium, (**a**) ventral view, (**b**) dorsal view, (**c**) right lateral view, and (**d**) left lateral view.

Type locality: Apollonia 1, Mygdonia Basin, Macedonia, Greece.
Age: Epivillafranchian (latest Early Pleistocene).
Material: Crania, APL-147, 148, 871, 872; partial crania 518, 519, 605; fragment of occipital bone, APL-813; maxilla with P4-M3 sin and P2-M3 dex, APL-129; fragment of the muzzle with I1-C, APL-268; fragment of the muzzle with I1-I3, APL-314, 574, 646, 812; maxillary fragment with M1, APL-816; tooth row P3-P4 sin, APL-343; P2 dex, APL-138; P3,4 sin, APL-469; M1,2, APL-142, 471, 500, 564; M3, APL-154, 830, 558, 566, 626 874;

mandible, APL-570; mandibular fragment with dp2-dp4, m1-m2 dex, APL-572; mandibular fragment with dp2-dp4, m1-m2 sin, APL-870; mandibular fragment with i1-i3, c, p2-m3 sin and dex, APL-785; mandibular fragment with i1-i3, c, p2-m2 sin and i1-3, c, p2-p4 dex, APL-633; mandibular fragment with i1-i3, c, p2-m2 sin and i1-i3, c, p2-m2 dex, APL-792; mandibular fragment with p3-m3 sin, APL-424; mandibular fragment with p2-m3 sin, APL-355; mandibular fragment with p2-m3 dex, APL-606; mandibular fragment with p4-m3 sin APL-295; mandibular fragment with m1-m3 dex, APL-486; mandibular fragment with p3-m2 sin, APL-315; mandibular fragment with p3-m3 dex, APL-557; mandibular fragment with m3 sin, APL-26; mandibular fragment with p2-p3 sin, APL-250, 834; mandibular fragment with p2-p4 dex, APL-622; mandibular fragment, APL-640; tooth row p2-p3 sin, APL-598; tooth row p2-p3 sin, APL-311; tooth row m2-m3 sin, APL-319; tooth row p4-m1 dex, APL-345; p2 sin, APL-562; p2 dex, APL-88 (fragment), 138, 186, 470, 563; p3,4 sin, APL-623; m1/2 sin, APL-119, 137, 185, 609; p3,4 dex, APL-608; m1,2 dex, APL-139, 140, 345, 153, 369, 496; m3 sin, APL-561; m3 dex, APL-301; third metacarpal, APL-74, 156, 165, 261, 306, 390, 445, 502, 612, 635, 742, 776, 777, 778, 787, 788, 793, 861; proximal part of McIII, APL-158, 396, 435, 637, 807, 850, 851; distal part of McIII, APL-164, 636, 851; third metatarsal, APL-76, 89, 91, 92, 130, 237, 293, 328, 329, 347, 449, 575, 610, 611, 621, 634, 789, 790, 794, 846, 848, 879, 880;proximal part of MtIII, APL-C, 81, 130, 167, 156, 160, 161, 162, 232, 248, 324, 362, 476, 517, 739, 805, 854, 859; distal part of MtIII, APL-166, 267, 360, 608, 779, 860, 877.

Measurements: The measurements are given in Tables S2–S4.

4.1. Description

4.1.1. Cranium

APL-148. It is the holotype of the species and was originally described by [41]. The cranium is almost complete, but it is laterally compressed; it belongs to a young adult individual (slightly worn M3); the large canines indicate a male individual (Figure 2). The cranium is elongated, and the muzzle is rather short and wide. The ratio muzzle breadth (meas. 15)/muzzle length (meas. 1)% is 49.2 mm. The palate is wide, but the palatal breadth cannot be measured accurately due to the lateral compression. On the right side, the major palatine foramen is located at the level of the mesial half of M2. The choanae are elongated and elliptical; their anterior border is situated at the level of M1/M2 contact. The medial border of the retroarticular process is almost straight. The narial notch is situated above the P2 mesostyle. The infraorbital foramen is quite large and deep, situated above the P4 parastyle. The anterior border of the facial crest is located above the M1 mesostyle. The facial crest is well-developed. Like all the other Apollonia 1 crania, the facial crest has a wavy shape (Figure 2c). The orbits are large and rounded. The occipital region is partially preserved (possibly due to carnivore attack). The external occipital protuberance is represented by a vertical crest. The foramen magnum is large, less wide and pentagon-shaped. The retroarticular processes are quite large and strong, and they are laterally outreaching the level of the articular surface of the mandibular fossa.

The dentition is completely preserved on both sides (Figure 2a). In lateral view, the cheek teeth are remarkably elongated. Both P1 are absent, but their alveoli are well distinguished. The anterostyle of P2 is elongated but not very wide. The parastyle and mesostyle on P2 and P3 are notched. The protocone is relatively elongated; its lingual border is concave except for P2 and M3 (where it is almost straight). The postprotoconal groove is deep, especially on the premolars. The hypoconal groove is always deep, elongated and pointed. The pli caballin is long and multiple in the premolars; in the molars, it is short and single. The fossettes are moderately plicated at their margins.

APL-871. The cranium is almost complete; it lacks the frontals, nasals, the left zygomatic arch and temporal bones; it is laterally compressed (Figure 3). There are no canines indicating that it is a female individual. In ventral view, the muzzle is rather short, and it is laterally compressed. The palate is not very long but relatively wide. The choanae are large, elliptical-shaped, and their anterior margin is situated at the level of M1/M2 contact.

The occipital bone is quite damaged, and the condyles are broken and misplaced. The orbit is relatively short, rounded, and its anterior border is placed above the posterior margin of M3. The infraorbital foramen is large, and it is situated at the level of the parastyle of P4. The facial crest is wavy shaped, well developed; its anterior border is situated caudally above the P4/M1 contact. The zygomatic arch runs almost parallel to the sagittal plane of the cranium.

