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Pleistocene vertebrates from the Kyparíssia lignite mine, Megalopolis Basin, S. Greece: Rodentia, Carnivora, Proboscidea, Perissodactyla, Ruminantia

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A B S T R A C T

The lignite mine of Kyparíssia is situated in the northern part of the Middle Pleistocene fluvio-lacustrine basin of Megalopolis (central Peloponnesus, Greece). During the years 2004–2008 numerous vertebrate fossils have cropped out in the mining sections and collected or excavated during short-term field expeditions. The finds derive mainly from organic-rich sediments (mostly lignites) and two fossiliferous horizons, which are stratigraphically closely situated. They are generally widely dispersed along the western margin of the palaeolake. Denser concentrations were found in four sites, dubbed KYP1–KYP4. The recovered fauna is diverse, dominated by hippopotamuses, deer and elephants. The present study describes the samples referred to castorids, carnivores, proboscideans, perissodactyls and ruminants. The following taxa are recognised: *Castor fiber*, *Canis* sp., Hyaenidae indet., *Felis* sp., *Panthera* sp., *Palaeoloxodon antiquus*, *Stephanorhinus* sp., *Equus* sp., *Praemegaceros verticornis*, *Cervus elaphus*, *Dama* sp., '*Cervus' peloponnesiacus*, and Cervidae indet. This fauna is of Galerian type, suggesting an early Middle Pleistocene age for the locality. The ecological character is that of a temperate, predominantly woodland/forest environment, with continuous presence of a large freshwater body.

1. Introduction

The lacustrine basin of Megalopolis (central Peloponnesus, Southern Greece) is well known since the beginning of the 20th century for its wealth in Pleistocene mammalian fossils, although sporadic mega-herbivore remains were continuously unearthed there since the antiquity (Mitzopoulos et al., 1862; Bürchner, 1903; Skuphos, 1905; Melentis, 1961; Sickenberg, 1976). The first large-scale palaeontological excavation was conducted by Prof. Theodore Skouphos (University of Athens) in 1902 in two or three locations within the basin (Bürchner, 1903; Skuphos, 1905; Melentis, 1961; Sickenberg, 1976). The produced material, which lacks specific provenance and stratigraphic information, was described much later in a series of publications by Melentis (1961, 1963, 1966a–g). During a geological prospecting project carried out during the years 1960, 1962 and 1963 in the area by a German team, working on the assessment of the mining potential of the organic-rich lacustrine deposits, additional palaeontological specimens were collected, all of which were non-stratified, surface finds. This material was studied by Sickenberg (1976). Since 1969 the exploitation of the basin's lignite seams in open-cast mines for electricity production has considerably facilitated the discovery of new sites, as the fossiliferous layers have been much more accessible in horizontal extent and depth. The mining activities have taken place in four fields, the Chorémi, the Marathoúsa, the Thoknía, and the Kyparíssia mine (Fig. 1), two of which, Kyparíssia and Marathoúsa have been recently investigated palaeontologically and are presented in the present issue. The Marathoúsa fauna is very well documented stratigraphically, as a product of a detailed systematic excavation, and is described by Konidaris et al. (this issue). The Kyparíssia fauna was discovered in October 2004, when a mine section collapsed during the mining operations, revealing skeletal remains of an elephant. This initiated a fieldwork project by the author, run from 2004 to 2008, on behalf of the Ephorate of Palaeoanthropology–Speleology (Hellenic Ministry of Culture). The project included the collection of surface material cropping out during the mining operations, as well as small rescue excavations in certain rich or important findspots, and produced a wealth of fossil skeletal elements of mammals, birds and reptiles. A part of the collected finds, referred to turtles, birds and suiform mammals, is described by Athanassiou et al. (this issue). The present paper completes the study of the Kyparíssia fauna with the description of the most complete and identifiable specimens belonging to mammals other than suiforms. A preliminary report of this study was presented by Athanassiou (2016).

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2. Material and methods

The studied osteological and dental material is stored in the collections of the Ephorate of Palaeoanthropology–Speleology (Ministry of Culture, Athens, Greece). Because of the fieldwork conditions (including collection of poorly stratified specimens within the highly disturbed environment of a lignite quarry) most of the available specimens are highly fragmentary. Consequently only a part of the collected sample is described below, that is those specimens that are fairly complete and attributable to a taxon. For the reader's convenience the catalogue numbers of the *in situ* specimens mentioned in this study include the site number where available (e.g., KYP3-456), though the actual specimens in the collection are invariably labelled as KYP (e.g., KYP-456). Surface finds are simply referred to as KYP throughout the text.

The description of the finds is based on standard anatomical terminology (König and Liebich, 2004; I.C.V.G.A.N., 2005). All measurements are in mm with an accuracy of up to one decimal digit, when possible. The use of parentheses in the tables denotes an inaccurate or estimated measurement because of specimen distortion or incomplete preservation. To avoid ambiguities about the cited sources, citations to figures, plates, tables etc. of published papers are given in lowercase, while citations to figures etc. of the present paper are given with a capital first letter.

Anatomical and dimensional abbreviations: I/i: upper/lower incisor; C/c: upper/lower canine; M/m: upper/lower molar; P/p: upper/lower premolar; trd: trigonid; DAP: craniocaudal (anteroposterior) diameter (p: proximal; d: distal; a: articular; pr: of protocone); L: length; DT or W: transversal diameter (p: proximal; d: distal; a: articular); H: height; Dmax: maximal diameter; Cf: circumference.

Institutional abbreviations: AMPG: Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece. IGF: Natural History Museum, University of Florence, Italy, NHMB: Natural History Museum of Basel, Switzerland.

3. Geological setting and taphonomy

The Megalopolis Basin originated from extensional tectonic movements, that created a continuously deepening graben along a NW–SE direction (Fig. 1A). Its basement consists of Mesozoic limestones and Palaeogene flysch that belong to Píndos and Tripolis geotectonic zones of the alpine orogen. The basin accumulated lacustrine (mostly phytogenic) and fluvial sediments during the Pleistocene, particularly the middle part of this epoch (van Vugt et al., 2000). An extensive, more recent, alluvial fan, as well as terrace deposits of the Alpheiós River, cover the sequence. The massive Middle Pleistocene series is characterised by an alternation of fluvial and biogenic lacustrine sediments that are interpreted as a sedimentary response to cold/arid (glacial) and warm/humid (interglacial) climatic alternations (Nickel et al., 1996; van Vugt et al., 2000; Okuda et al., 2002).

The Kyparíssia mine occupies the NW area of the Megalopolis Basin (Fig. 1A). Its basement consists of Jurassic – Early Cretaceous cherts and Late Cretaceous limestones of the Píndos geotectonic zone (Papadopoulos et al., 1997). The basin sedimentary fill in the area consists mainly of a thick lignite sequence, lacking the intermediate detritic layers, which are found elsewhere in the basin (Fig. 1C). On top of the lignite there is a red clay deposit of colluvial origin, which expands along most of the western margin of the basin (see Fig. 2A). According to the stratigraphic scheme used by Löhnert and Nowak (1965) and Vinken (1965), the sedimentary fill at Kyparíssia belongs to the Marathousa member of the Chorémi Formation.

The fossils crop out mainly along the western margin of the mine, that is along the western margin of the Megalopolis palaeolake, while they are extremely rare in the central and the eastern parts of the mine. They are usually found isolated at numerous findspots. Four areas that were characterised by increased density and/or importance of finds were dubbed sites 1 to 4 (KYP1 to KYP4; Fig. 1B). Their geographic coordinates are the following: KYP1, 37.4526°N, 22.0696°E; KYP2, 37.4569°N, 22.0697°E; KYP3, 37.4541°N, 22.0686°E; KYP4, 37.4537°N, 22.0696°E (WGS84 datum). KYP1 and KYP2 were partially exploited in 2004 but were subsequently destroyed or buried as a result of the mine development. KYP3 and KYP4 still exist and are promising for future research by means of a systematic excavation. An additional site tracked down in 2012, KYPT (Fig. 1B), is not considered in the present study, because it didn't yield identifiable specimens of the taxa described here (see Athanassiou et al., this issue). All sites are located near the top of the preserved palaeolake sedimentary sequence in this part of the basin, at an altitude of 330–340 m. Their exact position with regard to the stratigraphy of the whole basin is, however, difficult to assess, mainly because the characteristic lignite seams, which are distinct in the more southern parts of the basin, are merging to each other towards the North, forming the thick more or less uniform biogenic deposit without any significant detrital intercalations. Löhnert and Nowak (1965) correlate this lignite deposit with the lignite seams I and II, implying that the stratigraphically upper seam III is missing in the north of the basin and in Kyparíssia mine in particular (Fig. 1C). Indeed, a calcareous–marly layer situated at the base of the KYPT section (see Athanassiou et al., this issue, fig. 2) may be identified as the thin limestone layer that according to Löhnert and Nowak (1965) characterises the top of the lignite seam II. However, this layer is not present or exposed in the other sites at Kyparíssia, which would have been closer to the lake shore.

KYP1 is the initially located section-collapse site. It is a sequence of mainly dark-coloured lignite layers with intercalating gray sandy clays of variable thickness (Fig. 2A). The main gray layer has a thickness of about 3 m, situated at an altitude of 340 m. This is most probably the layer that contained an axial skeleton of an elephant (see Section 4.3). The underlying lignite layers were also rich in fossils, notably *Hippopotamus* specimens, most of which probably belong to a single individual (Athanassiou et al., this issue). Due to the disturbance of the site the stratigraphic relationship and the number of the existing fossiliferous horizons are not clear. The most probable reconstruction based on field data includes two fossiliferous horizons at about 340 m and 330 m above sea level.

KYP2 is the northernmost one at an altitude of 340 m. It was potentially very rich in fossils preserved within lignite, as shown by preliminary fieldwork (prospecting and small-scale rescue excavation), but it was destroyed before it could be excavated more extensively.

KYP3 (Fig. 2B) includes a rich fossiliferous lignitic layer at 340 m above sea level, which was horizontally exposed over an area of about 300 m^2. Part of this exposure was covered later because of the construction of a temporary road. The lignitic layer lays on an at least 1-m-thick green-brownish sandy clayey layer with numerous small (diameter of about 5–20 mm) angular gravel in certain places. A few meters to the North, the clay becomes chestnut-brown and contains nodules and intercalations of pure green sand. The site also includes an additional fossiliferous horizon in a sandy clay layer, poor in finds but only visible in a section, situated about 2 m higher than the main one.

KYP4 is situated on top of a limestone outcrop, apparently very close to the palaeoshoreline, at an altitude of 330 m (Fig. 2B). It consists of lignite layers with intercalations of sandy clays. The fossil finds are not accumulated but were found dispersed. The lacustrine sediment outcrop at this site is limited, less that 2 m thick, as most of it has been already mined.

The preservation quality of most recovered specimens is high, documenting every detail of their live morphology. They have suffered, though, recent fragmentation due to operations of the mining machinery. KYP1 and KYP3 yielded specimens that quite plausibly belong to individual skeletons (of an elephant and a hippopotamus in the former site, of a hippopotamus in the latter), but no relevant taphonomic data are available, because the sites were highly disturbed. Very few isolated surface finds show signs of rounding because of rolling

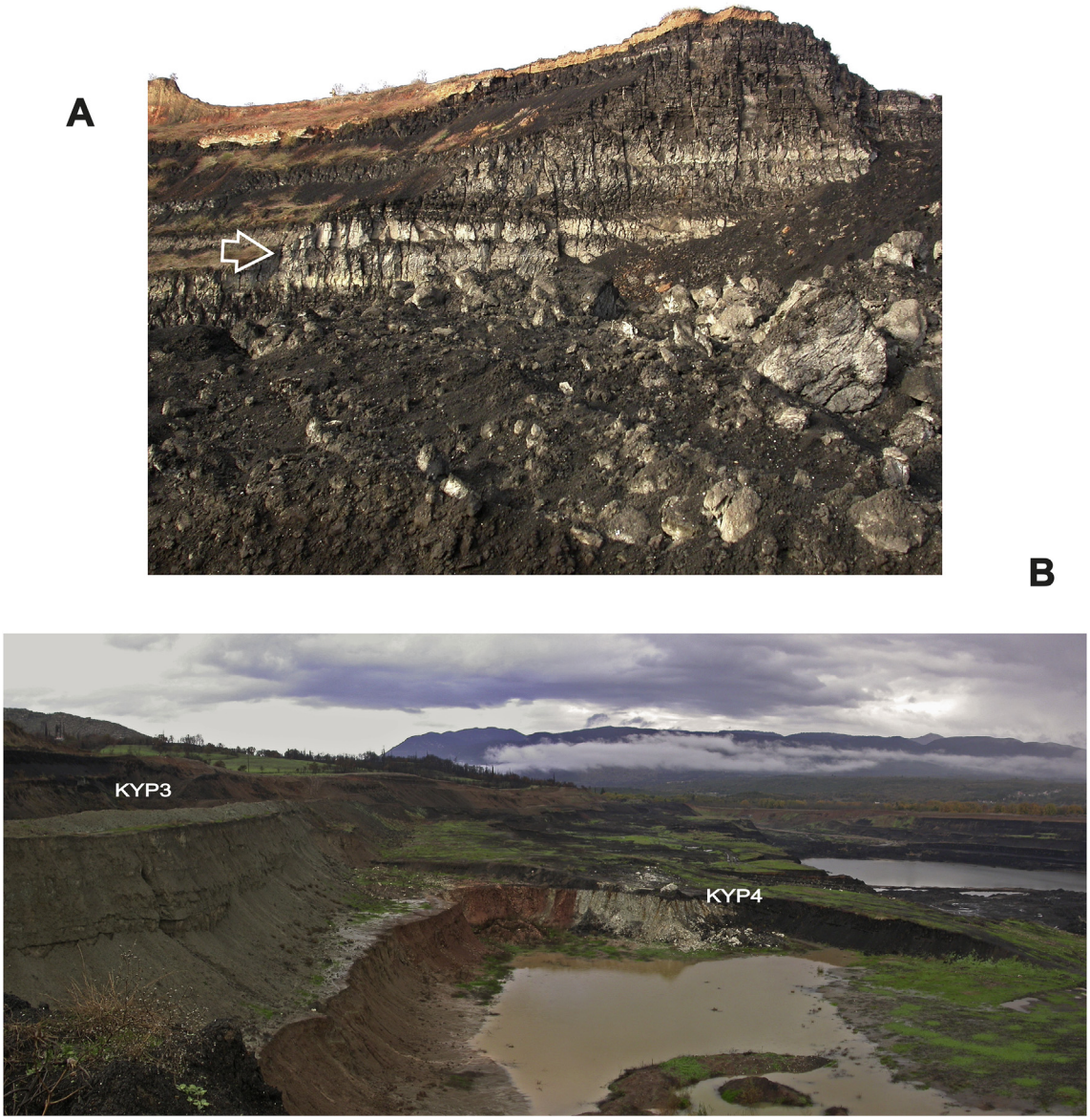

Fig. 2. Views of three sites at Kyparíssia mine: **A**, the collapsed section at KYP1 viewed from the East (October 2004). The layer where the elephant axial skeleton possibly derived from is indicated by an arrow. Note the red colluvial deposits on the top that cover the lacustrine layers. **B**, the location of the sites KYP3 and KYP4 viewed from the South (November 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

wear; their state of preservation, and their reddish colour in particular, indicates that they quite probably come from the colluvial formation that covers the lacustrine series. The specimens recovered from both horizons at KYP1 are in pristine condition, barring the fact that the section collapse caused severe fragmentation. The fossil preservation at KYP2–KYP4 varies according to local geochemical conditions and the effects of the mining operations. However, no specimen exhibits surface cracking or flaking, indicating quick burial without exposure to dry aerial conditions or to any stresses associated with high temperature and moisture changes (Behrensmeyer, 1978). Two cervid skulls excavated *in situ* at KYP2 and KYP4 were severely damaged during or shortly after deposition, which could have possibly happened due to trampling by animals moving in the lake close to the shore: KYP2-345 was reduced to a concentration of scattered fragments, except for the pedicels, the distal part of one antler, and most of its teeth, while KYP4-633 is badly crashed and twisted (see Fig. 9E). The mining operations may have also contributed to the further fragmentation of these specimens, particularly of the former one. Carnivore damage of the collected specimens is quite uncommon throughout the locality. Very few bone specimens, most notably the rhinoceros astragalus KYP-358 (see Fig. 8B), show signs of possible carnivore gnawing.

