



# ***Bos primigenius* Bojanus, 1827 (Mammalia, Bovidae) in Greece: New Finds and a Revision of the Species, with a Comparison with Body-size Variations of Aurochs from the Italian Peninsula**

***Eleni Samartzidou*<sup>1\*</sup>, *Luca Pandolfi*<sup>2</sup>, *Evangelia Tsoukala*<sup>3</sup>, *Yannis Maniatis*<sup>4</sup> & *Stelios Stoulos*<sup>5</sup>**

<sup>1</sup> School of History and Archaeology, Faculty of Philosophy, Aristotle University, 54124 Thessaloniki, Greece;  
E-mail: [helensam@hotmail.com](mailto:helensam@hotmail.com)

<sup>2</sup> Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira 4, 50121 Firenze, Italy;  
E-mail: [luca.pandolfi@unifi.it](mailto:luca.pandolfi@unifi.it)

<sup>3</sup> School of Geology, Aristotle University, 54124 Thessaloniki, Greece; E-mail: [lilits@geo.auth.gr](mailto:lilits@geo.auth.gr)

<sup>4</sup> Laboratory of Archaeometry, NCSR Demokritos Patriarchou Grigoriou E' and Neapoleos 27, 15310 Aghia Paraskevi, Attiki, Greece; E-mail: [y.maniatis@inn.demokritos.gr](mailto:y.maniatis@inn.demokritos.gr)

<sup>5</sup> Department of Nuclear and Elementary Particles Physics, School of Physics, Aristotle University, 54124 Thessaloniki, Greece;  
E-mail: [stoulos@auth.gr](mailto:stoulos@auth.gr)

**Abstract:** The present study deals with a new bovid assemblage from Kataphyto, Northeastern Greece, providing additional information concerning this species dispersal and stature in Greece. It consists of 155 teeth and bone remains attributed to the extinct species *Bos primigenius* Bojanus, 1827. The <sup>14</sup>C dating analysis of the fossils resulted in a Late Pleistocene age, with a median at 23,800 calBP, similar to the age obtained using the U-series geochronology. A brief outline of the evolutionary history, morphology and ecology of the Pleistocene aurochs is reported, with a comprehensive update of the palaeontological and archaeological records of the species in Greece reviewed here. Morphometric data have been investigated in order to provide an evaluation of the species body size variations through time in Greece. The results show that the populations of aurochs in Greece were small in size during the Middle Pleistocene, increased in size during the end of the Late Pleistocene, followed by a decrease during the Holocene. Moreover, aurochs remains from Greece, compared with those obtained from the Italian Peninsula, contribute to knowledge about body size variation during the Pleistocene and Holocene. This study revealed a different trend compared to other European sites and depict a more complex and articulated framework on aurochs body size variation than previously thought.

**Key words:** Aurochs, radiocarbon dating, U-series geochronology, body size, morphometry, trends, Quaternary, palaeontology.

## **Introduction**

Fossil large and small Bovidae are known from Neogene and Quaternary sediments in Greece. New findings, from Pleistocene palaeontological and ar-

chaeological sites, came to light during the last decades. This paper focuses on the extinct aurochs, *Bos primigenius* Bojanus, 1827, a well-known large bovid species, being recovered in numerous fossiliferous localities from Europe, Asia and Africa.

\*Corresponding author: [helensam@hotmail.com](mailto:helensam@hotmail.com)