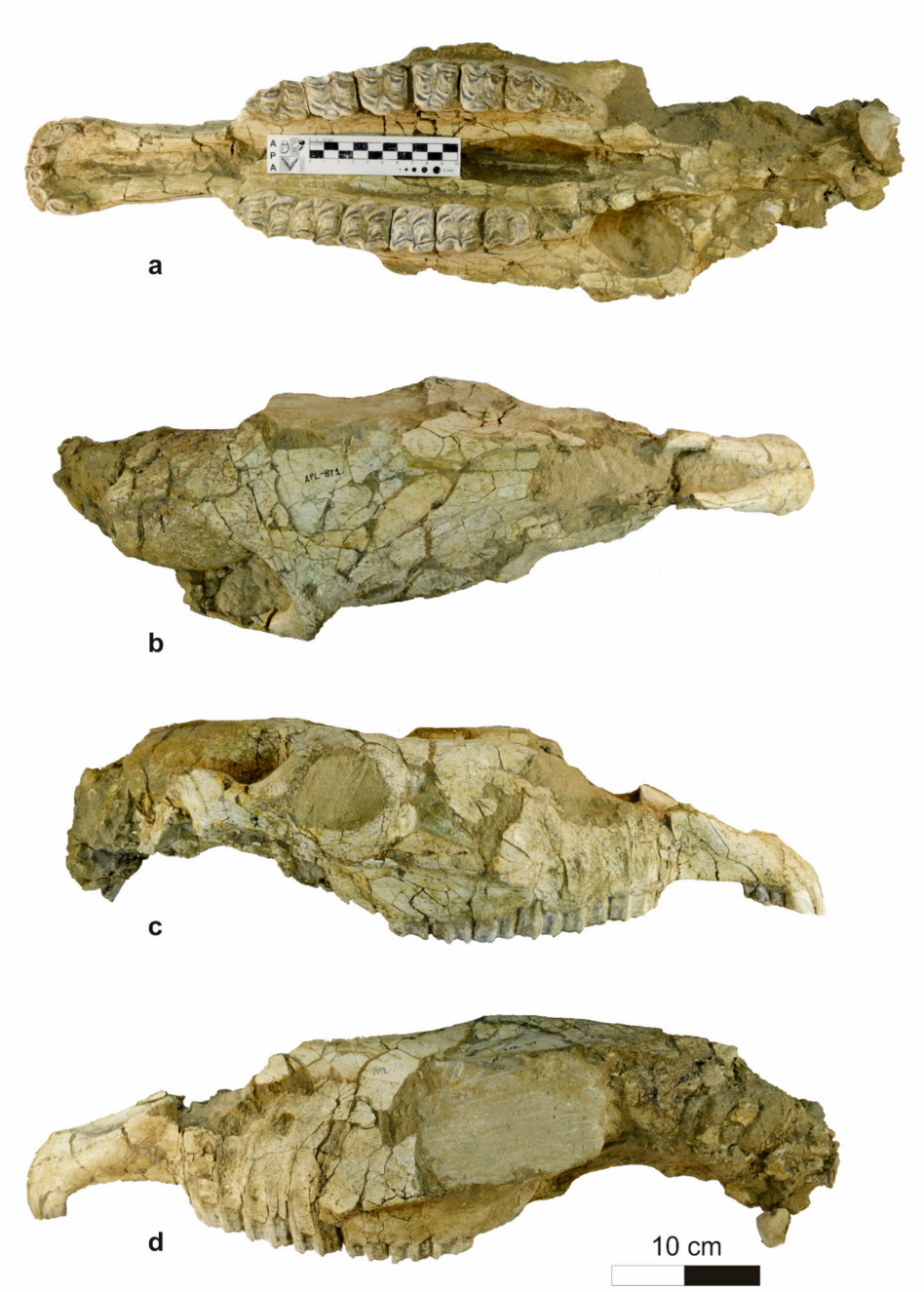


Figure 3. *Equus apolloniensis*, APL-871; (**a**–**d**) cranium, (**a**) ventral view, (**b**) dorsal view, (**c**) right lateral view, and (**d**) left lateral view.

The cheek teeth rows are parallel. The P1 is present on both sides; it is high, reaching the occlusal level of P2, quite elongated and elliptical-shaped. The anterostyle of P2 is wide and rounded. The protocone is relatively short on all cheek teeth; its lingual border is more or less concave. The fossette margin is moderately plicated.

APL-872. The cranium is mediolaterally compressed and lacks the frontal and nasal bones, the right maxillary sinuses and both orbits; only a part of the left braincase is preserved, and the occiput is completely missing (Figure 4). The occipital bone is quite damaged, and the condyles are broken and misplaced. It belongs to a relatively old individual, possibly female; the Galvayne' s groove on I3 is at its full length giving an age of ~20 years old. The muzzle is relatively short and wide; the ratio muzzle breadth (meas. 15)/muzzle length (meas. 1)% is 50.4 mm. The palate is relatively short and wide. The major palatine foramens are situated at the anterior half of M3. The choanae are elongated and elliptical; their anterior border is situated approximately at the middle of M2. The left orbit is partially preserved; it is possibly rounded with its anterior border far behind M3. The facial crest is well-developed but does not project laterally as in the other APL crania. The anterior border of the facial crest is placed above the mesostyle of M1; it is wavy shaped.

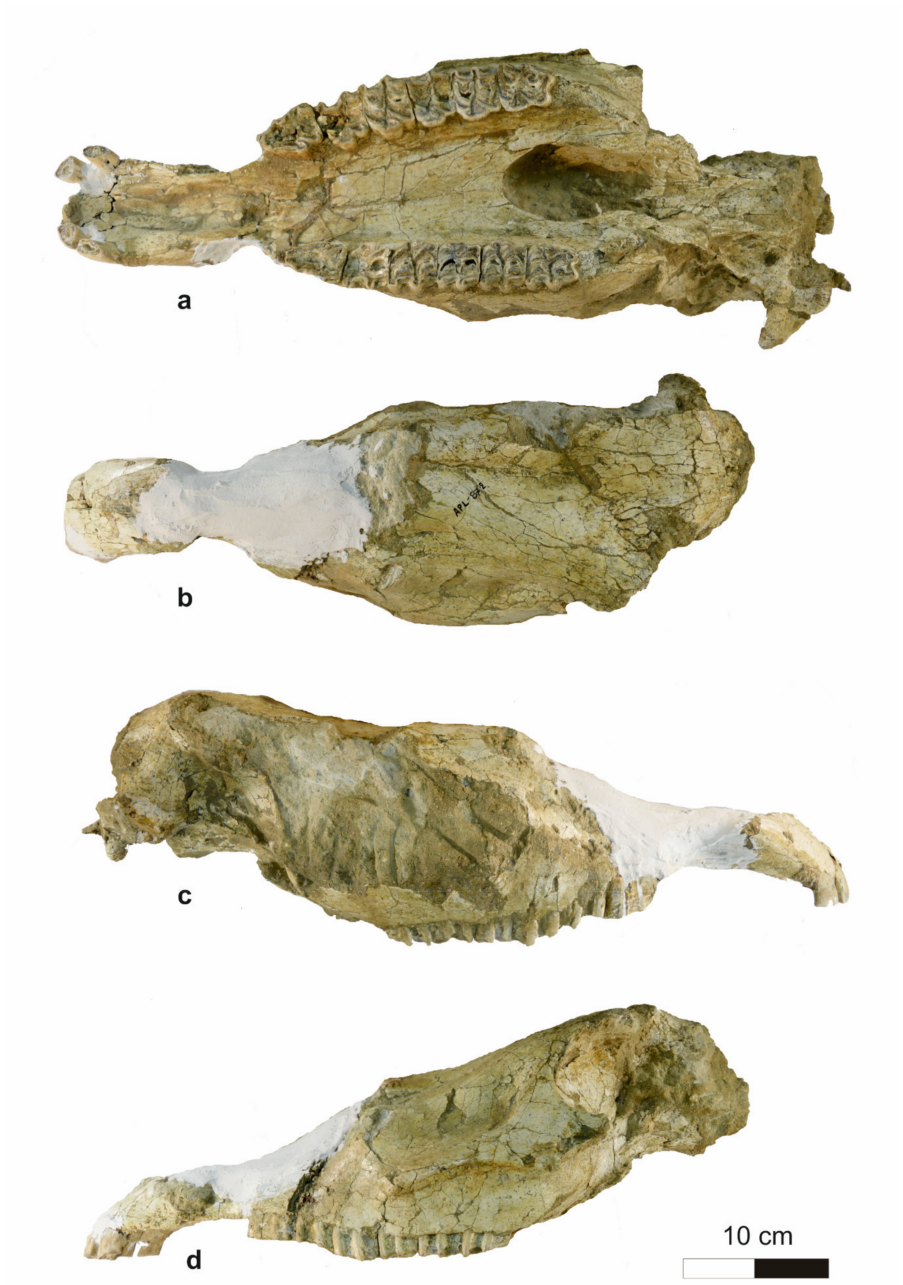


Figure 4. *Equus apolloniensis*, APL-872; (**a**–**d**) cranium, (**a**) ventral view, (**b**) dorsal view, (**c**) right lateral view, and (**d**) left lateral view.

The P1 is absent. The anterostyle of P2 is rounded and relatively wide. The protocone is relatively long and elliptical on all cheek teeth, except P2; its lingual border is always more or less concave (on P2, it is straight to convex). The second and third premolars are very worn, and most of the enamel in the fossette margin is worn. The enamel plication of the other cheek teeth is simple.