4. Systematic palaeontology

4.1. Rodents

The fieldwork in Kyparíssia mine did not include any micropalaeontological survey, thus there are no data on the microfauna of the locality. Nevertheless, the presence of a large-sized rodent was confirmed by two specimens.

Order: Rodentia Owen, 1848

Family: Castoridae Gray, 1821

Genus: *Castor* Linnaeus, 1758

Castor fiber Linnaeus, 1758

Material: KYP-166: right lower incisor; KYP4-310: right humerus part.

Description: The tooth (Fig. 3A) is a surface find spotted at about 100 m north of the site KYP2. It is moderately curved (radius of

Fig. 3. Rodent and carnivore finds from Kyparissia. *Castor fiber* Linnaeus, 1758: **A**, right lower incisor, KYP-166, mesial view and cross section (*l*, labial; *m*, mesial; *d*, distal side). *Canis* sp., right dentary with p3–m2, KYP-162: **B**, occlusal view; **B′**, labial view; **B″**, lingual view. **C**, Hyaenidae indet., right P4 part, KYP3-34, labial view. **D**, *Panthera* sp., left third metatarsal, KYP3-22, lateral view. *Felis* sp., right tibia, KYP3-144: **E**, lateral view; **E′**, cranial view. The graphical scale equals 5 cm for **A**, **D** and **E**, 3 cm for **B** and **C**.

curvature = 5 cm), of subtriangular cross section, and covered by enamel only on its labial side. The enamelled side is almost flat with rounded edges. The incisor's preserved length is 76.5 mm (90 mm, measured along its labial margin). Its linguolabial diameter is 9.2 mm and its mesiodistal 8.3 mm. The humerus lacks its proximal part proximally to the deltoid tuberosity, as well as the lateral part of its distal extremity. The specimen presents a typical castorid morphology, with medially expanded distal end and prominent crests along the diaphysis. Its general size is comparable to *Castor fiber*; no measurements can be taken, however, due to its bad preservation.

Among the European Pleistocene Castoridae, KYP-166 differs from *Trogontherium* morphologically, in its flat, not convex, enamel band, and its subtriangular, not pear-shaped cross section (Schreuder, 1931, p. 153; Fostowicz-Frelik, 2008, p. 767). It also differs metrically from this genus, as KYP-166 is somewhat smaller (Hooijer, 1959; Mayhew, 1978). Nonetheless, its dimensions are identical with the *Castor fiber* samples from Heppenloch and Mauer, and slightly smaller than the samples from Elbe and Iller (all in Germany) referred to the same species (Adam, 1975, p. 12; Mai, 1979, p. 45). *Castor fiber* is already known from an unspecified locality within the Megalopolis Basin (Melentis, 1964), as well as from the levels CHO2–CHO4 of the Chorémi mine (van Vugt et al., 2000). The species was also recently found in Marathousa 1, another locality within the Megalopolis Basin (Konidaris et al., this issue).

4.2. Carnivores

The specimens referred to carnivores are scanty, testifying the presence of four small to large-sized species. The Megalopolis carnivore guild was probably much more diverse, as indicated by the occurrence of additional taxa in non-stratified material (Sickenberg, 1976), as well as in the recently excavated locality of Marathousa 1 (Konidaris et al., this issue).

4.2.1. Canids

Order: Carnivora Bowdich, 1821
Family: Canidae Gray, 1821
Genus: *Canis* Linnaeus, 1758
Canis sp.
Material: KYP-162: right dentary with p3–m2.

4.2.1.1. Description. There is only a single specimen attributable to a canid, that is a right mandibular fragment preserving part of the dentition (p3–m2; Fig. 3B). It is a surface find in the area of KYP3. The rostral part, the ventral margin and the ramus are broken off. The p3 is preserved only distally, while p4 and m1 lack their mesial wall. All preserved teeth are worn, particularly the masticatory part of the dentition (talonid of m1, m2). Both premolars present an accessory cuspid distally to the protoconid, as well as a distal talonid that forms a small tubercle at its distal end, though both are almost totally worn out in p3. The carnassial (m1) is the largest and strongest tooth, characterised by a very prominent protoconid. Its paraconid is much lower, about as high or somewhat higher than the protoconid of p4 (accurate height comparisons are, however, impossible, due to the advanced stage of wear). The metaconid is low and not well separated from the protoconid, but this is quite probably due to its advanced wear stage. The trigonid makes up about 75% of the tooth's length. The talonid has a larger labial cuspid (hypoconid) and a smaller lingual one (entoconid), both worn almost till their base. The m2 is dimensionally comparable to the talonid of m1, which it is functionally related to. Its occlusal surface is rather elongate, not square. The mesial cuspids, protoconid and the metaconid, are still distinguishable, the former being stronger, while the distal ones are totally worn out. The presence of an m3 is witnessed by its partially preserved alveolus. The dental measurements of KYP-162 are given in Table 1.

4.2.1.2. Discussion. Compared to known Pleistocene mandibles of the genus *Canis*, KYP-162 has small dimensions. The m1 is metrically much smaller than Late Pleistocene *C. lupus* (Argant, 2010; Bertè and

Table 1
Dental dimensions (in mm) of the *Canis* mandibular fragment KYP-162 from Kyparíssia mine.

Canis sp.	L p3	W p3	L p4	W p4	L m1	L m1 trd	W m1	H m1	L m2	W m2
KYP-162	–	4.6	(13.0)	5.6	(20.5)	(15.5)	8.3	12.5	9.1	7.0

Pandolfi, 2014), marginally smaller than the Early and Middle Pleistocene *C. etruscus* and *C. mosbachensis* from European localities (Bonifay, 1971; Baryshnikov, 2012; Bartolini Lucenti et al., 2017; personal data), and similar to the smaller specimens from Petralona (Kurtén and Poulianos, 1977, 1981; Baryshnikov and Tsoukala, 2010), Ceyssaguet (Boudadi-Maligne, 2010), Poggio Rosso (Bartolini Lucenti and Rook, 2016), and Valdarno (IGF, NHMB, personal data), referred to the small-sized species *C. arnensis*. Moreover, *C. etruscus* and *C. mosbachensis* have proportionally longer lower carnassials with regard to the m2 length. Fig. 4 depicts graphically these metrical comparisons. The metrical similarity of KYP-162 to samples referred to *C. arnensis* indicates that it possibly belongs to this species. *Canis arnensis* is considered to have persisted in Southern Europe during the Middle Pleistocene, while *C. mosbachensis* was already established to northern territories (Rook and Torre, 1996; Brugal and Boudadi-Maligne, 2011). However, given the availability of only one specimen, with insufficiently identifiable dental morphology due to wear, and having in mind the still unresolved taxonomy of the pre-Late Pleistocene *Canis*, I will refrain from determining KYP-162 to the species level. Within the Megalopolis Basin *Canis* is also known from the recently excavated locality Marathousa 1 (Konidaris et al., this issue). Although no comparison is possible, as there are no common skeletal elements between Kyparíssia and Marathousa 1, the latter sample also represents a small-sized *Canis*, quite plausibly taxonomically identical to KYP-162.

4.2.2. Hyaenids

Order: Carnivora Bowdich, 1821
Family: Hyaenidae Gray, 1821
Hyaenidae indet.
Material: KYP3-34, right P4 fragment; KYP-669, coprolite.

The dental fragment is the mesial part of a right P4 (Fig. 3C). It lacks the protocone and the part of the tooth distally to the paracone tip. The specimen has a strong parastyle. Due to its partial preservation, which do not allow either any assessment of its morphology, or to take measurements, it cannot be determined further than the family level.

The coprolite was found in the area of KYP1. It is flattened in lateral view, circular in axial aspect with a diameter of 52 mm, and crescent-shaped in sagittal section (its one side being convex and the other concave). It is an ichnofossil of a large hyaenid species.

Hyaenid material is already known from old fossil collections in the basin of Megalopolis and referred by Melentis (1964, 1966d) to *Crocuta crocuta*, but the find (a dentary fragment with p2 and p3) is rather inadequate for a specific attribution.

4.2.3. Felids

The family Felidae is very rare in the studied material, as it is represented by just two specimens. One belongs to a small species, referred to the genus *Felis*, and the other to a rather large taxon, similar in size to *Panthera pardus*. The latter represents the first record of a leopard-like felid in the basin of Megalopolis. The Felidae were previously known in the same region by a single surface find (phalanx) collected in 1962–1963, which was referred by Sickenberg (1976) to a larger species, the lion *Panthera leo*. Recently, a partially preserved P4, referred to *Felis* sp., was found in Marathousa 1 (Konidaris et al., this issue).

4.2.3.1. *Wildcat*.

Order: Carnivora Bowdich, 1821
Family: Felidae Gray, 1821
Genus: *Felis* Linnaeus, 17581
Felis sp.
Material: KYP3-144, right tibia.

This specimen (Fig. 3E) belongs to a small felid. It is quite slender, and its general shape is weakly sigmoid in cranial and particularly in lateral aspect. The proximal articulation is low in cranial view, as its articular surfaces are only slightly concave and the intercondylar eminence is weak. The tibial tuberosity, situated in the proximal end of the shaft and projecting cranially, is even and low. The distal extremity of the specimen bears a fairly deep articular cochlea. Dimensions are given in Table 2. Compared to tibias of Pleistocene and recent small-sized felids, KYP3-144 is smaller and more slender than *Lynx*, including the extant small Iberian lynx L. *pardinus* (Temminck, 1827) (Testu, 2006, tableau 21) and somewhat larger than the largest specimens of the European wildcat *Felis silvestris* Schreber, 1777 (Fig. 5; Ballesio, 1980, p. 99; Linseele et al., 2007; O'Connor, 2007). In terms of proportions the studied specimen is more similar to the *Felis* tibias, which are also slender, thus KYP3-144 is referred to this genus. Its large size relative to known *Felis* samples indicates a possible relationship to the extant species *F. chaus* Güldenstädt, 1776, the largest species of *Felis*, which still occurs in the Eastern Mediterranean region. This species' preference for swampy areas (Sunquist and Sunquist, 2002, p. 61; Hutchins et al., 2003, p. 390) is raising the possibilities for its occurrence in the Megalopolis Basin. The presence of *F. chaus* in the Pleistocene of Europe has already been reported (Helbing, 1934; Kurtén, 1968, p. 80; Schreve, 2001), but the available finds are scanty and not comparable to the Kyparíssia specimen, as they don't include a tibia. More material from Kyparíssia is certainly needed in order to reach to a species-level attribution. Very large-sized wildcats were previously documented in Middle Pleistocene localities of Greece (Petralona, Apídima; Kurtén and Poulianos, 1977, 1981; Tsoukala, 1989, 1999) and may be related to the Kyparíssia *Felis*. The taxonomic relationship between the wildcat of Kyparíssia and the smaller *Felis* sp. described from Marathousa 1 (Konidaris et al., this issue) is currently unknown.

4.2.3.2. *Panther*.

Genus: *Panthera* Oken, 1816
Panthera sp.
Material: KYP3-22, left third metatarsal.

The metatarsal is slightly curved in medial or lateral view (Fig. 3D), but it looks like being much more curved because of an inflated laterodorsal ridge, that makes its dorsal profile markedly convex. This condition is quite possibly pathological. Otherwise, the specimen has a felid morphology. Its proximal end is flat and medially inclined in dorsal or plantar view. The proximal articular surface is mushroom-shaped in proximal view, being much wider in its dorsal part. Its narrow plantar part is situated closer to the medial side of the bone, and it is gracile, unlike the morphology observed in certain Machairodontini (Ballesio, 1963, p. 102; Berta, 1987, p. 38; Rawn-Schatzinger, 1992; Christiansen and Adolfssen, 2007). The medial and lateral sides of the proximal end bear articular facets for the second and fourth metatarsals respectively, the latter being much larger. The distal articulation is spheroid with a distoplantarly prominent median keel, which is visible in dorsal view. Dimensions are given in Table 2. The size of the specimen is comparable to that of a large felid, like *Panthera pardus*, and it falls within the range of samples referred to this species (e.g., Diedrich, 2013, p. 184; Ghezzo and Rook, 2015, suppl. data).