The origin and relationships of this species and, in general, of the tribe Bovini, is still a matter of debate. Based on the sequence of nucleotides for the mitochondrial b gene, *Bos* and *Bison* are grouped together but separately from Asian and African buffaloes, such as *Bubalus* and *Syncerus* (HASSANIN & DOUZERY 1999, MASSILANI et al. 2016). According to amplified fragment length polymorphisms (AFPL), bison and yak species (*Bison bison*, *Bison bonasus* and *Poephagus mutus*) on one side, and domesticated cattle (*Bos taurus*, *Bos indicus*) and gaur (*Bos gaurus*) on the other, are grouped separately. Both groups are also separate from *Bubalus* and *Syncerus* (BUNTJER et al. 2002). However, according to some morphological studies, *Bos*, *Bison*, *Poephagus* and *Bibos* are considered as subgenera of the genus *Bos* (GENTRY 1978, GROVES 1981, WRIGHT 2013). Other scholars also included *Leptobos* as subgenus of *Bos* (BRUGAL 1985, MOYÀ-SOLÀ 1987), proposing a form of *Leptobos* as the ancestor of *Bos* and other genera (DUVERNOIS 1990). However, the cranial anatomy of *Bos* is highly derived and a direct anagenetic evolution from *Leptobos* appears improbable (MARTÍNEZ-NAVARRO et al. 2014). *Bos primigenius* is possibly related to or derived from *Bos acutifrons*, about 2 Ma in the Siwalik Hills (PILGRIM 1947), whereas other authors considered it to be related to *Bos planifrons* and *Bos namadicus*, two Asian species (ZONG 1984, GUINTARD 1999). Another hypothesis indicates that the genus *Bos* probably evolved in Africa from the Olduvai buffalo *Pelorovis* Reck, 1928 (GERAADS 1981, GERAADS et al. 2004, MARTÍNEZ-NAVARRO et al. 2010, 2014, MARTÍNEZ-NAVARRO & RABINOVICH 2011) but it conflicts with the hypothesis that the early *Bos* species from the Siwaliks is the ancestor of *Bos primigenius* (see BAR-YOSEF & BELMAKER 2016, PORTER et al. 2016, TONG et al. 2018).

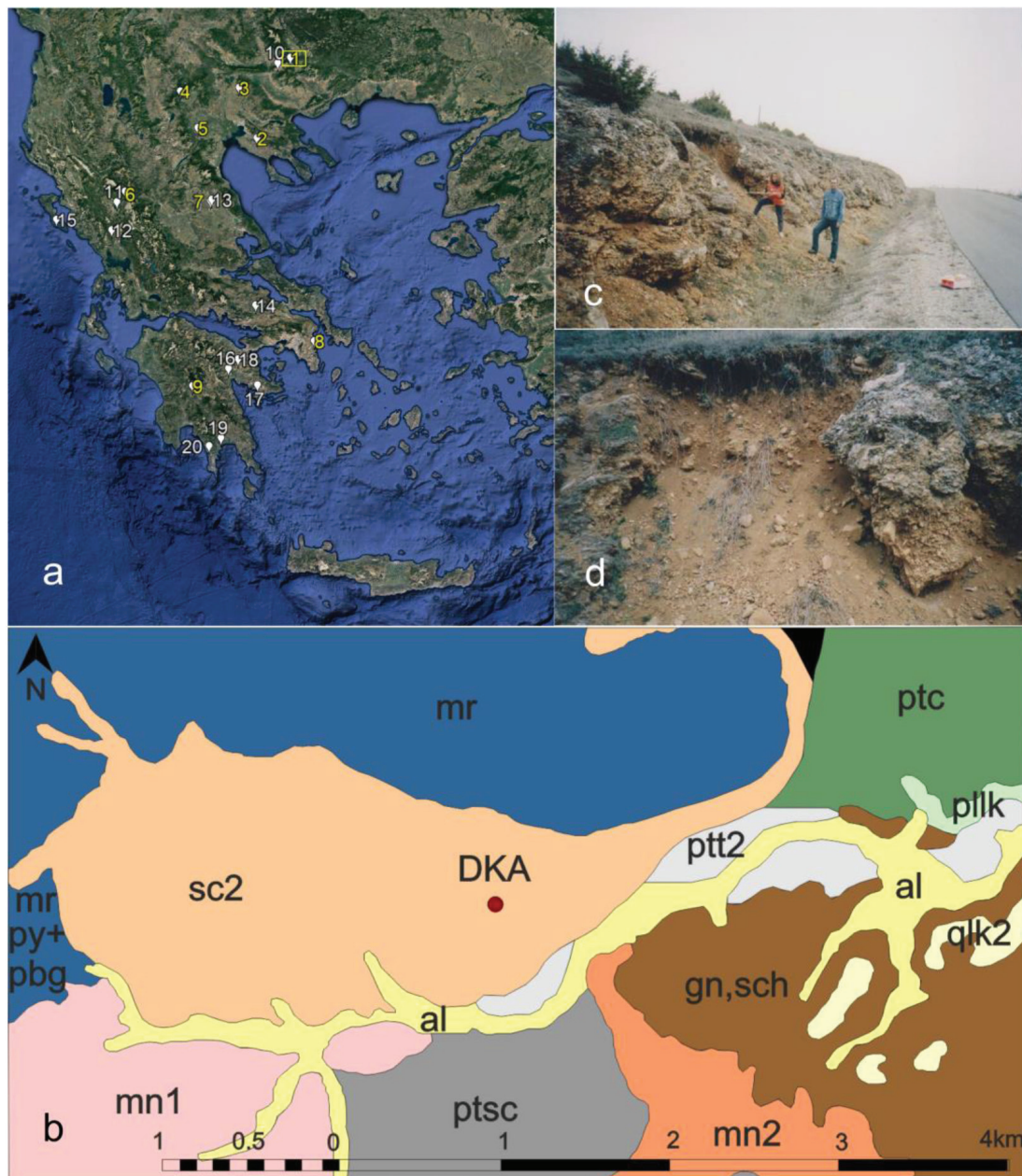
According to the classification based on their physiological, functional and dental morphology, the Early Holocene *Bos primigenius* and *Bison bonasus* are recognised as large mixed feeders (BRUGAL & CROITOR 2007, HOFMAN-KAMIŃSKA et al. 2018). Microwear and mesowear studies on Middle and Late Pleistocene (MIS7, MIS9, MIS 11) have also shown that aurochs were mixed feeders or browsers (RIVALS & LISTER 2016), whereas other studies suggested that in Northern Europe, during the Late Pleistocene, aurochs had a grazing diet on graminoids and forbs (BOCHERENS et al. 2015). Mesowear analysis conducted on aurochs from the Pleistocene-Holocene transition to the end of the Subboreal period in Denmark (SCHULZ & KAISER 2007) suggested that they were at first abrasion-dominated grazers, and later, in particular at the onset of the Boreal peri-