APL-147. The cranium belongs to an old individual (fourth stage of wear), and it was described earlier [41]; it is mediolaterally compressed and lacks the muzzle and the right P2 (Figure 5). The palate is wide, but the mean palatal breadth at the limit between P4 and M1 cannot be measured due to the deformation. The major palatine foramen is located at the posterior half of M2. The choanae are elongated and elliptical, and their anterior border is situated at the M1/M2 contact. The narial notch is situated above the parastyle of P2. The region of the facial crest is crushed; however, the anterior border of the facial crest is located above the P4/M1 contact. The right infraorbital foramen is situated above the posterior half of P4. The orbits are oval-shaped due to the deformation, and their anterior border is far behind the M3. The retroarticular processes are like those of APL-148. The dorsal edge of the zygomatic arch is directed horizontally at a point behind the orbit. The zygomatic process is strong and relatively broad (breadth 28.4 mm). In dorsal view, the nasal bones form a smooth groove along their sagittal suture. The greatest breadth of the cranium is behind the orbits. The frontonasal suture is straight like in *E. zebra* [74]. The upper part of the occipital bone is missing. The external occipital protuberance is represented by a vertical crest, and there is no depression. The foramen magnum and paracondylar processes resemble those of APL-148. APL-147 preserves the tooth rows P2-M3 dex and P3-M3 sin (Figure 5a). The P2 anterostyle is rounded and relatively short. The hypoconal groove is always shallow and rounded; on the right M3, the hypocone is isolated as an islet. The protocone is relatively long on all teeth, except P2; its lingual margin is almost straight on P2 and M3, while on all the other cheek teeth is concave. The pli caballin is absent. The inner fossettes are simply plicated. The enamel of the buccal side of the fossettes is wrinkled (Figure 5).

4.1.2. Mandible

Among the studied material, there is one almost complete mandible (APL-570), described earlier by [41] and several mandibular fragments, preserving complete tooth rows or part of them. APL-570 is strongly compressed laterally, and only the left condyle and the right coronoid process are missing (Figure 6). It lacks canines, indicating a female individual. The mandibular corpus is high with a relatively short and wide snout. The ratio snout breadth (meas. 7)/snout length (meas. 2)% ranges between 51.8 and 53.2 (mean = 52.6). The vascular notch is clear in APL-570, while in APL-792 is weak. The mental foramen is relatively large and single, situated in the middle of the i3-p2 diastema. In APL-570 and APL-633, there is no acute angle at the junction of the interalveolar border with the border of p2, while in APL-792 and APL-785, they join in a way that the junction forms an angle of almost 90°. In APL-792, possible hypoplasia is observed in M2 (Figure 6c). The p1 is absent in all specimens.

4.1.3. Upper dentition

The cheek teeth are elongated and wide. The length of the upper cheek tooth row ranges from 180.7–201.0 mm (mean = 193.26 mm), and the ratio molar length (meas. 8)/premolar length (7)% is 83.90 on average. The anterostyle of P2 is relatively long and wide. The parastyle and mesostyle are well-developed and wide projecting labially; in APL-148, the mesostyle of the right premolar row is more notched than that in the left one. The fossettes are always isolated except for the slightly worn teeth; the enamel of their borders is moderately plicated. The protocone is relatively elongated; in the worn teeth of APL-147 is remarkably long (especially in M3), while in APL-519, it is short.; the shape of the protocone varies from elongated-elliptical to semilunar-elliptical; in M3, it can be atractoid; the lingual border of the protocone is more or less concave except on P2

where it is sometimes straight; the protocone is usually more projected anteriorly in the molars than in the premolars; in the same tooth row, the postprotoconal groove is deeper in the premolars than in the molars (APL-148). The hypocone is rounded-elliptical shaped; hypoconal islets are common on M3; the hypoconal groove is pointed and relatively deeper in the premolars than in the molars. The pli caballin is usually present and single on all cheek teeth, and it disappears in the very worn teeth; on premolars, it is more elongated than on molars.

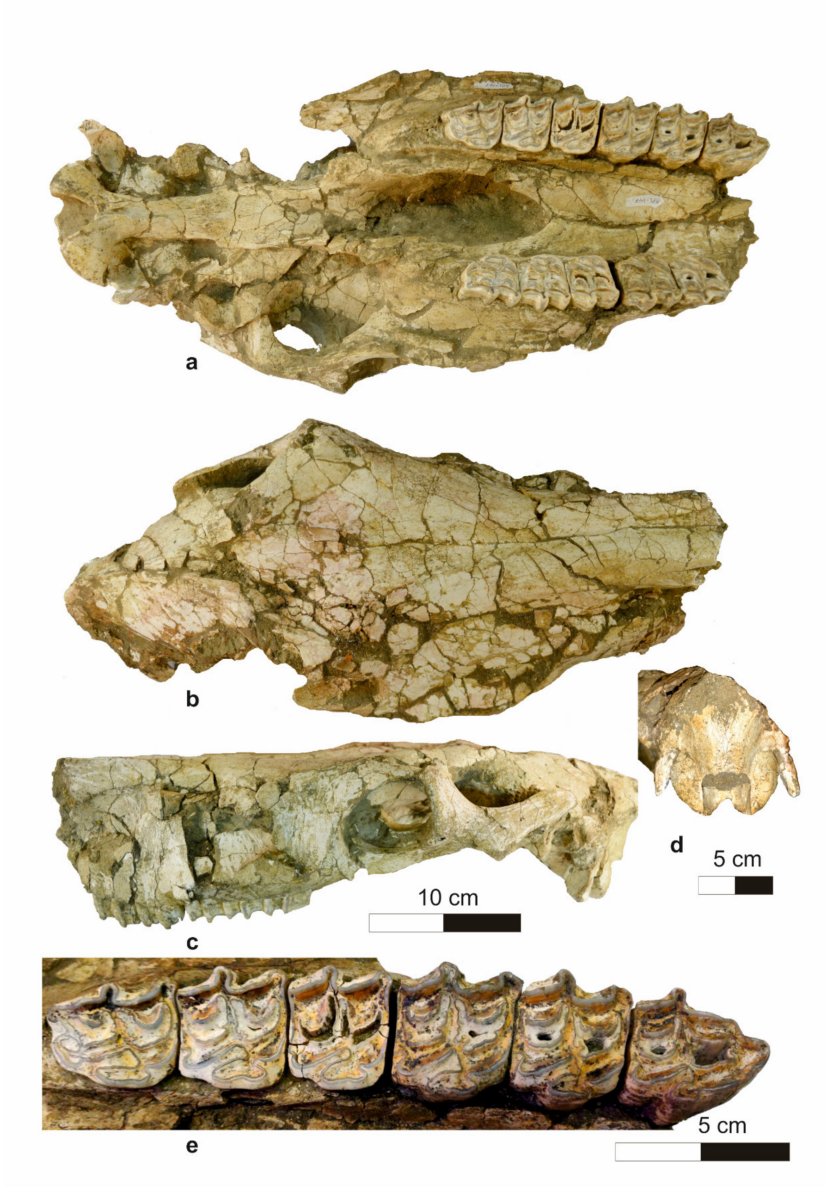


Figure 5. *Equus apolloniensis*, APL-147; (**a**–**e**) cranium, (**a**) ventral view, (**b**) dorsal view, (**c**) left lateral view, (**d**) occipital region, and (**e**) right tooth row.