4.3. Proboscideans

Order: Proboscidea Illiger, 1811
Family: Elephantidae Gray, 1821

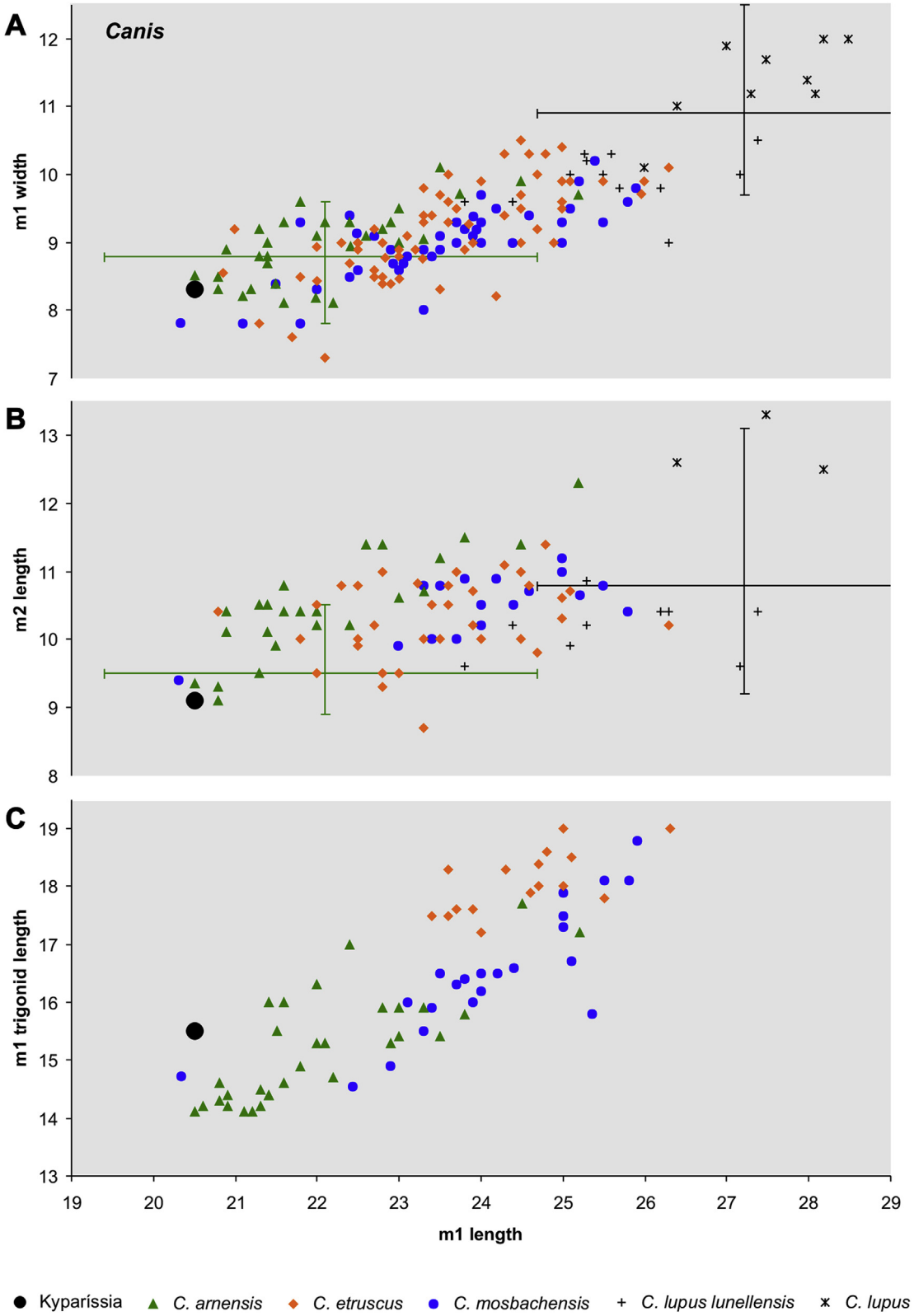

Fig. 4. Graphical comparison of the dental dimension of KYP-162 from Kyparíssia to selected rich European Pleistocene *Canis* samples: Scatter plots of the lower carnassial (m1) length in relation to the carnassial width (**A**), to the m2 length (**B**), and to the carnassial trigonid length (**C**). Data according to Argant (2010) and Bertè and Pandolfi (2014) [*C. lupus*, Romain-la-Roche (France), Avetrana (Italy), Late Pleistocene], Bonifay (1971) and personal data [*C. lupus lunelensis*, Lunel-Viel (France), late Middle Pleistocene; *C. etruscus*, L'Escale cave (France), Valdarno (Italy), Early Pleistocene], Sotnikova (2001), Baryshnikov (2012) and Bartolini Lucenti et al. (2017) [*C. mosbachensis*, Untermaßfeld (Germany), Vallparadís and Cueva Victoria (Spain), Early Pleistocene; Westbury Quarry Cave (England), Stránská skála (Czech Republic), Middle Pleistocene], Boudadi-Maligne (2010), Bartolini Lucenti and Rook (2016) and own data [*C. arnensis*, Ceyssaguet (France), Poggio Rosso and Valdarno (Italy), Early Pleistocene]. The green ranges in plots **A** and **B** correspond to the Petralona sample (Greece), which was originally referred to *C. etruscus* (Kurtén and Poulianos, 1977, 1981) and later transferred to *C. arnensis* (Baryshnikov and Tsoukala, 2010); the black ranges correspond to the Late Pleistocene *C. lupus* sample from Romain-la-Roche, France (Argant, 2010). The *C. lupus* samples extend beyond the plot areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Postcranial element measurements of Felidae (*Felis* sp. and *Panthera* sp.) from Kyparíssia (in mm).

Felis sp., tibia	L	DAPp	DTp	DTm	DAPd	DTd
KYP3-144	155.5	23.1	23.4	8.0	11.0	15.9

Panthera sp., MT III	L	DAPpa	DTpa	DAPda	DTda
KYP3-22	94.5	24.5	17.2	(14.5)	(15.5)

Genus: *Palaeoloxodon* Matsumoto, 1924
Palaeoloxodon antiquus (Falconer and Cautley, 1845)
Synonymy:

1961 *Archidiskodon meridionalis meridionalis* — Melentis, p. 229ff
1961 *Archidiskodon meridionalis cromerensis* — Melentis, p. 231
1961 *Palaeoloxodon antiquus antiquus* — Melentis, p. 178ff
1961 *Palaeoloxodon antiquus italicus* — Melentis, p. 208ff
1961 *Palaeoloxodon melitensis* — Melentis, p. 211ff
1965 *Palaeoloxodon antiquus germanicus* — Melentis, p. 198ff
1976 *Mammuthus (Archidiscodon) meridionalis* — Sickenberg, p. 28

Material: KYP4-52, KYP3-75, KYP3-76, KYP3-79, KYP3-121: tusk fragments; KYP3-160: right dentary bearing the m3; KYP-1: distal part of right m3; KYP-674: distal part of right m3; KYP-362: distal lower molar (m3?) part; KYP3-132: lower (?) molar fragment; KYP-613: molar fragment; KYP-146: atlas part; KYP1-464, KYP1-481, KYP1-482: cervical vertebrae; KYP1-167, KYP1-168, KYP1-479, KYP1-485, KYP1-486, KYP1-487, KYP1-488, KYP1-489, KYP1-549, KYP1-550, KYP1-551, KYP1-552, KYP1-553, KYP1-567, KYP1-792, KYP1-484, KYP-617: thoracic vertebrae; KYP1-149, KYP1-375, KYP1-376, KYP1-379, KYP1-381, KYP1-555, KYP1-556, KYP1-569: thoracic vertebral spinous processes; KYP1-475, KYP1-480: lumbar vertebrae; KYP1-446: sacrum; KYP-445: caudal vertebra; KYP1-396, KYP-756, KYP-757, KYP-758, KYP-765, KYP-769: left ribs; KYP3-483: left humerus; KYP1-675: left proximal radius; KYP4-74: right ulnar; KYP-643: left carpal IV; KYP-642: left metacarpal III; KYP-506, KYP1-686: pelvis parts; KYP-798: part of right femur distal end; KYP1-169: middle pedal phalanx III.

4.3.1. Description

The available dental material consists of numerous tusk fragments, several isolated or partly preserved lower molars (mostly m3s) and another complete m3 still in life position in a dentary fragment (KYP3-160; Fig. 6B). The tusk fragments are very small for an assessment of the tusk morphology and dimensions. However, several of them exhibit the Schreger pattern in their broken surfaces (Fig. 6A). The Schreger pattern is a special character of the proboscidean ivory (Espinoza and Mann, 1993; Palombo and Villa, 2001; Trapani and Fisher, 2003). In transverse sections, perpendicular to the sagittal plane, this pattern consists of two sets of radiating spiral lines that intersect with each other, forming the Schreger angles, and reflects macroscopically the dentine's internal structure. The Schreger lines in all examined specimens, where observable, form well obtuse angles of more than 120° near the tusk's cement/dentine junction (Fig. 6A).

The molar KYP3-132 consists of five lamellae worn down to the roots, plus a small part of a sixth lamella. It is probably a lower one, judging from the fact that the mesial face of the enamel loops is concave. The enamel is not intensely plicate. The tooth's maximal width is 72 mm (at the third lamella).

The partial m3s are high crowned. KYP-1 is preserved only distally: only the seven distalmost lamellae are available. The last three are still completely unworn, while the four mesial to them are slightly worn, presenting a series of small enamel loops on their occlusal surface. KYP1-674 also lacks its mesial part. Nine lamellae are preserved, five of which are only slightly worn, while the occlusal side of the rest four are still covered with cement. The two mesialmost lamellae exhibit a · – · wear pattern on the occlusal surface, i.e. the median enamel loops tend to be wider than the lingual and labial ones. The enamel of the mesial lamellae is rather thick (2–3 mm) and strongly plicate, particularly in their median area, where it also tends to form a slight loxodont sinus. The metrical characters of KYP1-674 are: maximal preserved width = 87 mm (at 6th lamella), height = 155 mm (at 5th lamella), lamellar frequency = 5.4 lamellae/10 cm, hypsodonty index = 178. Another distal molar part that might be identified as a right lower m3 is KYP-362, consisting of four slightly worn lamellae. The mesial one also exhibits the · – · wear pattern. The maximal lamellar dimensions are width = 86.5 mm and height = 172 mm, which results in a hypsodonty index of 199.

The m3 preserved in the KYP-160 mandibular fragment (Fig. 6B) is the only complete elephant molar available from Kyparíssia. However, its maximal dimensions cannot be measured accurately, as it is preserved within the dentary. The crown is elongate with proportionally narrow occlusal surface. It consists of sixteen lamellae, but one or two additional distal lamellae may also have existed and broken off. Twelve lamellae were in use, while the rest are totally unworn. A · – · wear pattern is very well pronounced in the ninth lamella. The enamel is strongly plicate in the moderately worn third to ninth lamellae, also exhibiting a prominent loxodont sinus. Its thickness is 2–3 mm. The molar measures about 330 mm in length and 84 mm in width (cement included), the widest point measured at the seventh lamella. The maximal lamellar height might be about 20 cm, judging from the dentary depth, but an actual measurement cannot be taken. The lamellar frequency is about 5 lamellae/10 cm.

4.3.1.1. Axial skeleton. Most of the vertebrae come from the site KYP1, found in close proximity, and quite possibly belong to the same individual, as implied by their very similar ontogenetic stage (all have unfused or incipiently fused vertebral discs), their comparable dimensions, and the good articulation between many of them. However, this association cannot be corroborated taphonomically, as they came to light after a quarry-wall collapse, thus recovered from disturbed sediments (see Section 3). The vertebral specimens not belonging to this skeleton are the KYP-146, KYP-484 and KYP-617.

The atlas is known from a single specimen (KYP-146, a surface find), of which only the left half is preserved. Moreover, the specimen is abraded or broken in many areas, particularly in its lateral end. Morphologically it is very robust and has a strong lateral wing (transverse process). The articulation for the left occipital condyle on the atlas' cranial face is bean-shaped and deeply concave in dorsoventral direction. A large transverse foramen opens laterally to it, perforating the wing in craniocaudal dimension. Another large foramen, the vertebral lateral foramen, opens in mediolateral direction through the dorsal arch, dorsally to the cranial articular surface. The caudal face preserves the left half of a continuous articular surface for the axis, as is the case in older individuals (Bezuidenhout and Seegers, 1996).

Apart from the atlas, three other vertebrae were identified as cervical: KYP1-464, KYP1-481 and KYP1-482 (Fig. 7A and B). All come from the KYP1 site and share the main characters of the post-axis cervical vertebrae, that is the craniocaudally very short body, the subtriangular vertebral foramen, the short and thin spinous process and the widely separated articular processes at the base of the vertebral arch. Of the three, the KYP1-482 belongs to the cranialmost part of the series, as

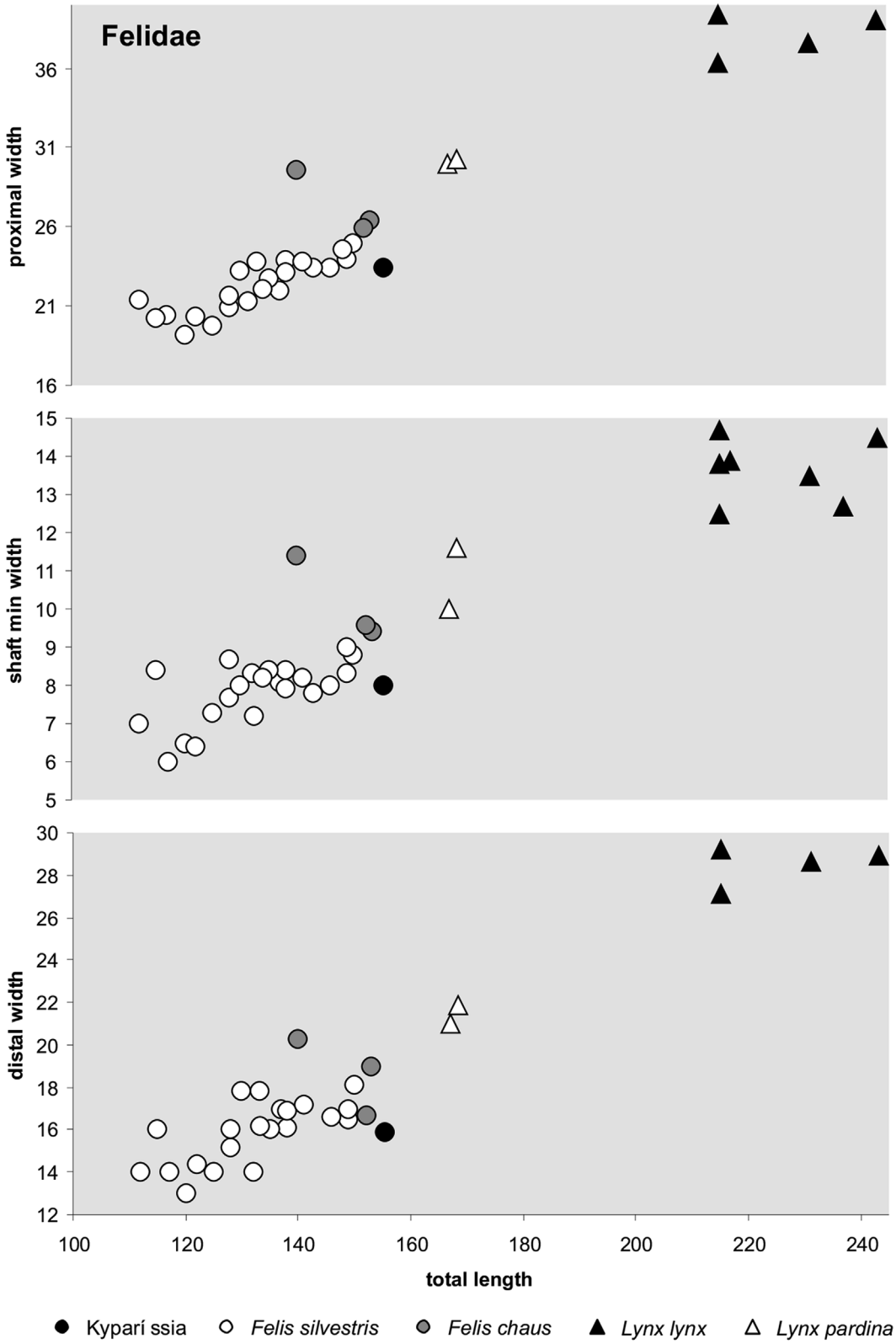

Fig. 5. Graphical comparison of the tibia KYP3-144 of *Felis* sp. from Kyparíssia to recent European *Felis* and *Lynx* samples. Metrical data according to Bonifay (1971), Kurtén (1978), Testu (2006) and Linseele et al. (2007). All dimensions are in mm.

it has the thinnest body and the most inclined facets on the articular processes. The KYP1-464 is especially characterised by the ventrolateral expansion of the transverse processes forming a ventral lamina on each side of the bone. This is a feature of the sixth cervical vertebra (Bezuidenhout and Seegers, 1996) thus KYP1-464 is identified as such. The KYP1-481 differs from the other two in the form of the transverse processes, which lack a transverse foramen, and in the presence of a caudal facet ventrolaterally on each side of the bone for the articulation of the head of the first rib; it is identified as the last (seventh) cervical vertebra. All three post-axis cervical vertebrae described here have