od, they changed to less abrasion-dominated mixed feeders. Similarly,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes analysis in eastern Denmark and southern Sweden revealed that aurochs' grass diet changed during the Preboreal toward a mixed diet (NOE-NYGAARD et al. 2005). Furthermore, dental microwear textural analysis (HOFMAN-KAMIŃSKA et al. 2018) applied to later Holocene *Bos primigenius* samples has shown that it was a variable grazer with an unchangeable diet over time (Neolithic-Middle Ages) or geographical distribution, indicating low flexibility in feeding preferences. In general, however, the highly variable ecological adaptation of aurochs in space and time implied by its variable habitat is also confirmed by its changeable feeding preferences.

Aurochs inhabited mainly temperate and subtropical zones (VAN VUURE 2005). It probably preferred swamps and swamp forests, along river valleys, river deltas and bogs but it possibly also lived in drier forests and, perhaps, in grasslands (CLUTTON-BROCK 1987, TIKHONOV 2008). In Europe, there might have been an ecological separation between the aurochs preferred habitat and that of the European bison (*Bison bonasus*), as the aurochs probably lived in wetter forests and the European bison in drier forests (TIKHONOV 2008), though the niches of these two species possibly overlapped (VAN VUURE 2002). Furthermore, according to HALL (2008), the aurochs could also be well adapted to open, steppe environments. In consequence, aurochs presents a highly variable ecological adaptation concerning habitat choice in space and time.

Aurochs is very common in the Middle and Late Pleistocene-Holocene faunas of Europe, Asia and Africa (LEHMANN 1949, GRIGSON 1969, DEGERBØL & FREDSKILD 1970, BRUGAL 1985, CERILLI & PETRONIO 1991, ESTÉVEZ & SAÑA 1999, GUINTARD 1999, VAN VUURE 2005, MARTÍNEZ-NAVARRO et al. 2010, 2014, RIVALS & ARELLANO 2010, PANDOLFI et al. 2011, 2013, TURVEY et al. 2013, MAGNIEZ & BOULBES 2014, MARRA et al. 2014, ÁLVAREZ-LAO et al. 2017, LENARDIĆ et al. 2018, TONG et al. 2018 among others).