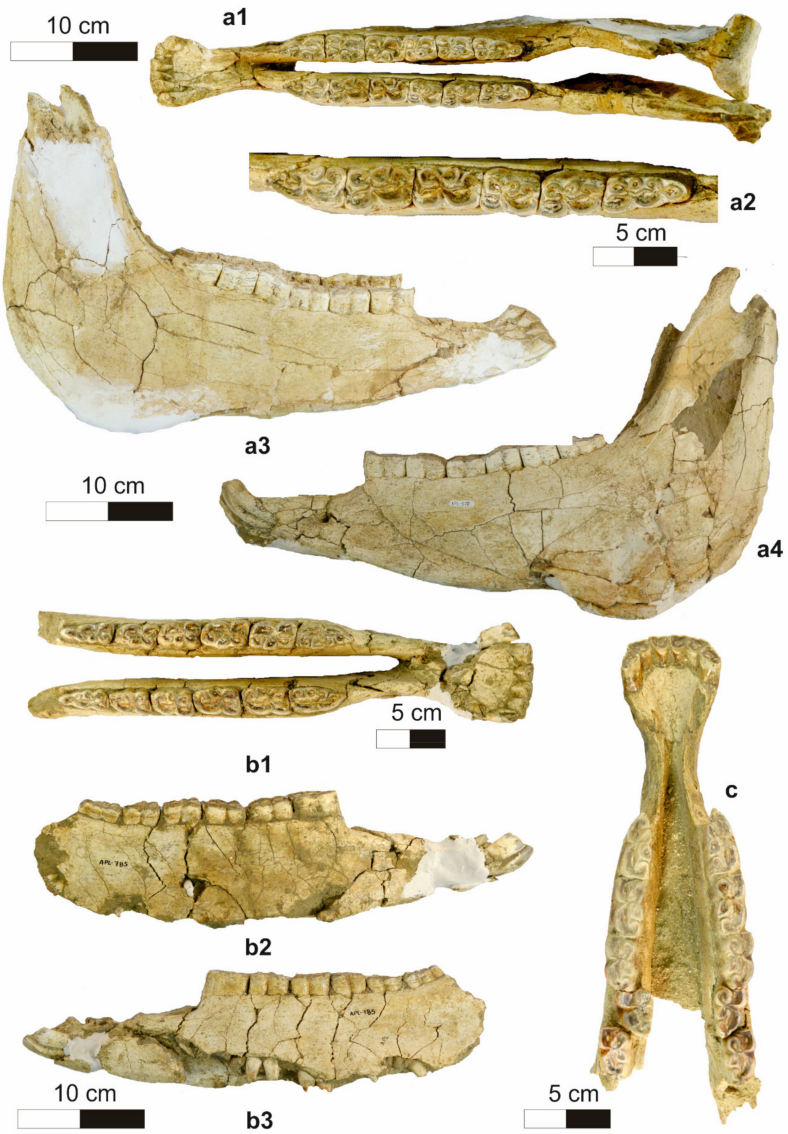


Figure 6. *Equus apolloniensis*, (**a1**–**a4**) mandible, APL-570, (**a1**) occlusal view, (**a2**) left tooth row, (**a3**) right lateral view, (**a4**) left lateral view; (**b1**–**b3**) partial mandible, APL-785, (**b1**) occlusal view, (**b2**) right lateral view, (**b3**) left lateral view; (**c**) partial mandible, APL-792, occlusal view.

4.1.4. Lower Dentition

The length of the lower cheek tooth row is 194.7 mm. The linguaflexid is V-shaped on the lower cheek teeth; on APL-295, 570, 785, it is deeper and pointed, while on APL-633, 792, it is shallow and wider. The linguaflexid is V-shaped. The metaconid is relatively wide and rounded. The metastylid is slightly smaller than the metaconid but also rounded, and its lingual border tends to be more pointed in the premolars than in the molars. On APL-295, there is a "bridge" between the metaconid and metastylid on the first molar. The entoconid is squarish in the premolars, while in the molars is more elliptical. The postflexid is longer than the preflexid in the premolars, while in the molars, it is shorter. The parastylid is usually half-open except in the advanced worn teeth (APL-355), where it is closed. Ectoflexid is shallow and pointed in the premolars, while in the molars is deeper, reaching the mesio-lingual corner of the postflexid, without, however, penetrating the isthmus; only in APL-355, the ectoflexid of m2 and m3 and in the m1/2, APL-369, is

very deep penetrating the isthmus. The pli caballinid is usually absent except for some slightly unworn teeth (APL-139, 137, 345, 369, 785), where it is small to rudimentary. In the same tooth rows, the enamel of the postflexid in the premolars is slightly plicated, while in the molars is mainly unplicated; there is a single pli in the preflexid of p4 in APL-345 and 295, as well as of m3 in APL-785 and 301. The protostylid is present in all cheek teeth, but it is more frequent in the premolars; it is not isolated, but it appears as a simple and shallow plication; in the same specimen (mandible APL-570), it is present in the left m1 and m2, while it is extremely weak (m1) or even absent (m2) in the right ones.

4.1.5. Metapodials

The third metapodials are elongated and relatively robust (Figure 7a–h). The slenderness index, distal maximal articular breadth (meas. 11)/maximal length (meas. 1)% ranges from 19.8–20.9 (n = 16; mean = 20.5) for the third metacarpals, and from 16.1–18.1 (n = 23; mean = 17.1) for the third metatarsals. The morphology of the articular surfaces for the lateral metapodials is variable. The distal maximal supra-articular breadth at the trochlea (meas. 11) is greater than at the tubercles (meas. 10) on the metatarsals. The distal keel is well developed; the keel index (distal maximal anteroposterior diameter of the keel (meas. 12)/distal minimal DAP of the lateral condyle (meas. 13)% varies between 125.1 and 132.9 (n = 20; mean = 128.1) for the third metacarpals, and from 127.5–146.0 (n = 28; mean = 134.6) for the third metatarsals.



Figure 7. *Equus apolloniensis*, (**a**–**d**) third metacarpals, (**a**) APL-777, (**b**) APL-801, (**c**) APL-157, (**d**) APL-788; (**e**–**f**) third metatarsals, (**e**) APL-848, (**f**) APL-92, (**g**) APL-880, (**h**) APL-237; *Equus* sp., (**i**) third metacarpal, APL-74.

5. Comparisons

As already mentioned by [41], one of the most important differences between *E. apolloniensis* and *E. stenonis* is the depth of the narial notch. *E. stenonis*, along with *E. stehlini*, *E. senezensis*, and *E. mygdoniensis*, are characterized by a deep narial notch ending above the third premolar [22,75,76]. In Apollonia 1 crania, the narial notch is shallow, and its hinder margin is situated above the mesostyle of P2. Furthermore, no preorbital fossa is traced in APL crania, unlike the typical cranium of *E. stenonis* (IGF 560), where it is weak but clearly developed [46,75,77]. A depression on the occiput of APL crania is also lacking, unlike in *E. stenonis* and *E. mygdoniensis*. Unfortunately, the supraoccipital crest, which could give more information, is missing from all crania of *E. apolloniensis*. Moreover, as the distance between the vomerine notch and the basion (meas. 4) can be interpreted as an estimation of the braincase [78]; the braincase of *E. apolloniensis* seems to be relatively larger than that of *E. stenonis vireti* compared to the basilar length (meas. 6).

The cranium of *E. apolloniensis* (n = 6) is distinguished easily from that of *E. mygdoniensis* from Gerakarou (Mygdonian Basin, Greece) by its larger dimensions (Figure 8). In comparison with *E. stenonis*, the cranium of *E. apolloniensis* is characterized by the shorter muzzle and palatal length (meas. 1, 2), wider choanae (meas. 12), longer cheek tooth rows (meas. 7, 8, 9), narrower muzzle (meas. 14, 15), quite shorter naso-incisival notch (meas. 30) and longer cheek length (meas. 31) (Figure 8).