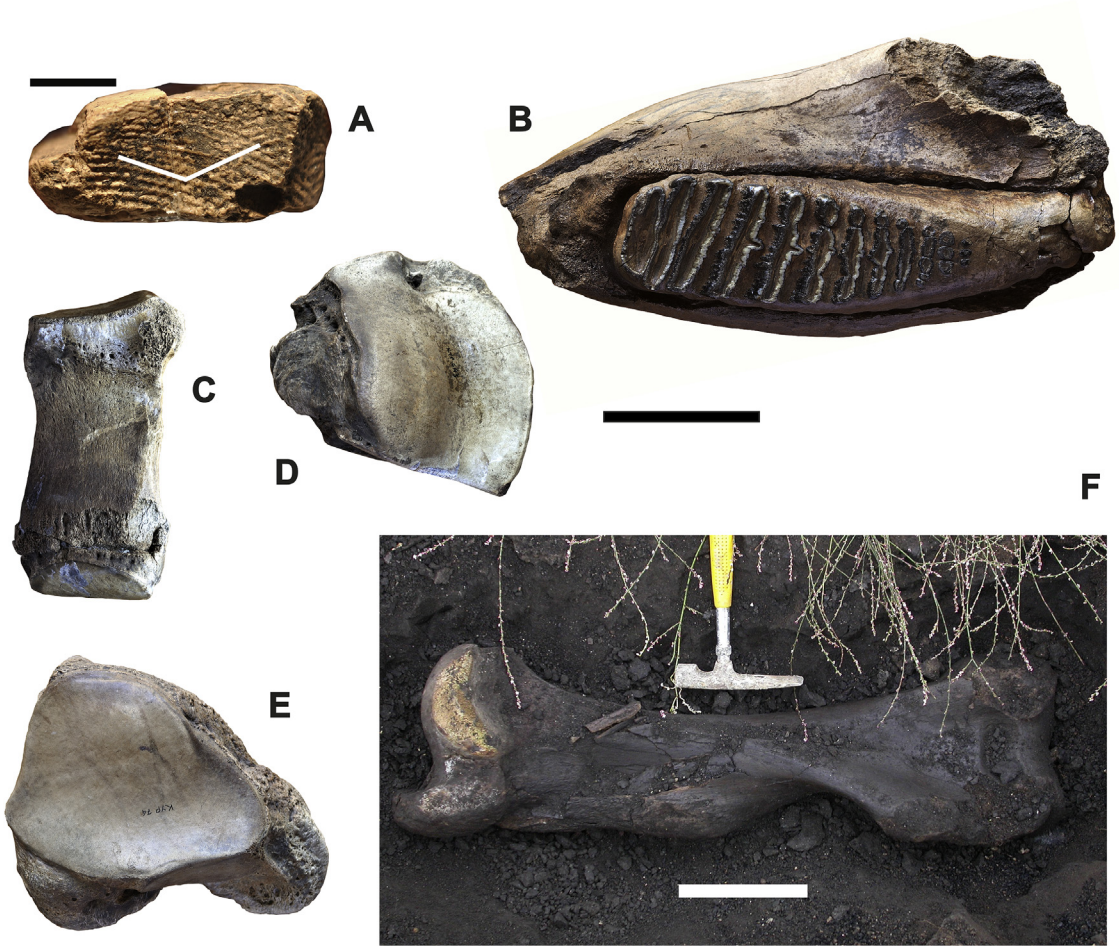

Fig. 6. *Palaeoloxodon antiquus* (Falconer and Cautley, 1845) from Kyparíssia: **A**, tusk (I2) fragment exhibiting the Schreger pattern in its cross section with well obtuse Schreger angles (white lines); **B**, right dentary with m3, KYP3-160, occlusal aspect; **C**, left metacarpal III, KYP-642, dorsal aspect; **D**, left carpal IV, KYP-643, proximal aspect; **E**, right ulnar, KYP4-74, proximal aspect; **F**, left humerus, KYP3-483, *in situ*, caudal aspect: the light coloured surface on the proximal articulation (on the left of the photograph) was exposed and is slightly eroded. The specimen was damaged during transportation. The graphical scales equal 1 cm for **A**, 20 cm for **F**, 10 cm for the rest of the figured specimens.

unfused or incipiently fused vertebral discs, have very similar size, and the two caudal ones (6th and 7th) articulate well to each other, indicating that all probably belong to the same individual. Measurements of the cervical vertebrae are given in Table 3.

There are seventeen thoracic vertebrae in the material (almost complete or bodies only), fifteen of which come from the site KYP1, are very similar in size and ontogenetic stage (usually have unfused vertebral discs, though some cranial discs are incompletely fused) and belong quite probably to the same individual. Following the gradual morphological changes observed in the *Loxodonta* thoracic vertebrae according to their anatomical position (Bezuidenhout and Seegers, 1996), the specimens of the supposed KYP1 skeleton were placed in the following relative order (cranially to caudally): KYP1-487, KYP1-479, KYP1-168, KYP1-549, KYP1-551, KYP1-486, KYP1-489, KYP1-550, KYP1-485, KYP1-488, KYP1-567, KYP1-167, KYP1-553, KYP1-782, KYP1-552. In terms of gross morphology they are grouped in three parts, cranial, middle and caudal, which are described below.

The cranial-part morphology is characterised by wide bodies with strong transverse processes, large articular facets for the costal heads, large bell-shaped vertebral foramina and high spinous processes. The latter is high and weakly caudally inclined in the cranialmost situated specimen (KYP-487; Fig. 7C), then they become much higher, more massive and more inclined (KYP-479; Fig. 7D), and more caudally they gradually get shorter. Four large broken off spinous processes (KYP-375, KYP-376, KYP-379, KYP-381) may also belong to the first thoracic vertebrae of this individual. A distal (dorsal) fragment of a thoracic spinous process that lacks its non-fused epiphysis (KYP-149) is distinctly larger (DAP = 89 mm, DT = 77 mm) and may belong to the third thoracic vertebra, which usually has the most robust spinous process. The cranial and caudal facets for the ribs are in contact in the first vertebrae, then gradually become more distant to each other. The bodies become narrower and higher cranially to caudally; in the same direction the transverse processes are positioned gradually more dorsally.

The middle part of the thoracic series is best represented by KYP-486 (Fig. 7E). The cranial side of the body has a pentagonal articular surface, while the caudal articulation is more triangular. The lateroventral sides of the body are lateroventrally straight and craniocaudally concave, joining to each other along a low sagittally-directed ridge. The transverse processes are very robust, high positioned, and direct laterally. Each bears on the ventral side of its distal end an articular facet for the costal tubercle. Medial to it, on the same side, there are two elliptical and deeply concave articular facets for the costal heads: a cranial one, facing cranioventrolaterally, and a caudal one, facing caudoventrolaterally. The caudal one becomes gradually smaller and facing more caudally in more caudally positioned vertebrae like KYP-488 (Fig. 7F). The spinous process is medium high, of triangular cross section, with a sharp cranial edge and a concave caudal one that forms a sagittally oriented groove. The caudal inclination of the spinous process becomes less pronounced caudally.

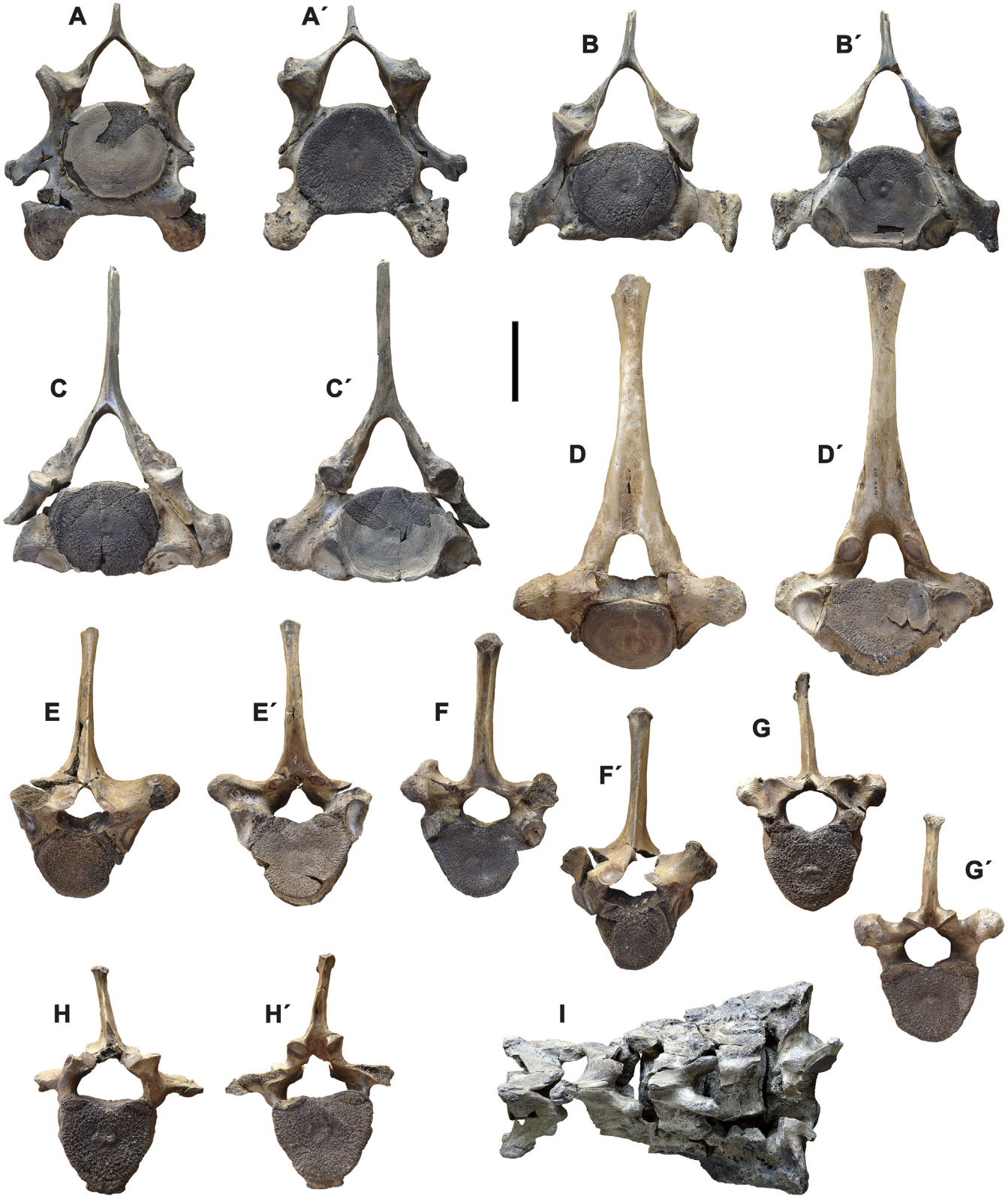

Fig. 7. Axial skeleton of *Palaeoloxodon antiquus* (Falconer and Cautley, 1845) from Kyparíssia, site KYP1: **A**, sixth cervical vertebra, KYP1-464, cranial view; **A′**, caudal view; **B**, seventh cervical vertebra, KYP1-481, cranial view; **B′**, caudal view; **C**, thoracic vertebra, KYP1-487, cranial view; **C′**, caudal view; **D**, thoracic vertebra, KYP1-479, cranial view; **D′**, caudal view; **E**, thoracic vertebra, KYP1-486, cranial view; **E′**, caudal view; **F**, thoracic vertebra, KYP1-488, cranial view; **F′**, caudal view; **G**, thoracic vertebra, KYP1-167, cranial view; **G′**, caudal view; **H**, lumbar vertebra, KYP1-480, cranial view; **H′**, caudal view; **I**, sacrum, KYP1-446, dorsal view. The graphical scale equals 10 cm.

Table 3
Cervical vertebral measurements of *Palaeoloxodon antiquus* from Kyparíssia (in mm).

cervical vertebrae	Atlas KYP-146	third–fifth KYP1-482	Sixth KYP1-464	Seventh KYP1-481
Maximal height	> 230	–	> 330	> 310
Maximal width	> 220	278	(286)	295
Cranial articular width	–	132	131	138
Cranial articular height	(123)	128	126	123
Caudal articular width	–	158	151	157[a]
Caudal articular height	116	138	137	126
DAP of the corpus (measured ventrally, at the middle sagittal plane)	(75)	–	–	–
DAP at the articular processes	–	94	91	86

[a] Excludes the articular surfaces for the first ribs.

The caudal part of the thoracic series is represented by KYP-167 (Fig. 7G). This specimen is characterised by a craniocaudally long, heart-shaped body in cranial or caudal aspect, a single and shallow facet for the articulation of the costal head (there is only one cranial and no caudal facet), and the short and almost vertical spinous process. The latter is much developed in the sagittal direction, but thin, forming sharp cranial and caudal margins. Dorsally it is considerably longer, expanding mainly to the cranial direction. All vertebrae of this part, except for KYP1-485, lack both articular discs of the body and the dorsal end of the spinous process (where preserved), all of which were still unfused. KYP1-485 has a partly fused cranial disc. The ventral side of the body bears a low sagittally-directed ridge. The transverse processes are robust and direct laterocaudally. The articular facets of the vertebral arch are almost horizontal in the craniocaudal direction; the cranial ones face dorsocranially and are separated by a deep notch, while the caudal ones face ventrolaterally. Three isolated spinous processes from KYP1 (KYP1-555, KYP1-556, KYP1-569) quite probably belong to vertebrae of this part of the series.

The best preserved lumbar vertebra is the KYP1-480 (Fig. 7H). It resembles the caudal thoracic vertebrae in general shape, but it lacks any articular facets for the ribs and has less robust spinous process, though of the same general morphology. The body is heart-shaped in cranial view, and rather inversed trapezium-like in caudal view. Its lateral surfaces are craniocaudally concave and converge to a slightly convex ventral side that bears two bilateral tubercles close to its cranial margin. The transverse processes are small. The vertebral foramen is pear shaped. The spinous process is flat, slightly inclined caudally, cranially expanded at its dorsal end, with sharp cranial margin. Its caudal side is sharp only dorsally, while towards its base it becomes wider and concave, forming a sagittal groove. KYP1-480 presents a bilateral asymmetry, as its spinous process bends to the right side. This is already observed, though less pronounced, in KYP1-167 (Fig. 7G), one of the last thoracic vertebrae.

The sacrum (KYP1-446; Fig. 7I) is a bone of triangular general shape in all aspects, dorsal, ventral and lateral, being wider and higher cranially. It is formed by the fusion of the five sacral vertebrae at the transverse processes. The arcs seem to be unfused to each other and the same is true for the spinous processes of the last three vertebrae (the processes of the first two are not preserved). The comparatively thin epiphyses (vertebral discs) of the individual vertebrae are also still unfused, or partly fused, to the corresponding bodies, and unfused to each other. All sacral vertebrae have triangular vertebral foramens that get smaller caudally, in accordance to the sacrum's general shape.

A large number of elephant rib parts was collected from KYP1 site, as well as surface finds. Most are very fragmentary to be mentioned here, but a couple of more or less complete specimens were prepared from available fragments. These include the very flat, sagittally expanded KYP-756, with sharp cranial and caudal body margins, unfused paired articular facets on the head, a neck that meets the body in almost right angle, and a robust tubercle. It belongs to the cranial part of the costal series, being quite probably the second one. More caudally positioned ribs possess a neck that follows the curve of the body (it does not form an angle with it), two articular facets on the head, and bodies that are much thicker mediolaterally with a shallow groove on their cranial side (they remain, though flattened distally). The most complete specimen, KYP-769, is 116 cm long, following its lateral side. The caudalmost studied specimen, KYP-758, has one articular facet, flatter body, and smaller dimensions.

4.3.1.2. Thoracic limb. A complete left humerus KYP-483 was excavated in site KYP3 (Fig. 6F). The specimen was laying horizontally, in N–S direction, parallel to the shore of the Megalopolis palaeolake, under a very thin layer of sediment of an artificially levelled surface. It is quite likely that the specimen has suffered heavy loads because of the quarry traffic, which may also have caused a small damage observed on the uncovered caudal margin of the proximal articulation and the distal end. Its proximal end is massive, and it is dominated by the large convex articular surface of the humeral head and the laterally positioned, craniocaudally directed greater tubercle. The lesser tubercle is low and flat, situated medially to the humeral head and directed sagittally. The diaphysis has a slightly concave medial margin. Its lateral margin is straight till the deltoid tuberosity, then becomes markedly concave forming the lateral supracondylar ridge. The distal articular trochlea is shallow. Proximal to it, on the caudal side, there is a small olecranon fossa, bordered laterally and mesially by the corresponding epicondyles, the lateral of which is more developed. The cranial side accommodates a wide but shallow radial fossa proximally to the trochlea. The specimen's dimensions are given in Table 4.