In Greece, fossil remains were found in 7 out of 43 Pleistocene sites (Fig. 1a, Table S1): Petralona cave (Chalkidiki, Middle-Late Pleistocene) (TSOUKALA 1989, 1991); Agios Georgios cave, Kilkis (Central Macedonia, Late Pleistocene), ESR-dated to  $12200 \pm 2500$  years based on an upper carnassial of the spotted cave hyaena (BASSIAKOS & TSOUKALA 1996), and radiocarbon-dated on dental elements of the cave hyena and the European wild ass at two different laboratories resulting in an age of 29,349 calBP for the former and 28,530 calBP for the lat-



**Fig. 1.a.** Map of Greece with the main palaeontological and archaeological sites with *Bos primigenius*: Palaeontological sites (yellow numbers): 1. Kataphyto, 2. Petralona Cave, 3. Agios Georgios Cave, 4. Loutra Almopias Cave, 5. Aliakmon basin (Veria), 6. Ambelia (Grevena), 7. Larissa, 8. Vraona Cave, 9. Megalopolis basin. Archaeological sites (white numbers): 10. Kapnophyto Cave, 11. Kastritsa rockshelter, 12. Asprochaliko rockshelter, 13. Peneios River, 14. Seïdi Cave, 15. Grava rockshelter, 16. Kephalaria Cave, 17. Franchthi Cave, 18. Klissoura Cave 1, 19. Lakonis Cave I, 20. Kalamakia Cave, Image exported from Google Earth Pro 7.3.3.7786 (2021) : Image Landsat/Copernicus, DATA SIO, NOAA, U.S. Navy, NGA, GEBCO, Imagery Date : 12/14/2015, 37°, 48', 55.54'' N, 26°, 15', 59.72'' E, elev. 183 m, eye alt 1382.91 km. **b.** Geologic setting of the Late Pleistocene Kataphyto fossil site (DKA, solid circle), Drama Basin, N. Greece: mn1, quartz monzonite of the Rhodopi Massif; al, deposits in the torrent beds, recent alluvial deposits (Quaternary undivided); ptsc, granite core-stones and tors (Quaternary undivided); mn2, porphyroid monzonite-monzodiorite; gn, sch, schists, schists-gneisses, augen-gneisses and gneisses; qlk2, fluvio-torrential deposits (Quaternary undivided); pll, fluvio-lacustrine sediments (Pliocene-Pleistocene); ptc, fluvioterrestrial deposits (Pliocene-Pleistocene); ptt2, lower terrace system, fluvio-torrential deposits (Quaternary undivided); mr, marble series; py+pb, Pyrite+P.B.G.; sc2, scree, breccioconglomerates of marble, slightly to very cohesive, with matrix of red sandy clay; usually they derive from marble cataclasis due to climatic changes (Quaternary undivided) (modified after STAIKOPOULOS & EFSTRATIADES 1987). **c, d.** The palaeontological site of Kataphyto.

ter (MAKRIDIS et al. 2013, TSOUKALA 1992a); Loutra Almopias cave (Pella, Late Pleistocene, radiometric dated to 37,880 BP, calibrated 42,361 BP (TSOUKALA et al. 2006, RABEDER et al. 2006, NAGEL et al. 2019); Aliakmon basin (Veria area, Middle-Late Pleistocene) (MELENTIS 1966); Ambelia (Grevena, Middle Pleistocene, ESR-dated to 165-170 ka, i.e. OIS 6) in association with *Elephas (Palaeoloxodon) antiquus* (see TSOUKALA & LISTER 1998); Larissa (Penios valley area, between the city of Larissa and the gorge of Kalamaki, Middle-Late Pleistocene), also in association with *Elephas (Palaeoloxodon) antiquus* (see ATHANASSIOU 2001); Megalopolis basin (Peloponnese, Middle-Late Pleistocene) in association with *Bison priscus* (see MELENTIS 1965).

The knowledge about Palaeolithic faunas in Greece is up to now limited. GALANIDOU (2014) summarised the last developments in the Palaeolithic and Mesolithic Archaeology of Greece. *Bos primigenius* was found in 11 out of 28 faunal assemblages of Middle or Upper Palaeolithic sites (Fig. 1a, Table S1).