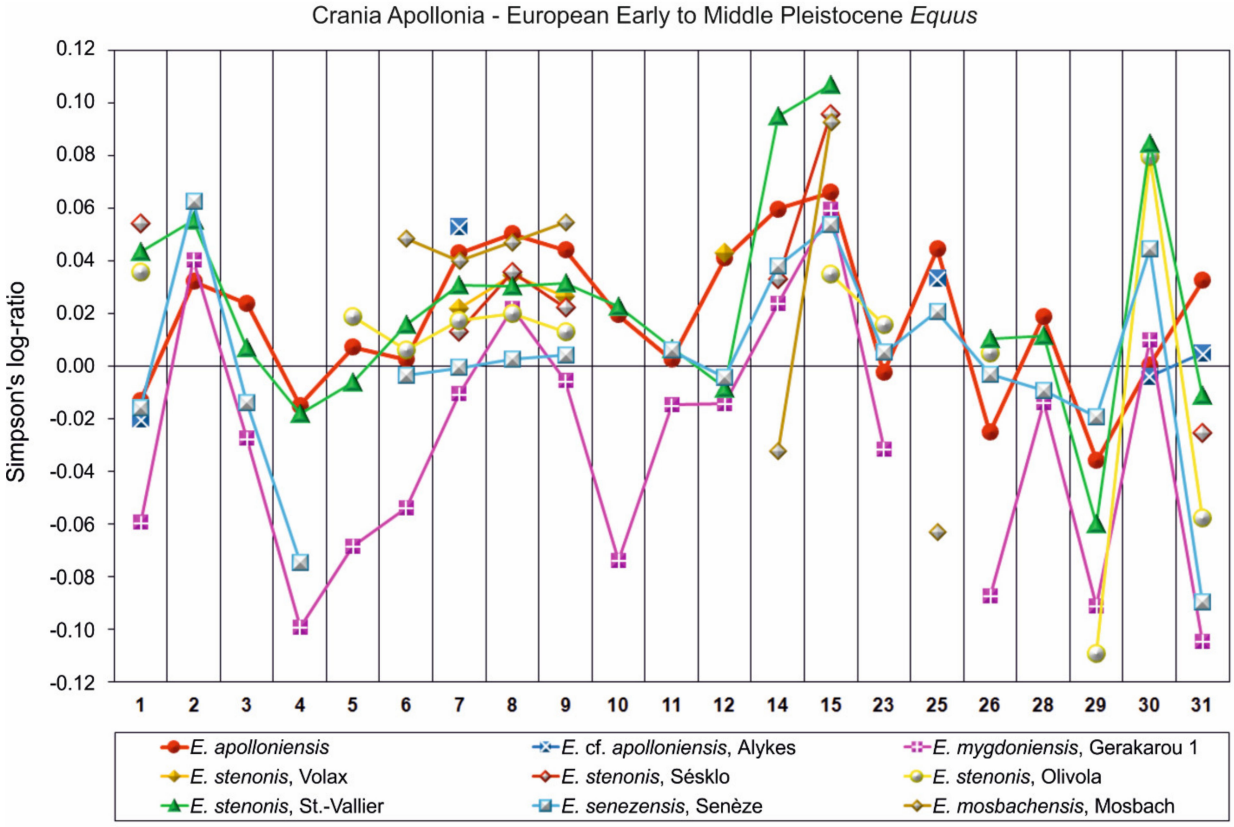


Figure 8. Simpson's log-ratio diagrams comparing the cranial dimensions of *E. apolloniensis* with other equids from Greece and Europe. Standard: *Equus grevyi* [69]. Data from [62,76] and personal dataset. For definitions of meas., see Supplementary Materials.

E. apolloniensis resembles *E. senezensis* in the basilar length and the short muzzle (meas. 6, 1), but it differs, having larger cheek tooth rows (meas. 7, 8, 9), wider choanae (meas. 12), wider muzzle (meas. 14, 15), shorter naso-incisival notch (meas. 30), and remarkably longer cheek length (meas. 31). In comparison with *E. mosbachensis*, *E. apolloniensis* has a shorter basilar length (meas. 6), similar cheek tooth rows length (meas. 7, 8, 9), and wider

muzzle at the incisors (meas. 15); the minimal muzzle breadth seems to be quite smaller in *E. mosbachensis.* In the Greek fossil record, there is a partial cranium from the locality Alykes in Thessaly (Αλ-20, University of Athens), the few dimensions, of which fits quite well with those of *E. apolloniensis* (Figure 8) and it is mentioned as *E.* cf. *apolloniensis* by [54]. Unfortunately, the lack of adult crania of *E. altidens*, *E. granatensis*, *E. suessenbornensis* and *E. wuesti* does not permit any further comparison.

The protocone of stenonoid horses is usually short, relatively to the tooth height. *E. mygdoniensis*, *E. senezensis* and *E., granatensis* display rather short protocones similarly to *E. stenonis* [22,76,79]. The lingual border of the protocone is concave on *E. apolloniensis* (see also [41]), and its distal part is clearly more pronounced like in *E. altidens* and *E. suessenbornensis* though not far from the condition seen in *E. s. vireti*. The postprotoconal groove of *E. apolloniensis* is deeper than in *E. stenonis*. Likely, *E. suessenbornensis,* the buccal side of the fossettes in APL-147 (teeth at the fourth stage of wear), is wrinkled (Figure 5e). On *E. apolloniensis*, pli caballin is present; on APL-148 (teeth at the first stage of wear), pli caballin is multiple on the premolars with a very large base, resembling sussemiones [80]; however, it reduces in size by the progressive attrition and disappears at the final wear stages. The shape of the double knot varies from a typically rounded stenonoid, separated by a pointed and deep linguaflexid (APL-295, 570, 785) to a rather hemionine type with an elongated metaconid and pointed metastylid separated by a shallow and wide linguaflexid (APL-633, 792). In these features, the APL horse resembles *E. granatensis* [81], from which (and sussemiones in general) differs in the shallow ectoflexid on the molars that recalls for hemiones and asses [71]. Ectoflexid on APL-355 (on m2 and m3) and APL-369 is very deep penetrating the isthmus. These specimens could belong to the second species identified in Apollonia 1; however, no other differences in the morphology or size were observed to assign them to a separate taxon. The presence of a "bridge" on the first molar of APL-295 is a character that appears on both wild asses and hemiones [71]. The presence of the pli protostylid on the lower premolars and molars (except on p2 of *E. apolloniensis*) is a character that usually occurs in the sussemiones [71,80].

The third metacarpal of *E. apolloniensis* is distinguished from *E. mygdoniensis*, *E. senezensis* and Libakos, due to its larger dimensions (Figure 9a,c) and from *E. suessenbornensis* and *E. mosbachensis* due to its smaller dimensions. *E. apolloniensis* has longer metacarpals (meas. 1) than almost all *E. stenonis* samples from Europe and Greece (Figures S1 and S2) except for Olivola, and the isochronous *E. granatensis,* which both seem rather like APL (Figure 9b,c). However, *E. apolloniensis* has deeper and narrower metacarpal diaphysis (meas. 3,4) than *E. stenonis* from Greece and Europe (Figure 9a,b). This means a relatively slenderer metacarpal, unlike all *E. stenonis* samples, except for that from Volax; this is probably due to the small number of specimens from the latter site (only three). Some more differences are seen in the distal epiphysis. The metacarpal of the Volax equid is wider with a slightly stronger keel and the deeper trochlea (meas. 10–14). The metacarpal proportions of *E. apolloniensis* seems to be closer to those of *E. stenonis* from St.-Vallier, from which it differs in the greater maximal length (meas. 1), the narrower diaphysis (meas. 3), the less wide breadth at the tubercles (meas. 10), the deeper trochlea (meas. 13, 14), the larger articular facet for os magnum, and the quite larger articular facet for os hamatum (meas. 8) (Figure 9b). Although the maximal length of the third metacarpal of *E. apolloniensis* is close to those of the European taxa *E. granatensis* and *E. altidens,* all the other dimensions are quite larger, distinguishing it well from them and suggesting for it a more robust appearance (Figure 9c). The third metacarpal of *E. apolloniensis* and *E. wuesti* seem to have similar proportions, but the latter is significantly longer (meas. 1). Thus, the metacarpal of *E. wuesti* appears slenderer with narrower trochlea (meas. 11), weaker keel (meas. 12), and considerably wider articular facet for the os hamatum (meas. 8) than those of *E. apolloniensis* (Figure 9c).