The radius in known from a proximal part (KYP-675), preserving the elongate subtriangular articular facet for the humerus. This is concave

Table 4
Selected postcranial element measurements of *Palaeoloxodon antiquus* from Kyparíssia (in mm).

humerus	L	DAPp	DTp	DTm	DAPd	DTd	DTda
KYP-483	940	> 202	251	121	–	275	213

ulnar	H	DAP	DT	DAPpa	DTpa	DAPda	DTda
KYP-74	100	160	197	123	149	124	175

carpal IV	H	DAP	DT	DAPpa	DTpa	DAPda	DTda
KYP-643	126	171	141	121	144	121	139

metacarpal III	L	DAPp	DTp	DAPpa	DTpa	DAPm	DTm	DAPd	DTd	DAPda	DTda
KYP-642	225	> 120	106	(117)	(102)	61	89	100	111	100	87

laterally and saddle shaped medially. Caudally it contacts the elongate and shallow articular facet for the ulna. The small preserved part of the diaphysis is triangular in cross section, as the proximal end of the bone, the apex of the triangle facing laterally.

The ulnar (a.k.a. triquetrum or pyramidal; Fig. 6E) is preserved in pristine condition. In proximal or distal aspect is triangular in shape, with a marked lateropalmar process. The proximal side bears a large subtriangular articular facet for the ulna with almost equally-long, wavy (sigmoid) margins. Its mediolateral profile is convex, while the dorsopalmar one is slightly sigmoid (convex dorsally, concave palmarly). The distal side is almost totally occupied by the facet for the articulation of the fourth carpal (unciform). This is almost square in shape, with a large lateropalmar tongue-like extension. Its profile is, again, slightly sigmoid in dorsopalmar direction, and slightly concave in mediolateral direction. The palmar face accommodates an almost elliptical articular facet for the accessorium (pisiform) with straight proximal margin. On the medial face there is a small elliptical facet for the intermedium, situated in the dorsodistal part of the face. Another tiny facet for the intermedium is located proximally, being essentially a continuation of the ulna facet that curves distally. The specimen's dimensions are given in Table 4.

The carpal IV (a.k.a. unciform or hamatum; Fig. 6D) is a massive bone of trapezoid shape. It is the lateralmost element of the distal row of the carpus. Its proximal face is almost totally occupied by the saddle-shaped articular surface for the ulnar. The distal face is also articular, consisting of three facets for the articulation of the metacarpals III, IV and V. The first is flat and elongated in the dorsopalmar direction, the second is slightly concave and triangular, being much wider dorsally, and the third is crescent-shaped and slightly convex. All form obtuse angles between them, but the separating ridges are blunt. In medial view two facets for the articulation with the carpal III (magnum) are observed: a proximally situated flask-shaped one, and a distal one with the shape of a low disc segment. They are confluent at their middle. The distally situated facet for the metacarpal II is also visible in medial aspect. The dorsal and palmar faces have rough surfaces, perforated by vascular foramina. The latter forms a large tuberosity in its distal part. The specimen's dimensions are given in Table 4.

The metacarpal III (Fig. 6C) is a large, robust bone, and it is preserved in good condition. Its proximal end is triangular bearing four articular facets, two for the adjacent metacarpals II and IV on the medial and lateral sides respectively, and two on the proximal face for carpals III and IV. The metacarpal facets are vertical, elongate in the dorsopalmar direction, and rather deeper dorsally. The carpal III facet is triangular (wide dorsally), somewhat convex in the dorsopalmar direction, and inclined slightly medially. It is separated from the laterally-inclined dorsopalmarly elongate carpal IV facet by a rather blunt ridge. The diaphysis has a cross section of a blunt triangle. Its dorsal surface is slightly concave in proximodistal direction. The distal end is widest at the suprarticular tubercles, at the sides of the bone. The distal articulation for the proximal phalanx III is strongly convex dorsopalmarly but straight mediolaterally. Its palmar part is divided in two faintly concave surfaces by a low sagittal ridge. The specimen's dimensions are given in Table 4.

The middle phalanx KYP-169 is a very short and wide. It is almost symmetrical bilaterally, thus it is attributed to the digit III. Its comparatively much wider proximal end with regard to the distal one indicates that it belongs to the pelvic limb (compare Smuts and Bezuidenhout, 1993, fig. 26; 1994, fig. 18). The proximal end accommodates an elliptical in proximal view, saddle-shaped articular surface. The dorsal end is shaped like a trochlea; it doesn't form a true articular surface, however, as the middle an the distal phalanges do not articulate to each other.

The recovered parts of pelvises are very fragmentary to reconstruct their morphology. KYP-686 preserves an almost complete acetabulum which has a maximal diameter of 183 mm.

4.3.1.3. Pelvic limb. The available specimens are very few and in fragmentary condition, so that their morphology cannot be described.

4.3.2. Discussion

The proboscidean remains of the Megalopolis basin are mainly known from the publications of Melentis (1961, 1963, 1965), who assigned the finds to no less than four species (*Mammuthus meridionalis*, *Palaeoloxodon antiquus*, *Palaeoloxodon melitensis* and *Mammuthus primigenius*), also further split to the subspecies level. More recent studies have attributed most of the observed morphological features within the available sample to intraspecific variation of *Palaeoloxodon antiquus* (e.g., Sondaar and Boekschoten, 1967, pp. 562–563). Indeed, all the dental material studied by Melentis, except for the specimens referred to the woolly mammoth, are characterised by high and narrow crowns and strongly plicate enamel, all typical characters of *P. antiquus*. The postcranial material studied by the same author (Melentis, 1963) is not diagnostic, but is fully consistent with an attribution to *P. antiquus*. Furthermore, geochemical and archival data (Lyras, 2007; Iliopoulos et al., 2010), have shown that the *Mammuthus primigenius* specimens published as coming from old excavations in the Megalopolis Basin, come in fact from the Ukrainian locality of Telichka. Consequently only one species, *P. antiquus*, is recognised in the published sample from Megalopolis basin.

The material studied here corroborates this view, as the examined dental specimens show clear characters of this species: obtuse Schreger angles in the tusks, and narrow hypsodont molars with moderate lamellar frequency and plicate enamel (Maglio, 1973; Palombo and Villa, 2001). *Mammuthus trogontherii*, which coexisted in Europe with *P. antiquus* during the Middle Pleistocene and was present in Peloponnesus during this epoch (Athanassiou, 2012), had also hypsodont molars with moderate lamellar frequency and plicate enamel, but its molar crowns are wider (Maglio, 1973) and, more importantly, its tusks exhibit acute Schreger angles (Palombo and Villa, 2001). *Palaeoloxodon antiquus* is the only European elephant exhibiting an obtuse Schreger angle, and this feature permits the attribution of the tusk fragments from Kyparíssia to this species. Although the distinction among elephantid taxa can be difficult based on molars (let alone postcranial elements), the currently available data do not support the presence of any other proboscidean in the Megalopolis Basin except for *P. antiquus*.

4.4. Perissodactyls

4.4.1. Rhinoceros

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

Material: KYP-531: right radial carpal (scaphoid); KYP-341: right third metacarpal; KYP-358: left astragalus. All are isolated surface finds.

Description: The radial carpal (scaphoid; Fig. 8A) is a massive bone. It almost completely preserved, lacking only a small proximo-lateral part. Its vaguely trapezoid shape, in cranio-medial view, is characterised by a large strongly concave proximal articular surface for the radius, as well as two smaller concave distal articular surfaces for the second (trapezoid) and the third carpal (magnum). In the same aspect, the cranial margin is almost straight, showing a slight inflation distally, while the caudal margin is markedly convex. In caudo-lateral aspect, there is a flat, sagittally directed, semi-elliptical proximal articular surface for the intermedium (lunatum). In distal view, the distal articulation is elongated in craniolateral–caudomedial direction. Measurements in mm, taken according to Guérin (1980, p. 90): H = 64.0, DAP = 71.2, DAPpa = 45.5, DAPda = 61.6, DT > 46. This specimen is metrically comparable to *Stephanorhinus hemitoechus* and *S. etruscus brachycephalus* (sensu Guérin, 1980) (currently usually synonymised with *S. hundsheimensis*) and is generally smaller than *S. kirchbergensis* (= *S. mercki*) (Guérin, 1980, p. 679).

Fig. 8. Dental and osteological specimens from Kyparíssia referred to Perissodactyla: *Stephanorhinus* sp.: **A**, right radial carpal (scaphoid), KYP-531, cranial aspect; **B**, left astragalus, KYP-358, cranial aspect. *Equus* sp.: **C**, right upper third molar (M3), KYP-640, occlusal aspect; **D**, right lower molar (m2?), KYP-546, occlusal aspect. The graphical scale equals 5 cm for **A** and **B**, 2 cm for **C** and **D**.

The metacarpal III is preserved in its proximal part. It appears to be extremely narrow, as the transverse diameter of the proximal end is smaller than any Middle Pleistocene rhinocerotid sample (Guérin, 1980, p. 704); its craniocaudal diameter (DAPp) falls, though, within the lower range of *Stephanorhinus hemitoechus* and *S. etruscus brachycephalus* (sensu Guérin, 1980). Probably it belongs to a juvenile or subadult individual. Dimensions: DAPp = 45.2, DTp = 42.0, DTpa = 40.0.

The astragalus (Fig. 8B) is incompletely preserved distally and laterally, because of breakage, rolling wear and quite possibly carnivore gnawing. The trochlea is large and wide, and dominates in cranial view. Its lateral part is more robust than the medial one, but has a blunter keel. The caudal face preserves two articular facets for the calcaneus, which are separated by a deep groove. The larger lateral one is deeply concave, but not angular. The other is elliptical and is situated more medially, but close to the centre of the bone. Dimensions: H > 67, DT > 70.

The scanty available rhinocerotid material does not allow any inference on its specific identity. Metrically it better fits, nevertheless, to a small-sized species like *S. hemitoechus* (Falconer, 1868). The presence of this species has been already mentioned in Megalopolis, together with "*S. merkii*" [a synonym of *S. kirchbergensis* (Jäger, 1839)] and *Coelodonta antiquitatis* (Blumenbach, 1799) (Melentis, 1966b). The latter is based on a skull, which in fact comes from the Ukrainian locality of Telichka (Lyras, 2007; Iliopoulos et al., 2010), while the rest of the already published rhinocerotid material is rather inadequate for a specific determination and fits biometrically better to the ranges of *S. hemitoechus* given by Guérin (1980).

4.4.2. Horse

Family: Equidae Gray, 1821

Genus: *Equus* Linnaeus, 1758

Equus sp.

Material: KYP-640: right upper third molar (M3); KYP-546: right lower molar (possibly m2); KYP1-706: left intermedium (lunatum); KYP-678: left astragalus fragment.

Description: The upper third molar (Fig. 8C) is not much worn. Its main characters include a rather simple enamel plication, very long protocone with straight lingual margin, and simple and narrow labial styles (the parastyle being the strongest). The lower molar (Fig. 8D) is tentatively identified as m2 because its distal root is bent caudally. It is rather small, with simple enamel plication, U-shaped linguaflexid, and very deep ectoflexid that penetrates the isthmus of the double knot. The metaconid and the metastylid are rather rounded. Dimensions in mm: M3: H = 84.5, DAP = 27.3, DT = 23.0, DAPpr = 15.7; m2: H = 43, DAP = 25.0, DT = 13.3 (cement excluded).

The intermedium is broken caudally and craniomedially. Dimensions in mm: DT > 31.5, H = 32.3. The astragalus fragment preserves part of the distal articulation and most of its caudal face. No measurements can be taken.

This scanty equid material seems to belong to a medium-sized population, but it is inadequate for an attribution to a species. The shape of the protocone and the linguaflexid merely point to a caballoid horse. A small number of *Equus* remains are already known from the Megalopolis Basin (Melentis, 1966f; Sickenberg, 1976), but they cannot be compared to the new ones, due to the lack of common elements among the samples.

4.5. Deer

The cervid family is abundantly represented at Kyraríssia, though the available material is generally fragmentary. Five antler types and four skeletal element size classes are recognised, which according to their morphology and dimensions are referred to five distinct species.

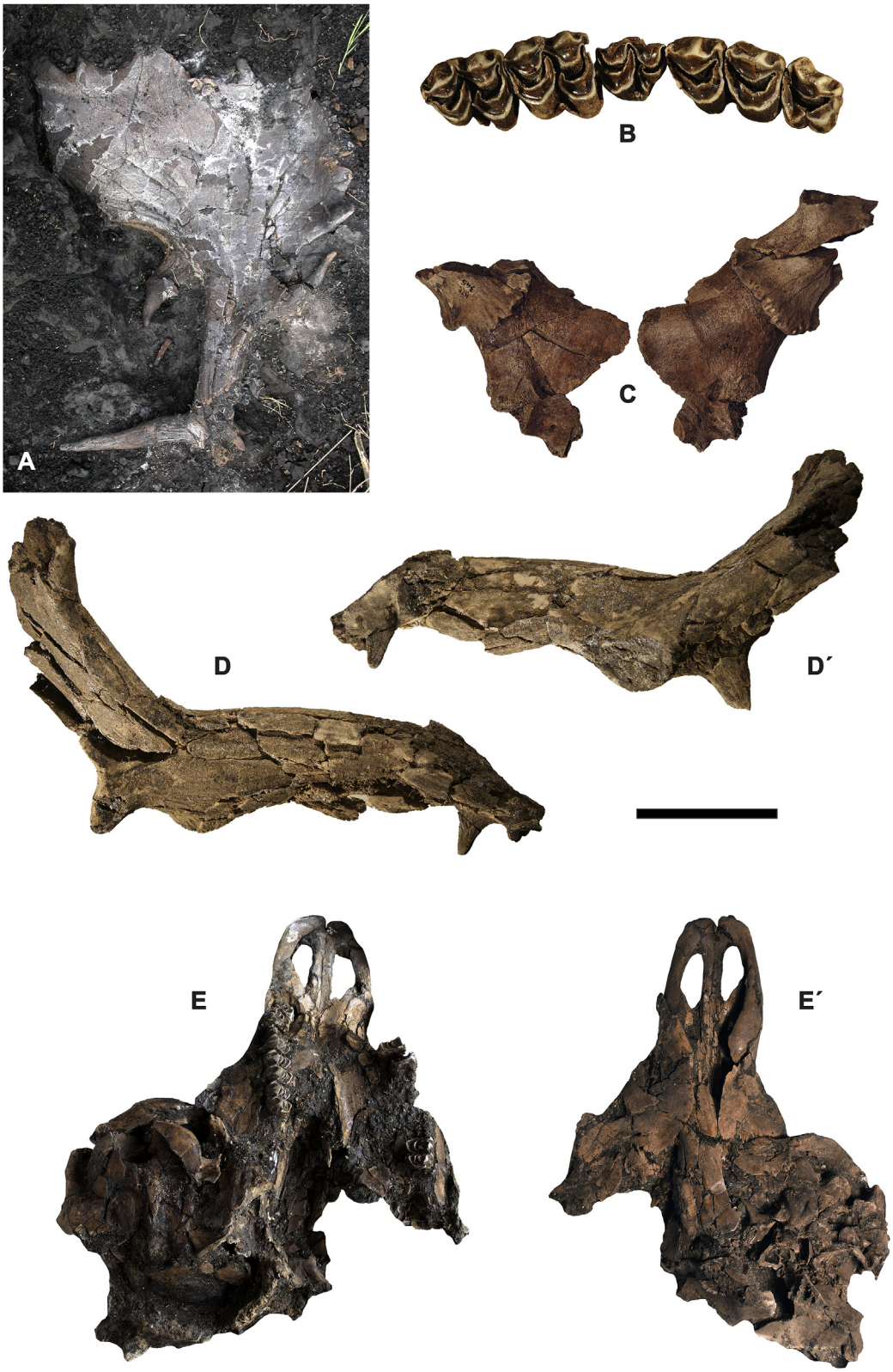

Fig. 9. Cervid specimens from Kyparíssia. *Praemegaceros verticornis* (Dawkins, 1872): **A**, distal antler part belonging to the skull KYP2-345, *in situ*; **B**, right upper dentition of the skull KYP2-345, occlusal aspect; **C**, fragmented frontal with antler pedicels and burrs of the skull KYP2-345, dorsal aspect; **D**, left proximal beam part, KYP4-150, caudal aspect; **D′**, rostral aspect; **E**, skull, KYP4-633, ventral aspect; **E′**, dorsal aspect. Note the twisted braincase. The graphical scale equals 20 cm for **A**, 5 cm for **B**, 10 cm for **C** and **D**, and 15 cm for **E**.