In Eastern Macedonia, *Bos primigenius* and few other species were found at Kapnophyto cave possibly of Upper Palaeolithic age (TRANTALIDOU 1996). In Epirus, the faunal assemblage at the rockshelter of Kastritsa (Upper Palaeolithic; GALANIDOU et al. 2000, GALANIDOU & TZEDAKIS 2001) is composed among other taxa by *Bos primigenius* bones (BAILEY et al. 1983a, KOTJABOPOULOU 2001). In addition, at Asprochaliko, a Middle/Upper Palaeolithic rockshelter in the Louros Valley (BAILEY et al. 1983a, b, 1992, HUXTABLE et al. 1992, STARKOVICH 2011), among other taxa from the Middle Palaeolithic layers, *Bos primigenius* was also found. In Thessaly, along the Peneios River, south from the prehistoric site of Argissa Magula, bones of various species, including *Bos primigenius*, were collected associated with stone tools of Middle and Upper Palaeolithic Age (BOESSNECK 1965). In Central Greece, in Boeotia, according to SCHMID (1965), the recorded faunal assemblage from the Upper Palaeolithic Seidi cave consisted possibly of *Bos primigenius* and few other species. In Corfu island, the Upper Palaeolithic rockshelter of Grava, on the southern slopes of Agios Mathias Mt, yielded the remains of several mammal species including *Bos primigenius* (see SORDINAS 1969). In northeastern Peloponnese, in Kephalaria cave, 5 km southwest from the town of Argos (Upper Palaeolithic, Mesolithic and Historical Times), the diversified Upper Palaeolithic fauna also included *Bos primigenius* (see REISCH 1976). Also on the southwestern shore of the Argolid Peninsula, near the modern town of

Kiladha, the well-known cave of Franchthi is located (Upper Palaeolithic to Final Neolithic; JACOBSEN 1973, DE VIVO et al. 2001); from the Upper Palaeolithic layers, *Bos primigenius* and many other taxa were identified (PAYNE 1973, 1975, 1982, STINER & MUNRO 2011, STINER et al. 2012). Klissoura Cave 1 (Middle Palaeolithic to Mesolithic, KOUMOUZELIS et al. 1996, 2001a, b, TOMEK & BOCHEŃSKI 2002, KUHN et al. 2010, STARKOVICH 2011, 2014, LOWE et al. 2012) is one of several karstic cave sites in Klissoura Gorge, in northeastern Peloponnese; there, STARKOVICH (2011) identified *Bos primigenius* among many other taxa. In southern Peloponnese, on the eastern coast of the Mani Peninsula, in Lakonis I cave (Early-Middle Upper Palaeolithic), the fauna also comprised of aurochs (PANAGOPOULOU et al. 2002–2004, ELEFANTI et al. 2008). Kalamakia cave, in the western coast of Mani Peninsula (Middle Palaeolithic), seems to be coeval to Laconis cave. It yielded a rich fauna, including *Bos primigenius* (see LUMLEY & DARLAS 1994, GARDEISEN & TRANTALIDOU 1996, GARDEISEN et al. 2001, LEBRETON et al. 2008, ROGER & DARLAS 2008a, b, HARVATI et al. 2013). Finally, Holocene archaeological sites with *Bos primigenius* finds in Greece are not presented in detail here, as this would exceed the scope of the paper but indicative measurements of the species from selected sites have been included in the measurement analysis (Tables S6 and S7): Lerna (GEJVALL 1969), Argissa (BOESSNECK 1962), Megalo Nisi Galanis (GREENFIELD & FOWLER 2005), Platia Magula Zarkou (BECKER 1991), Sitagroï (BÖKÖNYI 1986) and Magula Pefkakia (JORDAN 1975, AMBERGER 1979). In addition, selected measurements of *Bos primigenius* bones from additional Holocene sites are indicatively presented here with the related references (Table S6).