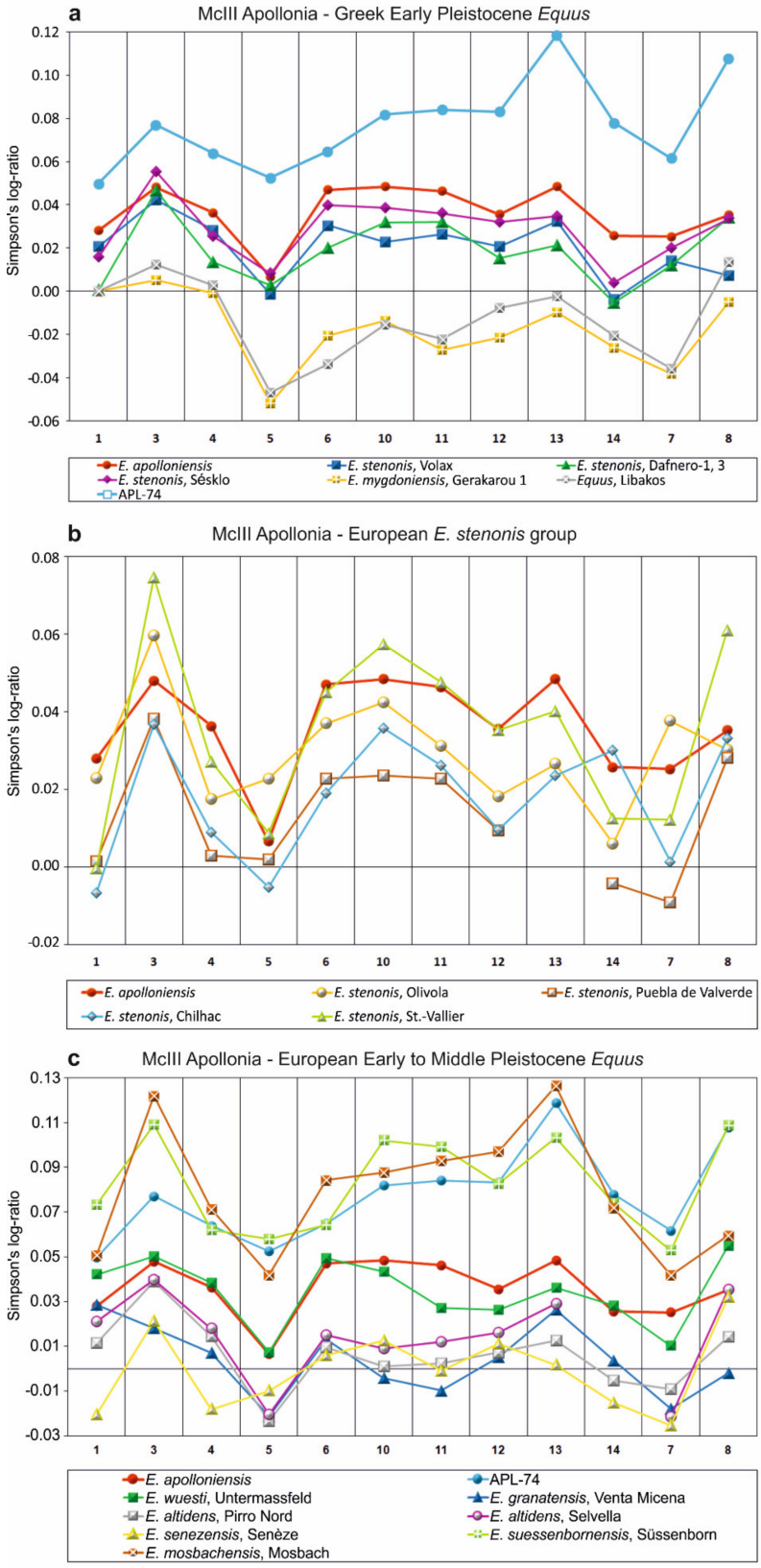


Figure 9. Simpson's log-ratio diagrams comparing the dimensions of the third metacarpal of *E. apolloniensis* with (**a**,**b**) Greek and European *E. stenonis* (**c**) and other Early/Middle Pleistocene horses. Standard: *Equus grevyi* [69]. Data from [61–65,76] and personal dataset. For definitions of meas., see Supplementary Materials.

The third metatarsal of *E. apolloniensis* is longer (meas. 1) than all *E. stenonis* samples from Greece and Europe (Figure 10a,b and Figures S1 and S2). Along with *E. wuesti*, it seems intermediate between the metatarsals of *E. stenonis* and the middle Pleistocene equids *E. suessenbornensis* and *E. mosbachensis* (Figures S1 and S2). Its diaphysis and proximal epiphysis have similar proportions with *E. stenonis*, except for *E. stenonis* from Dafnero 1, 3, which is characterized by a less deep diaphysis (meas. 4) and from Sésklo and Dafnero 1, 3, both showing a less deep proximal articular facet (meas. 6). Furthermore, the articular breadth at the trochlea (meas. 11) is greater than the suprarticular breadth at the tubercles (meas. 10), unlike all *E. stenonis* except for Dafnero 1, 3 and Volax (Figure 10a,b). Comparing with the European *E. stenonis, E. apolloniensis* has a longer metatarsal (meas. 1) with deeper trochlea (meas. 13, 14) and a larger articular facet for cuboid (meas. 8) (Figure 10b). Like the third metacarpals, the third metatarsal of *E. stenonis* from St.-Vallier is close to *E. apolloniensis*, but its remarkably shorter maximal length (meas. 1) distinguishes it well from the latter taxon (Figure 10b). The third metatarsal of *E. granatensis*, *E. altidens*, and *E. senezensis* are smaller than that of *E. apolloniensis* (Figure 10c). *E. wuesti* is slightly longer (meas. 1) than *E. apolloniensis,* but it clearly differs in the larger proximal articular dimensions (meas. 5, 6) and the considerably larger articular facets for cuneiform and cuboid (meas. 7, 8). *E. apolloniensis* and *E. suessenbornensis* metatarsals have similar proportions, but the latter species has a significantly larger third metatarsal (Figure 10c). In both taxa, the distal articular breadth (meas. 11) seems larger relatively to the suprarticular breadth at the tubercles (meas. 10). The third metatarsals of *E. apolloniensis* are well separated from those of *E. mosbachensis* and *E. suessenbornensis* by their quite smaller size (Figures 9 and 10c).

The PERMANOVA results for both the metacarpals and metatarsals indicate a significant difference between the species (Table S1), and they agree with Simpson's ratio diagrams and PCA (Figures 9 and 10 and Figure S2). Metacarpals of *E. apolloniensis* appear statistically different from almost all *E. stenonis* representatives apart from *E. stenonis* from Olivola, Sésklo and Volax, the latter, however, known by a single complete specimen. *E. wuesti* is close to *E. apolloniensis* yet statistically different. Metatarsals of *E. apolloniensis* are again different from all the other species; Volax is also represented here by only one specimen.

Equus sp.

Locality: Apollonia 1, Mygdonia Basin, Macedonia, Greece.

Age: Epivillafranchian (latest Early Pleistocene).

Material: Third metacarpal, APL-74; third phalanges APL-394, 429, 868

Measurements: The measurements are given in Table S3.