Most common are the middle to large-sized forms, and least common the two small-sized ones. Previous publications on the fauna of the Megalopolis have documented the presence of three or four cervid species in the basin (Melentis, 1966a; Sickenberg, 1976). The recent excavation at Marathousa 1 has only yielded *Cervus* and *Dama* finds (Konidaris et al., this issue).

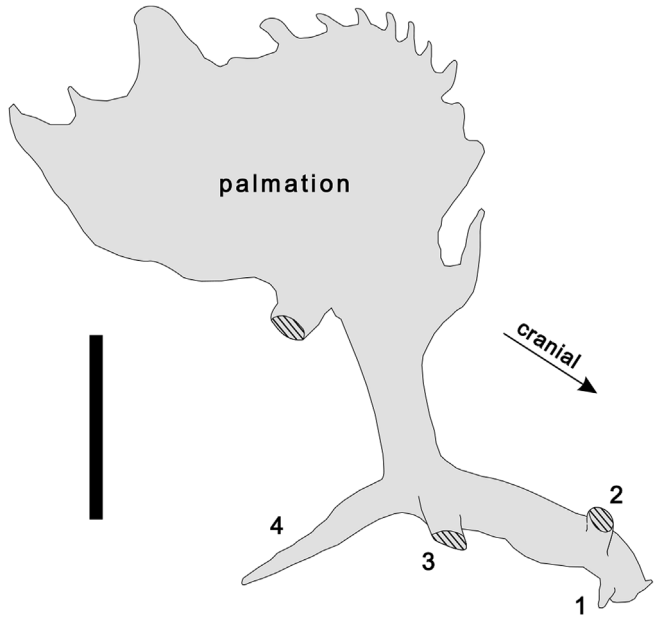

Fig. 10. Tentative reconstruction of an antler of *Praemegaceros verticornis* from Kyparíssia in craniolateral aspect. The numbers refer to the individual tines (1st, 2nd, etc.). The arrow points to the cranial direction. The drawing is mainly based on a combination of the specimens KYP2-345 and KYP4-150. The graphical scale equals 20 cm.

4.5.1. Giant deer

Order: Artiodactyla Owen, 1848

Family: Cervidae Gray, 1821

Genus: *Praemegaceros* Portis, 1920

Praemegaceros verticornis (Dawkins, 1872)

Material: KYP2-345: fragmentary skull and antler part, and associated atlas; KYP4-633: skull; KYP-527, KYP-542, KYP-543, KYP3-28, KYP3-451, KYP4-150, KYP4-151, KYP4-634, KYP4-635: antler fragment; KYP4-653: upper premolar; KYP4-331: left scapula; KYP-524: radius; KYP3-70: proximal radius part; KYP3-453: left calcaneus; KYP4-301: right metatarsal; KYP4-302: left metatarsal.

4.5.1.1. Description. Skull: There are two cranial specimens referred to this species. The first (KYP2-345), collected at KYP2 in 2004, was found badly crashed under a very thin layer of lignite, in a place formerly frequented by heavy machinery. One partial antler (Fig. 9A), several cranial fragments including both antler pedicels (Fig. 9C), and most of the teeth (the complete right series, figured in Fig. 9B, P2, P3 and M1 of the left side, as well as two incisors and the right m3 of the lower series) were recovered. Unfortunately, it was impossible to reconstruct the cranial morphology based on the available fragments. Both pedicels bear the burrs, the left of which is measurable (diameter: 83 mm. A rather small tine, judging from its preserved base (diameter: 22 mm), emerges 72 mm above the burr. The preserved antler part is the distal one and includes the palmate section and the distal part of the beam bearing the posterior tine (Fig. 9A). The latter is 21 cm long, sigmoid in shape, and has a laterally compressed elliptical cross section (diameters at the base 39 × 28 mm). The distal (vertical) beam is about 25 cm long from the posterior tine to the palmation, and it is also laterally compressed. The palmation is flat, without any markedly concave or convex areas, and it is almost sagittally directed. Its caudal part is much more expanded. Its sagittal diameter is 50 cm and its height 30 cm. Its rostral and dorsal margins are decorated by several prongs. At the palmation base there are two tines, on rostral and caudal margins of the antler respectively, which are stronger and longer than the palmation prongs, and remain separated from the palmate part of the antler.

The second cranial specimen (KYP4-633; Fig. 9E) was excavated at the site KYP4. It is also very badly preserved, as it is severely fragmented. Moreover, the praeorbital part of the skull is broken off, turned dorsally and found in contact to the postorbital part. The ventral side of the former was found facing up. This taphonomic arrangement is possibly indicative of trampling during deposition (see also Section 3). The specimen preserves parts of both pedicles. A left proximal beam part (KYP4-150; Fig. 9D) was found 60 cm east of the skull and probably belongs to the same individual. The same is possibly true for two palmate antler fragments (KYP4-151) located 80 cm west of the skull; however, it is impossible to restore them in their life position and corroborate this assumption. The preserved beam part is 40 cm long and includes the weakly-developed burr, the first tine, and the bases of the second, third and fourth tines. In rostral aspect it is sigmoid: The beam emerges in dorsolateral direction, turns almost horizontal, extending laterally at the level of the second tine, and then bents dorsally at the level of the third and fourth tines. The 'horizontal' part is dorsoventrally flattened (cross section diameter approximately 75 × 45 mm, perimeter 24 cm). The distal, almost sagittally-oriented part, of which only a basal portion is preserved, begins 30 cm distally to the burr, and forms an angle of about 45° with the 'horizontal' one. It is markedly flattened, but there is no clear evidence of a palmation, as it is inadequately preserved. The two palmate antler fragments found nearby might, though, constitute such an indication, if they truly belong to the same individual. The first tine is small (4 cm long), rostroventrally directed, conical but somewhat flattened rostrocaudally, and situated very close to the burr (3 cm laterally to it). The second tine ('brow tine') is located very close to the first one (4 cm dorsolaterally to it), is much larger judging from its base, has an elliptical basal cross section (43 × 33 mm), and initially directs dorsorostrally. The third tine ('middle tine') originates 25 cm distally to the burr, is directed rostroventrally, and is the strongest. Its cross section is elliptical, measuring 60 (mediolateral) × 44 (dorsoventral) mm at its base. The forth tine ('posterior tine') emerges next (distally) to the third one, is directed caudoventrally and has a circular cross section with a diameter of 28 mm.

Another large-sized antler fragment from K4, KYP4-635, was identified as the part bearing the third tine of a right antler. The specimen preserves a 16-cm-long part of the beam and a 95-mm-long part of the third tine. It is estimated that the latter would be at least 16 cm long, expanding in a rostromedial direction. Its cross section is elliptical (67 × 40 mm at its base, 32 × 23 mm at its preserved end). The beam's cross section is triangular, with a flat or slightly concave caudal surface (beam diameters about 65 mm). A lateral widening may correspond to the origin of the fourth tine. Combining the morphological characters of the partly preserved *Praemegaceros* antlers from Kyparíssia, a provisional reconstruction of an almost complete antler was drawn (Fig. 10), in order to present its tentative life appearance.

The cranial morphology is not well recognisable because of the fragmentary preservation and distortion of KYP4-633. The pedicles are divergent, inclined laterally and slightly caudally, their axes forming almost a right angle between them. The frontal morphology is not observable, as it is badly crashed. The nasals are long, expanding caudally at least to the imaginary line connecting the rostral margins of the orbits. The premaxillaries are laterally convex, taper rostrally, and their rostral border is rather rounded (Fig. 9E). The snout is moderately long, the distance prosthion–P2 being about equal to the dental row length. The occipital is semicircular in caudal view and exhibits a moderately prominent nuchal crest. The occipital condyles are strong and border a wide foramen magnum. Measurements are given in Table 5.

Dentition: Only the upper dentition is known, mainly from the two cranial specimens, as well as the right m3 of KYP2-345. An isolated cervid premolar is also referred to this species, judging from its large size. The wear stage of the KYP2-345 dentition is moderate (Fig. 9B), indicating a middle-aged individual, while that of KYP4-633 is somewhat more advanced (Fig. 9E). Both toothrows exhibit the typical cervid morphology of wide teeth with prominent labial styles, partly

Table 5
Cranial measurements of *Praemegaceros verticornis* from Kyparíssia (in mm). Due to the fragmentary state of the specimens, all given values are rather inaccurate.

	KYP2-345	KYP4-633
Prosthion – P2	–	120
Inter-pedicel line – inion	–	98
Muzzle width	–	99
Width at M1 level	–	124
Width at pedicels	–	206
Parietal minimal width	–	145
Temporal width (at the mastoid processes)	–	187
Occipital width (at the paroccipital processes)	–	155
Occipital height	–	114
P2–P4 length	61.5	55
M1–M2 length	88	80.5
P2–M2 length	147	135

separated labial and lingual crescents, and rugose enamel surface. The premolar series is rather long with respect to the molar one, the premolar length making up the 41–42% of the whole dentition length and the 71–73% of the molar length. A particular character of the dentition is the structure of the P2, the lingual crescent of which consists of two completely separated cusps, the protocone and the hypocone. A similar tendency is observed in P3, were the two cusps remain partially separated forming a bilobe lingual crescent with a marked vertical groove in the lingual wall of the tooth. In P3 the protocone and the hypocone are not distinct from each other. The molars exhibit protoconal and hypoconal folds, which are diminished or completely absent in the much worn specimens. Weak cinguli, in the form of a flattened entostyle, are present in each molar. The toothrow dimensions are given in Table 5. The m3 has weak lingual stylids in the mesial lobe, but only rudimentary ones more distally. All cuspids and the talonid are rather rounded, not angular, lingually and labially. There are weak protostylid and ectostylid.

Postcranial skeleton: Several postcranial elements, most notably two complete metatarsals, are referred to *Praemegaceros*. All have typical cervid morphology, as described e.g., in Heintz (1970), and are referred to this taxon because of their very large size (e.g., largest specimen in Fig. 11D). Dimensions are given in the supplementary material.

4.5.1.2. Discussion. This sample represents a deer species of very large size, characterised by laterally expanded antlers with well-developed distal palmation. This morphology points to the giant deer species formerly grouped under the generic name *Megaloceros* Brookes, 1828, the nominal species of which, *M. giganteus* (Blumenbach, 1799), is famous for its extremely large palmate antlers. The current taxonomic practice usually confines this genus to its type species, and groups the less advanced similar forms of Early and Middle Pleistocene age to the genus *Praemegaceros* Portis, 1920 (Abbazzi, 2004; Croitor, 2006, 2014; Vislobokova, 2012, 2013). This taxonomic scheme, based on several cranial characters, is also followed here. *Praemegaceros* includes several continental large-sized forms of specific or subspecific status (according to authors), all of which show close similarities with the most common species referred to the genus, *P. verticornis*. The relative development and the orientation of the beam and the tines, as well as the development of palmation among the distal tines have been used, and debated on their validity, as characters of specific or subspecific taxonomic value. In addition to *P. verticornis*, the continental species commonly included in this genus are *P. obscurus* (Azzaroli, 1953), *P. solilhacus* (Robert, 1830) and *P. dawkinsi* (Newton, 1892) (Croitor, 2006, 2014; Vislobokova, 2012, 2013, 2018), though they have also been considered as variants of *P. verticornis* (e.g., Pfeiffer, 2002, p. 293).

The studied material differs from *Megaloceros* in its comparatively much smaller antler, the high position of the palmation and somewhat smaller dental and bone dimensions. The absence of cingulum in the upper dentition of KYP2-345 and KYP4-633 is another potentially differentiating feature, as its presence has been considered a character of *Megaloceros* (e.g., Vislobokova, 2013, p. 879; but other authors, e.g., Croitor, 2018, regard it as a variable non-diagnostic character). However, the skull KYP4-633 resembles *Megaloceros* in its fairly rounded rostral end of its praemaxillae in dorsal or ventral view. It is unknown, though, if the square-ended praemaxillae is a truly consistent character of *Praemegaceros*, as it is observable only in a few specimens (Abbazzi, 2004). The tendency of *Megaloceros* to have concave frontals between the antler pedicles (Azzaroli, 1953; Abbazzi, 2004) cannot be observed in the studied material due to its fragmentary preservation. Nevertheless, the Kyparíssia giant-deer antler form and skeletal element size are sufficient to distinguish it from *Megaloceros*.

Leaving aside the genotypical species *P. dawkinsi*, which is small in body size, derived in several characters, and endemic of Great Britain, other species than *P. verticornis* that belong to this genus differ from the studied material. *P. obscurus* and the not universally accepted *P. pliotarantoides* (De Alessandri, 1903) are characterised by antlers that do not form a distal palmation (Croitor, 2014, 2018). The former also has extremely developed first and second tines, while the latter lacks the third tine, unlike KYP4-150. *P. solilhacus* is characterised by absence of the first tine, frequently also of the second one, and the formation of a very high and pointed palmation with numerous small prongs along its caudal margin (Vislobokova, 2013; Croitor, 2014, 2018; Breda et al., 2015). In the recently described, nicely preserved, complete shed antler from Isernia la Pineta, Italy, the distal palmation starts just above the posterior tine, is more than 1 m high, and lance shaped (Breda et al., 2015), quite unlike the much shorter, forming in high position above the posterior tine, and more circular-shaped palmation of the Kyparíssia specimen KYP2-345.

The divergent, sigmoid in rostral view beam with a dorsally bent distal part, the distal palmation of elliptical shape, and the very small first tine observed in the studied specimens (mainly KYP2-345 and KYP4-150) point to the species *P. verticornis* (Vislobokova, 2012, p. 690; 2013, p. 913; Croitor, 2014, 2018). Typically this species has, though, rudimentary or even absent first tine and more cylindrical, not rather flattened beam as in the studied sample. We attribute these differences to individual variation, which is rather high in *Praemegaceros* (see e.g., Abbazzi, 2004; Croitor, 2006), though it is yet unclear if this variation is population-depended in some extent. The species is already known in the Megalopolis Basin mainly from a frontlet bearing the proximal part of the left antler (Sickenberg, 1976, pl. 8, fig. 1), a specimen which is morphologically closer to the typical *P. verticornis*.