## Materials and Methods

The osteological fossil assemblage from Kataphyto site (DKA, Drama Kataphyto, Fig. 1a,b) has been discovered by Stelios Lazaridis during public works in April 2000. The bones were hand collected under the supervision of one of us (E.T.). The bones were found as a single accumulation buried in reddish loose clay sediments close to the eroded surface, on the slopes of a country road. The sediments, which were not sieved, consist of a cemented conglomerate covering an area of about 2 m<sup>2</sup> (Fig. 1c, d). Further search around the accumulation or at a greater depth did not result in other findings. The bones were treated as originating from a single context, as we did not observe different deposition layers. The

bone assemblage was stored in the Archaeological Museum, Ephorate of Antiquities of Drama.

Kataphyto (41°21'6"N 23°41'28"E) is located on the slopes of Orvilos Mt. at an altitude of 760 m, Prefecture of Drama (eastern Macedonia). This is a mountainous area of particular geological interest (Fig. 1b, STAIKOPOULOS & EFSTRATIADIS 1987), intersected and separated by Nestos River and lakes into two parts. The northern part consists of the Central Rhodope Mountains. The Greek Rhodope massif is separated into three, structurally complicated tectonic units: (a) the uppermost – Kimi unit; (b) the middle – Sidironero unit, and (c) the lowermost – Paggaiio unit. The uppermost and middle units consist mainly of ortho- and paragneisses, mica schists, amphibolites, metaophiolites, thin layers of marbles, migmatites and granites intrusions. The lowermost unit is composed by schists and marbles intercalations that at its higher levels develop into a thick marble sequence. Oligocene-Miocene granitoids intrusions are also abundant in the lowermost Rhodope Paggaiio unit (KROHE & MPOSKOS 2002, JAHN-AWE et al. 2010). Eocene-Oligocene molassic sediments intercalated with large volume of volcanic products are mainly developed in the eastern Greek Rhodope province, the so-called Thrace Basin (TSIFTSIS 2009, KILIAS et al. 2013). In the southern lowlands, there are lignite and peat deposits. Drama basin is a post-Alpine tectonic graben, located in the western part of Rhodope massif (DEL MORO et al. 1990, KILIAS & MOUNTRAKIS 1990). Metamorphic and granitoids rocks constitute the basement of the area. The metamorphic rocks are marbles, ortho- and para-gneisses, schists and amphibolites of Paleozoic and Mesozoic age (DEL MORO et al. 1990, KILIAS & MOUNTRAKIS 1990). The granitoids intrusions are of Jurassic – Cretaceous to Oligocene – Miocene age (SKLAVOUNOS 1981, SOLDATOS & CHRISTOFIDES 1986, DINTER et al. 1995, TURPAUD & REISCHMANN 2010). The thickness of the sediments in the basin exceeds 2 km. During Miocene and Pliocene, fluvial, lacustrine and terrestrial sediments were formed, which crop out at the central-western border (BORNOVAS & RONDOGIANNI-TSIAMBAOU 1983). After Lower Pleistocene, lacustrine and telmatic sediments dominated. In the central part of the plain, peat accumulated until the Eemian interglacial resulting in the deposition of lignite (BROUSSOULIS et al. 1991). In the southwestern part, peat accumulated until the recent drainage (1931, 1944) (MELIDONIS 1981). Alluvial sediments and talus cone deposits extend to the rest of the plain (GEORGAKOPOULOS et al. 2001).

Two quantification methods were followed for the recording of the material: (1) NISP (Number of