Description and comparison. Among the Apollonia 1 metacarpals, APL-74 (Figure 7i) is quite larger than the mean of *E. apolloniensis* (Figure 9c). The slenderness index (distal breadth at the tubercles (meas. 11)/maximal length (meas. 1) % is 21.2 for APL-74 versus 20.4 (n = 16, min = 19.6, max = 20.9) on average for *E. apolloniensis*, indicating a more robust metacarpal. The keel index (distal maximal anteroposterior diameter of the keel (meas. 12)/distal minimal DAP of the lateral condyle (meas. 13) % is 121.4 for APL-74 versus 128.2 (n = 23, min = 125.1, max = 132.9) for *E. apolloniensis* indicating a relatively less developed keel.

These features of APL-74 are closer to *E. mosbachensis* and *E. suessenbornensis* (Figure 9c). Nevertheless, compared to *E. mosbachensis,* APL-74 has a similar maximal length (meas. 1) and proportions, but narrower diaphysis, deeper proximal articular facet (meas. 6), less developed keel (meas. 12) and wider articular facets for the os magnum and os hamatum (meas. 7, 8). In comparison with *E. suessenbornensis*, APL-74 is shorter with narrower diaphysis (meas. 3) and distal epiphysis (meas. 10, 11) (Figure 9). APL-74 could belong to one of these large equids, but the poor material cannot go any further. Furthermore, three third phalanges were separated from *E. apolloniensis* because they are much wider. Their maximal breadth is 72.6 (n = 3, min = 69.8, max = 74.5) versus 63.31 (n = 7, min = 62.19, max = 64.75) in *E. apolloniensis.* Besides these specimens, there are some more postcra-

nial fragments, which also have larger sizes and could belong to the same equid taxon. Thus, it is better to separate this metacarpal from the *E. apolloniensis* sample, waiting for more material.

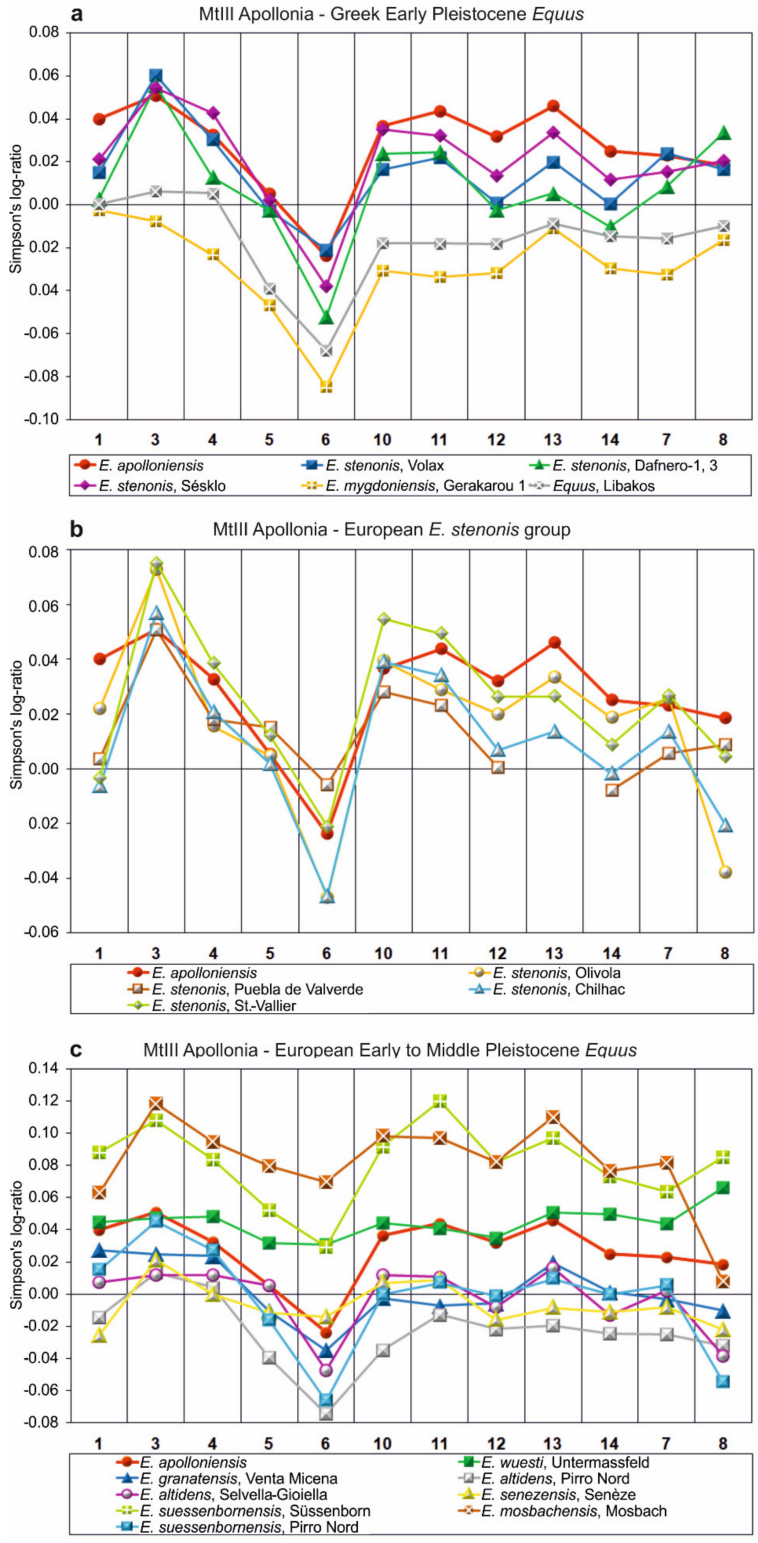


Figure 10. Simpson's log-ratio diagrams comparing the dimensions of the third metatarsal of *E. apolloniensis* with (**a**,**b**) Greek and European *E. stenonis* and (**c**) other Early/Middle Pleistocene horses. Standard: *Equus grevyi* [69]. Data from [61–65,80] and personal dataset. Definitions of meas., see Supplementary Materials.

6. Discussion

The arrival of the monodactyl equids in Eurasia and their dispersal towards Europe is one of the most significant events that mark the beginning of the Quaternary period (*Equus–Elephant* event) [82]. Despite the rich fossil record of equids from several localities and the numerous studies upon them, their taxonomy, phylogenetic relationships and chronological distribution are still discussed ([47,60,65,75,77,79,80,82–98] and ref. therein). The lack of complete or well-preserved crania from the Early Pleistocene European record makes the comparisons rather difficult.

Authors disagree regarding the phylogeny of the Early and Middle Pleistocene equids (*E. granatensis*, *E. altidens*, *E. suessenbornensis*, *E. wuesti*, *E. apolloniensis*) and whether these species originated from America, Asia, and/or Africa. According to [80], species like *E. suessenbornensis*, *E. granatensis* and *E. altidens* are included in the sussemione-group due to their peculiar dental features; this group is supposed to originate from North America, and it is not linked with stenonoid equids (e.g., *Allohippus*). However, other authors do not consent to this approach, considering these species belonging to the stenonoid group [65,77,79,83,94–96]. According to these authors, these species were locally evolved in Europe from a stenonoid stock adapting to environmental conditions and climatic changes [96].

The exact taxonomic position of *E. apolloniensis* and its phylogenetic relationships to the stenonoid equids is a matter of debate [41,61,96,99,100]. *Equus apolloniensis* was originally described as a species with both stenonoid and caballoid features [41]. The shorter muzzle, the more elongated protocones (which occurred at 1.2–0.7 Ma, [100] and the slender metapodials indicate an advanced species adapted to dry-cool habitats. According to [41], *E. apolloniensis* could "*represent a transitional form from the typical E. stenonis to the middle Pleistocene horses* (*Equus ex gr. E. suessenbornensis*). According to [61], *E. apolloniensis* shares great similarities in the morphology of the teeth and the general proportions of the metapodials with extant wild asses (*E. africanus*), and thus it could represent "*a step within the lineage of asses soon after their differentiation*". Furthermore, similarities with *E. mygdoniensis*, *E. altidens* from Pirro Nord, *E. granatensis* and *E. wuesti* on either the metapodials and/or the tooth morphology make relationships of *E. apolloniensis* more complicate.