4.5.2. Red deer

Genus: *Cervus* Linnaeus, 1758

Cervus elaphus Linnaeus, 1758

Material: KYP-492, KYP-494, KYP-497, KYP-500, KYP-751, KYP1-702, KYP1-707, KYP3-28: antler part; KYP1-668, KYP1-733, KYP3-61, KYP3-449, KYP4-645, KYP-696: humerus part; KYP1-703: radius; KYP1-736: ulna; KYP-357, KYP-434: metacarpal III-IV; KYP1-734, KYP1-740, KYP-157: femur part; KYP1-671: tibia part; KYP-323, KYP-646, KYP3-105: astragalus; KYP1-692, KYP3-654, KYP4-605: calcaneus; KYP1-676: centrotarsal; KYP4-603, KYP-417, KYP-435, KYP-647, KYP3-21, KYP3-123: proximal phalanx; KYP-436: medial phalanx; KYP-754: distal phalanx.

4.5.2.1. Description. Antlers: There is an unusual high number of red-deer antlers with regard to the rest of the material attributable to this species. Both shed and unshed specimens are available, all fragmentary, preserving only the proximal part (Fig. 11A–C). All present an initially straight beam that higher becomes convex in caudal direction, and two basal tines (first or brow tine and second or bez tine, mostly preserved only at their bases) situated almost in contact to each other close to the burr (about 3 cm above it). The second tine is placed somewhat external to the first one. It is completely preserved in one specimen (KYP-492)

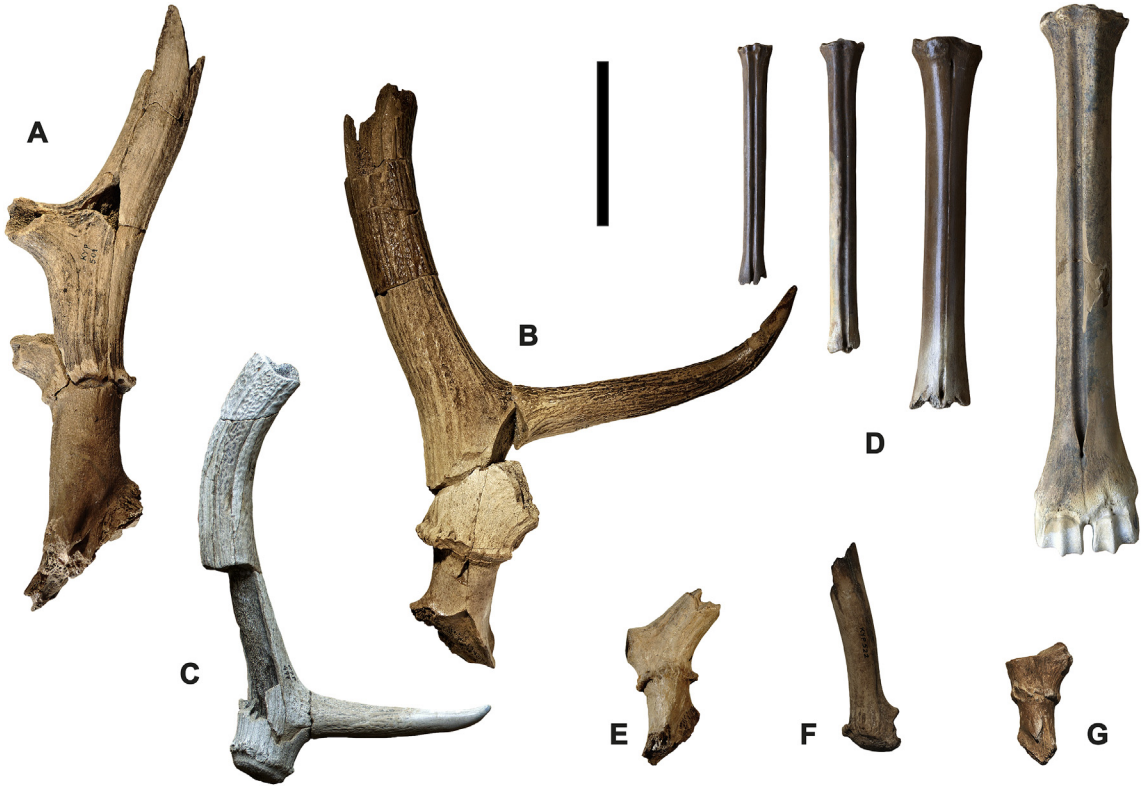

Fig. 11. Cervid specimens from Kyparíssia. *Cervus elaphus* Linnaeus, 1758: **A**, left antler with pedicel, KYP-500, lateral aspect; **B**, left antler with pedicel, KYP-492, medial aspect; **C**, right shed antler, KYP-497, lateral aspect. **D**, metapodial size variety; from left to right: *Capreolus*- and *Dama*-sized metatarsals III-IV, *Cervus elaphus* metacarpal III-IV, *Praemegaceros verticornis* metatarsal III-IV. **E**, *Dama* sp., left proximal antler part with pedicel, KYP-493, lateral aspect; **F**, Cervidae indet., right proximal shed antler part, KYP-522, lateral aspect; **G**, '*Cervus' peloponnesiacus* Sickenberg, 1976 right proximal antler part with pedicel, KYP-705, lateral aspect. The graphical scale equals 10 cm.

Table 6
Antler measurements (in mm) of Cervidae, excluding *Praemegaceros*, from Kyparíssia. '1st' and '2nd' refer to the first (brow) and second (bez) tine respectively. The pedicel circumference was measured just below the burr. The beam circumference was measured above the second tine. The tine length was measured along their convex side.

		pedicel H	pedicel Dmax	pedicel Cf	Burr Dmax	burr Cf	beam Cf	1st L	1st Cf	2nd L	2nd Cf
Cervus elaphus	KYP-494	53.0	39.0	124.0	55.0	155.0					
	KYP-500	53.0	39.0	124.0	57.0	(155)	114.0				101.0
	KYP-492	37.0	38.0	124.0		(195)	132.0			225.0	110.0
	KYP-751						135.0				
	KYP1-702				67.0	202.0	147.0				
	KYP3-28				(61)	180.0	140.0		(120)		(130)
	KYP-497				44.0	131.0	111.0	125.0	87.0		
Dama	KYP-329	24.5	30.5	98.0	43.0	133.0	95.0		75.0		
	KYP-354				41.0	122.0			65.0		
	KYP-499	16.0	36.5	119.0	(41)	(125)					
	KYP-493	21.5	33.0	106.0	45.0	(130)	98.0		82.0		
	KYP1-719	26.0	33.5	114.0	56.0						
'Cervus' peloponnesiacus	KYP1-705	19.0	22.0	73.0	(32)	(105)					
Cervidae indet.	KYP-522				(37)	(101)	69.0				

and it is rather long (Fig. 11B). However, it cannot be compared to the first tine, because the latter is not preserved beyond its base in any available specimen. The beam and the tines have an almost rounded cross section and form a slightly obtuse angle between them (Fig. 11A–C). The pedicles, where preserved, are rather high. The studied specimens exhibit considerable metrical variation (Table 6), but this is normal in any given cervid population, as the antlers are shed each year and grow again stronger each spring, changing through ontogeny: e.g., KYP-500 (Fig. 11A), as well as KYP-494 that quite possibly belongs to the same individual, have higher pedicels and more slender beam and tines than KYP-492 (Fig. 11B), which belongs to an older individual. KYP-497 (Fig. 11C) is a peculiar case, because it has only one basal tine (identified as the first or brow tine), not two as the previously described specimens. Otherwise the beam and basal tine configuration is very similar to the other antler specimens referred to *Cervus elaphus*. KYP-497 is attributed here to a young individual that hadn't yet developed a second tine. This is common in recent and fossil samples of this species, where the second tine emerges in a later ontogenetic stage, after the first and the third tines, or may be totally absent (Lister, 1987, p. 91; Pfeiffer, 1999, p. 34; Croitor, 2018, p. 98). The very large and strong KYP1-702 may also have lacked a second tine, unless the two basal tines were virtually merged at their bases.

Postcranial skeleton: Several postcranial elements having the typical cervid morphology, as described e.g., in Heintz (1970), are referred to

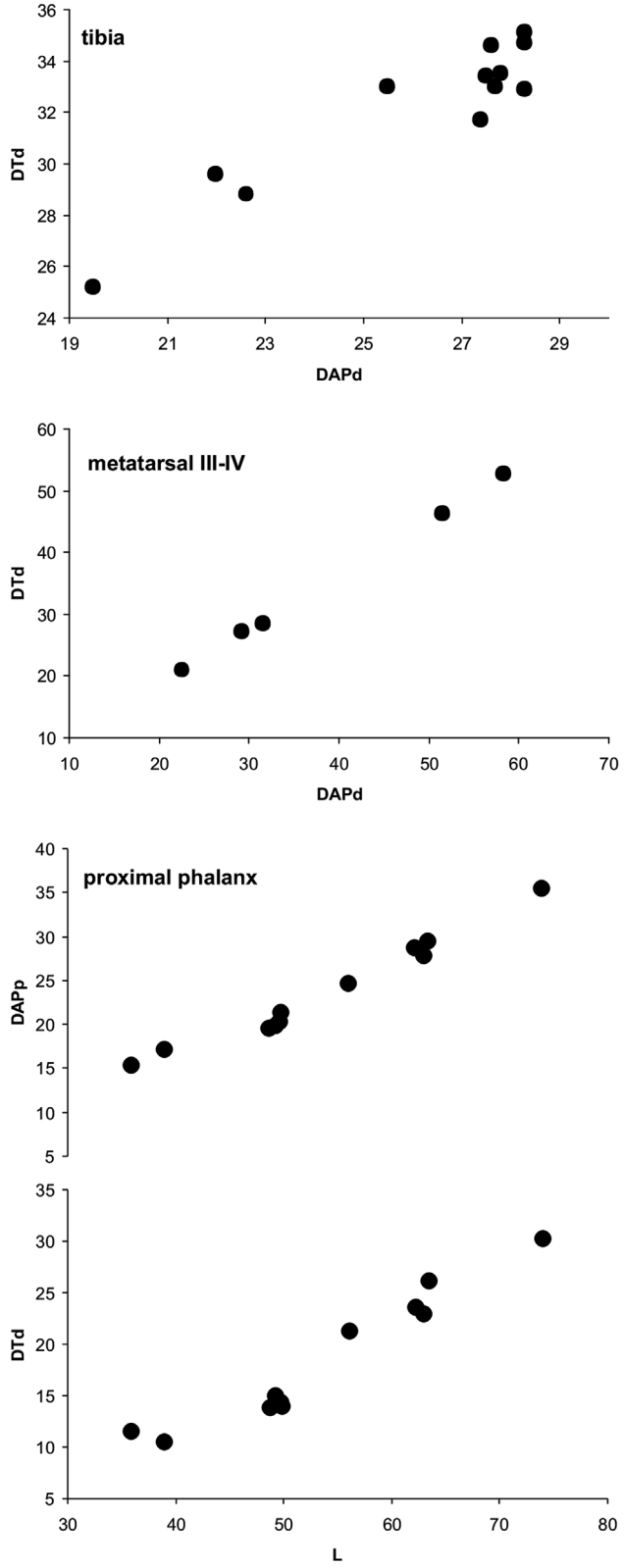

Fig. 12. Size distribution of cervid postcranial material (tibia, metatarsal III-IV and proximal phalanx) from Kyparíssia. Three to four size groups are identifiable depending on the skeletal element, which are attributable to small deer (*'Cervus' peloponnesiacus* and Cervidae indet.), *Dama* sp., *Cervus elaphus* and *Praemegaceros vericornis*. All dimensions are in mm. The relevant measurements are given in the supplementary material.

this taxon because of their large size, comparable to other samples of this species (e.g., the metacarpal III-IV in Fig. 11D; see also Fig. 12). Dimensions are given in the supplementary material.

4.5.2.2. Discussion. The presence of the two basal tines and their arrangement (almost in contact to each other, slight lateral shift of the second one), as described in the studied material, is the most characteristic feature of the red deer antlers (Lister, 1987, p. 91; 1990, p. 179; Pfeiffer, 1999, p. 34). The species is already described from the Megalopolis Basin by Melentis (1966a). This material, deriving from the 1902 excavations and kept in the AMPG, is morphologically identical to the Kyparíssia one.

4.5.3. Fallow deer

Genus: *Dama* Frisch, 1775

Dama sp.

Synonymy:

1966 *Dama somonensis* — Melentis, p. 3ff, pl. III, Figs. 1–3

1976 *Cervus* sp. — Sickenberg, p. 44ff, pl. IX, Fig. 1

Material: KYP-329, KYP-354, KYP-493, KYP-499, KYP-719: antler parts.

Description: All available material consists of antler fragments united under the generic attribution to *Dama* because of their similar size, short pedicel (distinctly shorter than antler fragments of similar diameter referred here to *Cervus elaphus*), the wide angle of departure of the beam from the pedicle (about 45°), and the well obtuse angle (about 135°) formed between the beam and the first tine (Fig. 11E). However, the first tine braches more than 2 cm above the burr and it is much weaker than the beam, unlike typical *Dama* (e.g., Lister, 1990, 1996; Croitor, 2014, 2018). The basal beam is of almost circular cross section, while the tine's section is elliptical, elongated dorsoventrally. Very similar specimens from the Megalopolis Basin have been published before as *Dama somonensis* and *Cervus* sp. (Melentis, 1966a; Sickenberg, 1976; respectively). The available material from the whole basin is, though, very fragmentary for a secure taxonomic assessment of the available samples. Dimensions are given in Table 6.

A considerable number of cervid postcranial finds, not mentioned in the referred-material list above, which are characterised by middle size (see Fig. 12) similar to that of the extant *Dama dama*, probably belong taxonomically with the previously described antler fragments. Dimensions are given in the supplementary material.

4.5.4. Small-sized deer

There are two distinct types of small-sized deer antlers, one of which was not identified to the genus and species level. A small number of postcranial bones, which are metrically close to *Capreolus capreolus* (Linnaeus, 1758) (see supplementary material) may be taxonomically related to either of these antler specimens (Fig. 12). However, there is no taphonomic association between any of the antler and postcranial specimens that could indicate conspecifity.

Genus: *Cervus sensu lato*

'Cervus' peloponnesiacus Sickenberg, 1976

Material: KYP-705: proximal antler fragment.

Description: A small-sized right antler fragment, also preserving the pedicel (Fig. 11G), is indistinguishable in size and morphology to Sickenberg's species, defined on scarce surface finds from the Megalopolis Basin. The Kyparíssia specimen is broken just 2.5 cm above the base, so little, if at all, can be said on its morphology. Similar specimens published by Sickenberg (1976) exhibit a rather *Dama*-like obtuse angle formed by the beam and the first tine. However, the first tine branches off well above the burr, unlike *Dama*, in rostrodorsal direction. The antler size is also rather small for this genus. '*Cervus' peloponnesiacus* still remains an obscure species in dire need of more material to figure out its morphology and its phylogenetic affinities. Dimensions are given in Table 6.

Cervidae indet.

Material: KYP-522: proximal antler part.

Description: KYP-522 is a proximally-preserved small-sized shed antler (Fig. 11F) that features a basal first tine situated very low, in contact with the burr, and an almost round in cross section, slightly convex laterally beam without any other branching till 9–10 cm above the burr. The specimen does not resemble the similarly-sized *Capreolus*, which lacks a tine close to the burr. The overall shape of the find reminds the antler morphology of the SE Asian genus *Muntiacus* Rafinesque, 1815. On the basis of the currently available morphological data the taxonomic affinities of this find are unknown.