Based on the basicranial proportions, [61,99] consider *E. apolloniensis* as a true *Equus* along with *E. suessenbornensis* and other equids. [78,101] distinguish the crania of true *Equus* from the primitive *Plesippus* and *Allohippus*, using Franck's index (vomerine length (meas. 3)/post-vomerine length (meas. 4)%) and the palatal index (palatal length (meas. 2)/vomerine length (meas. 3)%). In the best-preserved specimen APL-148, Franck's index is 112, indicating that vomerine length is longer than post-vomerine one, contrary to the true horses, and it is similar to asses and donkeys [78]. On the other hand, the palatal index on APL-148 and APL-872 is 103 and 104.3, respectively, indicating a slightly longer palate than vomerine length, a character of true *Equus*. Consequently, *E. apolloniensis* must be assigned to *Equus*, though not to the caballine forms. It is likely the oldest occurrence of a cranium belonging to a true *Equus* (non caballine) in Europe [99,100], while *E. mosbachensis* von Reichenau, 1915 dated at 0.5 Ma, is believed to be the first evidence of a caballine equid [101,102].

Considering all mentioned above, the following hypotheses could be formulated:

(a) *E. apolloniensis* could be an intermediate form between *E. stenonis* and the middle Pleistocene equid, *E. suessenbornensis*. Although the general size of the metapodials of *E. apolloniensis* is similar to those of *E. stenonis*, the proportions fit better with the slender but smaller *E. altidens* from Pirro Nord and *E. mygdoniensis*. In other words, there is an obvious proportional analogy associated with a size increase through time from the metapodials of *E. mygdoniensis* and *E. altidens* from Pirro Nord to those of *E. apolloniensis* (Figure 9) (see also [41]). *E. apolloniensis* may originate from an *E. mygdoniensis–E. altidens* stock-keeping similar proportions on the metapodials but increasing in size. Ref. [103] suggested that *E. mygdoniensis*, *E. altidens*, and perhaps *E. wuesti* and *E. apolloniensis* could represent different local species or ecomorphotypes

of the same lineage. Although this scenario cannot be ruled out with the available data, differences on the crania (at least with the better-known *E. mygdoniensis*) contradict the hypothesis of local ecomorphotypes and rather support the idea of different species from the same lineage. The affinities with *E. suessenbornensis* at the distal articulations of the metapodials (analogies between meas. 10–11) could also support a link between the two species. This hypothesis rather supports the idea that both species, *E. suessenbornensis* and possibly *E. apolloniensis*, evolved in Europe and belonged to stenonoid lineage.

(b) Based on similarities of both upper and especially lower teeth and metapodials, Ref. [61] noted affinities between *E. apolloniensis* and the modern wild asses (*E. africanus*). If indeed, as these authors state, *E. apolloniensis* represents an early step in the lineage of asses, it cannot be linked to stenonoid s. s. and *E. suessenbornensis* [100]. Although the lower teeth of the mandible APL-570 are ass-like, the revised description of both old and new material suggests that *E. apolloniensis* resembles asses as much as hemiones.

Considering all mentioned above, similarities of *E. apolloniensis* with the stenonoid horses and the proportional similarities of its metapodials with *E. mygdoniensis* and *E. altidens* from Pirro Nord rather support the first hypothesis.

7. Conclusions

As Apollonia is dated at the beginning of the 1.2–0.9 Ma interval [58], it represents the most complete Epivillafranchian faunal assemblage in southeastern Europe, a period with increased climatic variability in subtropical Africa [104] and a significant faunal turnover in the western Palearctic [59]. The result of these progressive environmental-related modifications of the faunal assemblages is recorded in the Mygdonia Basin by the replacement of the primitive stenonoid horses (*E. stenonis, E. mygdoniensis*) by the medium-large size *E. apolloniensis*, which was adapted to the open landscapes indicated by its shorter muzzle (following Allen's rule) and slenderer metapodials. In Southwestern Europe, primitive equids are being replaced at about 1.5–1.4 Ma by the slender, middle-sized *E. granatensis* (Venta Micena LFA, Spain) and *E. altidens* (Selvella, Pirro Nord LFA, Italy), while the larger *E. suessenbornensis* also occurred in Selvella and Pirro Nord (Italy) and in Barranco León 5 and Fuente Nueva 3 (Spain) [65,105]. The presence of two species of *Equus* in Apollonia 1 fits its young age. According to [106], usually, one equid species was present in the European faunas from the Early Pleistocene (~2.5–1.7 Ma).

The co-existence of two species becomes more frequent in younger localities, such as in Tsiotra Vryssi (Greece), Akhalkalaki (Georgia), Selvella-Gioiella and Pirro Nord (Italy), Fuente Nueva-3 and Barranco León-5 (Spain), and maybe three species in Süssenborn (Germany) [31,60,65].

The geographical distribution of *E. apolloniensis* seems to be rather limited in southeastern Europe (Eastern Mediterranean), with the possible first occurrence in Tsiotra Vryssi, Greece (1.78–1.5 Ma, [31,107]), Platanochori-1 [31] and Alykes (~1.6 Ma, [54]). A similar form is also reported from the *Homo erectus* bearing Kocabaş-Denizli mammal locality (1.3–1.1 Ma; [108,109]).

Supplementary Materials: The Supplementary Materials includes the principal component analysis and the box-plot diagrams of the maximal length of the Apollonia 1 metapodials than other early middle Pleistocene equids from Europe. It also includes the raw data and their statistics for the crania, mandibles and metapodials of the Apollonia equids. The following are available online at https://www.mdpi.com/article/10.3390/quat4020012/s1, Figure S1: Box-plot diagrams comparing the maximal length of the metapodials of E. apolloniensis with various Greek and European taxa of Equus, Figure S2: principal component analysis (PCA), loading the metapodial dimensions of E. apolloniensis and various equid taxa from Greece and Europe, Table S1: Results of One-way PERMANOVA for the metacarpals (lower left) and metatarsals (upper right) of Equus apolloniensis and other European equids (*p*-values, A 95), Table S2: Cranial and mandibular dimensions and statistics of Equus

apolloniensis, Table S3: Metacarpal dimensions and statistics of Equus apolloniensis, Table S4: Metatarsal dimensions and statistics of Equus apolloniensis.

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Abbreviations

Localities:

ALK	Alykes (Thessaly, Greece);
APL	Apollonia (Macedonia, Greece);
CH	Chilhac (France);
CHR	Chrysavgi, (Macedonia, Greece);
DFN, DFN3	Dafnero 1, 3 (Macedonia, Greece);
GER	Gerakarou 1 (Macedonia, Greece);
KAL, KLT	Kalamoto 1, 2 (Macedonia, Greece);
KRI, KRM	Krimni 1, 2 (Macedonia, Greece);
LIB	Libakos (Macedonia, Greece);
MAR	Marathousa 1 (Macedonia, Greece);

PLN	Platanochori (Macedonia, Greece);
PN	Pirro Nord;
RIZ	Riza 1 (Macedonia, Greece);
RVL	Ravin Voulgarakis (Macedonia, Greece);
SES	Sésklo (Thessaly, Greece);
SU	Süssenborn (Germany);
SE	Senèze (France);
SG	Selvella-Gioiella;
StV	Saint-Vallier (France);
TSR	Tsiotra Vryssi (Macedonia, Greece);
VOL	Volax (Macedonia, Greece);
VSL	Vassiloudi (Macedonia, Greece)
Other:	
McIII	third metacarpal;
MtIII	third metatarsal;
DAP	antero-posterior diameter;
meas. X	measurement X;
PCA	principal component analysis;
Fm	Formation

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