4.6. Bovids

Order: Artiodactyla Owen, 1848

Family: Bovidae Gray, 1821

Genus: *Bison* Hamilton Smith, 1827

Bison sp.

Material: KYP-347, upper right premolar (P3/4); KYP-346, left upper molar (M3?); KYP-612, left upper molar (M3?); KYP4-321, left tibia; KYP1-315, right metatarsal III-IV; KYP-701, left metatarsal III-IV.

Description: The available dental material (Fig. 13B and C) is unworn, or slightly worn and has all the characters of Bovini: very hypsodont, presence of prominent labial styles, as well as of an entostyle. The enamel is rugose, particularly lingually. The molars are quite probably identified as M3 because of the asymmetry of their lobes. Measurements are given in Table 7.

The dental material is only provisionally referred to *Bison*, as an attribution to *Bos* cannot be excluded either morphologically, or metrically.

The long bones referred here to *Bison* are characterised by robust build. The distal end of the tibia KYP-315 has a divided malleolus facet, a feature that characterises *Bison* (Gee, 1993). In *Bos* this facet is usually united. Measurements are given in Table 7. Both available metatarsals lack their distal ends (Fig. 13A). KYP-701 is also damaged proximally, so that its articular dimensions cannot be measured. In the metatarsal proximal end the facets for the tarsals II and III and the cubonavicular are in contact to each other in the anterior part of the articu lation, forming a small ridge (Fig. 13B). This is considered a stable *Bison* character, as in *Bos* these facets are well separated (Gee, 1993). Measurements are given in Table 7. The length of KYP-315 is estimated to about 25 cm. The articular dimensions are within the range of both *Bison priscus* Bojanus, 1827 and *Bison schoetensacki* Freudenberg, 1910, but the length appears to be shorter in the Kyparíssia material (see Sala, 1986, table 20).

The Megalopolis Basin has already yielded large bovine finds referred to both *Bos primigenius* Bojanus, 1827 and *Bison priscus* (see Melentis, 1966e), or to *Bison* sp. with affinities to *B. schoetensacki* (Konidaris et al., this issue). The material available from Kyparíssia is still insufficient for specific attribution, while a small part of it may in fact belong to *Bos*. The pronounced individual (including sexual) variation within and between *Bos* and *Bison* frequently makes their distinction very difficult, requiring rich fossil samples, which are yet to be found in Kyparíssia and other localities of the Megalopolis Basin.

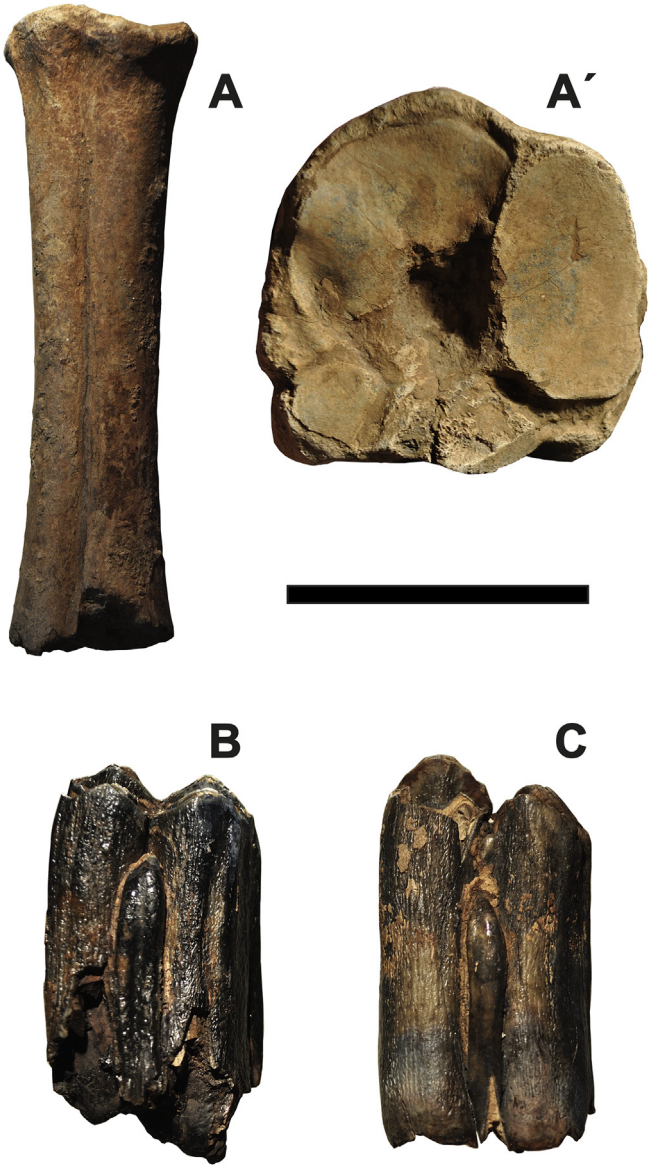

Fig. 13. Dental and osteological specimens from Kyparíssia referred to *Bison* sp.: **A**, right metatarsal III-IV, KYP1-315, dorsal aspect; **A′**, proximal aspect; **B**, left upper molar (M3?), KYP-612, lingual aspect; **C**, left upper molar (M3?), KYP-346, lingual aspect. The graphical scale equals 10 cm for **A**, 5 cm for **A′–C**.

5. Biochronology

The general biochronological character of the Kyparíssia fauna is of Middle Pleistocene (Galerian) type, in accordance to what is already known from other sites within the Megalopolis Basin (Sickenberg, 1976; van Vugt et al., 2000; Konidaris et al., this issue). Athanassiou et al. (this issue) based on the suiform material date the Kyparíssia fauna to the latest Early – early Middle Pleistocene. The more diverse mammal taxa studied in the present paper bring new data to this issue and further support an early Middle Pleistocene age as detailed below. The presence of two main fossiliferous horizons in the Kyparíssia mine (see Section 3) raises an issue of possible faunal mixing and time averaging. However, the preservation of very large-sized megaherbivore skeletal elements within the basin, including at least three elephant skulls (Melentis, 1965; Konidaris et al., this issue) indicates rapid sedimentation that prevented long subaerial exposure and consequent surface cracking and flaking, or even the ultimate destruction of the specimens. Moreover, van Vugt et al. (2000), based on magneto- and cyclostratigraphic data, calculated a sedimentation rate of 21 cm/kyr for the sedimentary filling of the basin, which is rather fast. A similar or even higher sedimentation rate (depending on the preferred magnetostratigraphy-based chronology) was recently calculated by Tourloukis et al. (this issue). Using this rate the stratigraphic distance of maximum 15 m between the lower and the upper fossiliferous horizons in Kyparíssia corresponds to an estimated chronostratigraphic range of no more than 70 kyr, which is not expected to be important biostratigraphically in the Middle Pleistocene. Based on the currently available data no significant faunal difference is traced between the two levels

Table 7
Dental and postcranial measurements of *Bison* sp. from Kyparíssia (in mm).

P3/4	H	DAP	DT
KYP-347	40.7	21.0	24.9
M3?	H	DAP	DT
KYP-346	67.0	37.0	31.2
KYP-612	67.2	36.0	27
tibia	DAPm	DTm	DAPd	DTd
KYP4-321	42.5	57.6	60.9	81.2
metatarsal III-IV	DAPp	DTp	DAPm	DTm
KYP-315	63.2	64.5	44.0	43.0
KYP-701	–	–	44.8	43.6

Table 8
Comprehensive faunal list of Kyparíssia with taxon representation in each site (KYP1–KYP4, KYPT), as well as in the non-stratified material (KYP). Combined data from Athanassiou et al. (this issue) and the present study. Note that *´Cervus´ peloponnesiacus* is distinguishable from Cervidae indet. only in the non-stratified material (KYP), which includes antlers. KYP1, KYP3 and KYP4 yielded only non-diagnostic finds, and may include either one or both of these small cervid taxa (their possible presence is indicated by '?').

Order	Family	Genus and species	KYP	KYP1	KYP2	KYP3	KYP4	KYPT
Testudines	Emydidae	*Emys orbicularis*	+	+		+		+
	Testudinidae	*Testudo marginata*	+	+		+		
Anseriformes	Anatidae	*Anas crecca*	+					
		Anas platyrhynchos	+				+	
		Cygnus olor				+		
		Mareca strepera	+					
		Spatula clypeata						+
		Spatula querquedula	+					
Gruiformes	Rallidae	*Fulica atra*	+					
Suliformes	Anhingidae	*Anhinga* sp.						+
	Phalacrocoracidae	*Phalacrocorax carbo*						+
Rodentia	Castoridae	*Castor fiber*	+					
Carnivora	Canidae	*Canis* sp.	+					
	Hyaenidae	Hyaenidae indet.	+			+		
	Felidae	*Panthera* sp.				+		
		Felis sp.				+		
Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	+	+		+	+	
Perissodactyla	Rhinocerotidae	*Stephanorhinus* sp.	+					
	Equidae	*Equus* sp.	+	+				
Artiodactyla	Suidae	*Sus scrofa*	+			+		
	Hippopotamidae	*Hippopotamus antiquus*	+	+		+	+	+
	Cervidae	*Praemegaceros verticornis*	+	+	+	+	+	
		Cervus elaphus	+	+		+	+	
		Dama sp.	+	+		+	+	
		´Cervus´ peloponnesiacus	+	?		?	?	
		Cervidae indet.	+	?		?	?	
	Bovidae	*Bison* sp.	+	+			+	

and among the taxonomically rich sites (Table 8), at least when considering the most abundantly represented taxa.

Castor fiber is a minimally changed species during the Pleistocene. It appeared during the Early Pleistocene in Central and Western Europe, but reached Italy (possibly also other South European regions) at the beginning of the Middle Pleistocene (Barisone et al., 2006). The small *Canis* is also not very helpful for biochronological purposes as it is found in both Early and Middle Pleistocene faunas. The worn dentition from Kyparíssia does not help to trace any resemblance to the more advanced wolf-like dentitions that appeared with the late populations of this canid (Rook and Torre, 1996). Large felids like *Panthera pardus* appear in the fossil record just before the beginning of the Middle Pleistocene (O'Regan et al., 2002) and the same is true for the straight-tusked elephant and the red deer (Palombo, 2014). *Bison* may be older depending to species, but this is not identifiable in the studied material. Somewhat later, at the Early/Middle Pleistocene transition, appear in the fossil record the caballoid horses and the giant deer *Praemegaceros verticornis* (Forsten, 1988; Croitor, 2006). Thus the earliest possible age of the Kyparíssia fauna coincides with the beginning of the Middle Pleistocene, some 0.8 Myr ago.

Most of the taxa represented in Kyparíssia, such as the beaver, the canid, the wild cat, the panther, the horse, the red and fallow deer, and the bison survived till the Holocene, so they are not good indicators about the fauna's latest possible age. *Palaeoloxodon* died out earlier, but still in the latest Pleistocene (Mol et al., 2007); it was present in Greece as late as about 40 ka (Athanassiou, 2011). The only taxon that has a shorter biochronologic span is *Praemegaceros verticornis*, which is unknown in the European faunas after the medial Middle Pleistocene (Croitor, 2006). The latest locality that yielded this species is Bilshausen (Germany), dated to 0.4 Ma (Pfeiffer, 2002) and this can be regarded as the minimum age of the Kyparíssia fauna. In conclusion, the Kyparíssia locality is dated according to the available biochronologic data to the early Middle Pleistocene, its age being confined between 0.8 and 0.4 Ma (Galerian large mammal age).

6. Palaeoecology

The depositional environment of the Megalopolis palaeolake had an excellent preservation potential of organic material and has provided abundant data for reconstructing the environment of the area. The study of organic remains (wood, fruits, seeds, ostracodes, molluscs, vertebrates etc.) documented the existence of an expanded permanent lake with rich aquatic vegetation, surrounded by mixed deciduous forests and woodlands (Lüttig, 1968; Mädler, 1971; Sickenberg, 1976; Schütt et al., 1985; Nickel et al., 1996; Okuda et al., 2002; Athanassiou et al., this issue; Field et al., this issue). This is corroborated by the present study. *Castor* is certainly an animal that depends on water, and together with the aquatic chelonian and avian species, *Hippopotamus* (Athanassiou et al. this issue) and *Bubalus* (Sickenberg, 1976) is a strong indicator for the presence of a permanent freshwater body in the basin. Although frequently named as the forest elephant, *Palaeoloxodon antiquus* seems to have been adaptable to a wide range of environments from temperate grasslands to wooded lands (Palombo et al., 2010; Rivals et al., 2012); thus it cannot serve as a good palaeoecological guide species. Assuming a sense of pleasure for water, similar to that observed in extant elephants, it can be supposed that the palaeolake was an attraction place for the population of the wider area. Deer is generally considered as a habitual browser and forest dweller, particularly the small-middle sized ones. *Cervus elaphus* is more versatile ecologically, both in terms of dietary habits and habitat, as it can be also found in open areas, usually, though, in the vicinity of forested areas (Gebert and Verheyden-Tixier, 2001). *Praemegaceros* might have favoured more open areas due to its very large body size and laterally expanded antlers. Typical open landscape dwellers, such as the horses, the rhinoceroses and the bisons, are, though, rare in the studied fauna. As a whole the fauna of Kyparíssia quite probably indicates an environment with widespread forests or woodlands around a large lake, interrupted by wide open or open woodland areas, under temperate climatic conditions.

7. Conclusion

Fieldwork carried out in the lignite mine of Kyparíssia in the northern part of the Megalopolis Basin, central Peloponnesus, during the years 2004–2008 and 2012 produced a diverse fossil fauna of turtles, birds and mammals, which are presented in Athanassiou et al. (this issue) and the present paper. The complete faunal list is given in Table 8. The main faunal elements are *Hippopotamus antiquus*, *Palaeoloxodon antiquus* and deer, the latter exhibiting a remarkable diversity of five species. Other mammals are less frequently represented in the locality's fossil record: *Castor fiber*, carnivores, *Equus*, *Stephanorhinus*, *Sus scrofa* and *Bison* are described based on rather scanty material. The turtle finds are referred to two species of different ecology, while a rich in taxonomic diversity aquatic bird assemblage is documented (Athanassiou et al., this issue).

The identified mammalian faunal composition is of Galerian character and place biochronologically the locality in the Middle Pleistocene. Among the identified taxa *Praemegaceros verticornis* is the most characteristic species biochronologically and constrains the age of the fauna within the timeframe of 0.8–0.4 Ma. The currently collected faunal data do not allow any biostratigraphic distinction of the studied sites within the Kyparíssia mine according to their taxonomic content, and the age difference among the sites is not expected to be significant.

The fauna as a whole indicates the presence of an expanded freshwater body with rich aquatic vegetation able to sustain a population of *Hippopotamus* and offer shelter to a diverse aquatic avian fauna. The surrounding land was mostly forested with patches of open landscapes.

The studied fauna from Kyparíssia is very similar to the samples recovered at other sites of the Megalopolis Basin since the Skouphos excavation in 1902 (see mainly the numerous publications by Melentis, as well as Sickenberg, 1976), including the recently discovered Marathousa 1 (Konidaris et al., this issue; Michailidis et al., this issue). The richness of the material collected at the sites KYP1, KYP3 and KYP4 calls for a future more detailed and systematic research in the mine focusing on undisturbed fossiliferous layers, in order to recover more complete specimens, more informative about the morphology of the taxa, the basin's palaeoecology, and the potential impact of humans on the local palaeoecosystem.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2018.06.042.

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