Identified Specimens; KLEIN & CRUZ-URIBE 1984) and (2) MNI (Minimum Number of Individuals, KLEIN & CRUZ-URIBE 1984). The age at death of the individuals represented in the assemblage was attributed according to SILVER (1969). Sex determination was based on proximal breadth measurements of the metacarpus (Bp: Greatest breadth of the proximal end, N=2), as cattle metapodials show strong sexual dimorphism (ALBARELLA 1997, HIGHAM 1969), including the same measurement from other sites (Argissa, Lerna, Peneios, Petralona, Sitagroi, N=15). It was also based on measurements (N=3) of the proximal phalanx, as a larger sample of measurements for this bone was available for comparison with Kataphyto phalanges (Ph1; GLpe: Greatest Length of the peripheral/abaxial half and Bd: Greatest distal breadth), which were plotted in a scattergram with those from Stavroupoli Neolithic site (N=16). Additionally, robustness index (Bd\*100/SD) was plotted for GLpe of proximal phalanges from Kataphyto and Stavroupoli. According to DOTTRENS (1946) and SALA (1986), forelimb proximal phalanx is shorter and stouter than the corresponding hindlimb phalanx. In each subsample of forelimb and hindlimb phalanges, more robust are those of males and slenderer are those of females. The measurements of the afore-mentioned sites (Argissa, Lerna, Peneios, Petralona, Sitagroi, Stavroupoli) were compared to those of Kataphyto, as the individuals therein represented were found to be of the same size, after the conducted statistical analysis (see relative section). Age determination was based on fusion stage of *Bos taurus* bones (diaphyses and epiphyses were recorded as fused and unfused) and age was attributed after Silver (1969). The taphonomic history of the sample was investigated following mainly the protocol of the Environmental Archaeology Unit of York and the protocol of the York system database (DOBNEY & RILLY 1988, DOBNEY et al. 1999, HARLAND 2001, HARLAND et al. 2003). Moreover, the following quantitative method was used for the recording of the degree of bone fragmentation; each fragment was recorded as a percentage of the original bone preserved (0–20%, 21–40%, 41–60%, 61–80%, 81–100%) (MARLEAN 1991, BARRETT 1998, HARLAND et al. 2003). In addition, scavenger attrition was assessed by the frequency of gnawing marks on the bones, whereas severity of scavenger attrition by the fragmentation patterns of bones, i.e. by estimating the frequency of bones in the shape of cylinders versus those, which preserve at least a part of an articular end, as according to BINFORD (1981), scavengers' attack results in the production of bones in the form of "cylinders" or "shaft splinters".

The measurements on the postcranial material have been taken following the methodology by VON DEN DRIESCH (1976). The elements considered in the statistical analysis include: radius, metacarpus, tibia, metatarsus, calcaneus, astragalus and phalanges. These elements were the most abundant within the considered sample and easily comparable with the standard used for the Size Variation Index (SVI). SVI is commonly used in zooarchaeology (UERPMANN 1982, 1986, MEADOW 1986, 1999, EISENMANN & KUZNETSOVA 2004, DI STEFANO et al. 2015, PANDOLFI et al. 2015) and it was performed in order to study the size variation of aurochs during the Pleistocene and Holocene. This index is useful to investigate the body size in a population when the remains are numerous but fragmented. The values of the SVI were obtained by means of the following formula:  $SVI = (x-M)/SD$  where “x” is the measurement of a specimen to compare, “M” is the mean of the measurement of the standard sample and “SD” is the standard deviation of the measurement of the standard sample. The SVI for each distinct anatomical element was calculated. In the present paper, the values of the SVI for each locality are plotted into a time-calibrated series following the methodology introduced by PANDOLFI et al. (2015). The number of measurements and the age for each locality are reported in Tab. 1. The standard is represented by the population of aurochs from Avetrana (Italy), data from PANDOLFI et al. (2011, 2013) and Supplementary Data (Table S2). This choice was made because the population is large, homogeneous and comes from a distant geographical region. Thus, it fits the requirements to be considered as a standard population. The sample is divided into nine groups based on the chronology of the considered localities; the variations of SVI for each group is graphically represented by box-plots. A permutational univariate analysis of variance (perANOVA; in order to deal with unbalanced sample size) has been performed using the function “adonis()” in “vegan” R package (OKSANEN et al. 2013). The differences in SVI among the different groups have been evaluated performing a pairwise permuted ANOVA using the function `pwperanovac` provided by SANSALONE et al. (2016). In addition, we used the Mann–Whitney U test to compare the differences between two independent samples (here the temporal groups) using the function “`wilcox.test()`”. The results obtained from the analysis of aurochs populations from Greece were also compared with the results obtained from the Italian Peninsula in order to detect the presence of body size variations in different areas of the Mediterranean Basin.

The data on aurochs from the Italian Peninsula are from PANDOLFI et al. (2011, 2013).

The following anatomical abbreviations were used: (M/m) upper/lower molar; (Mc) Metacarpal; (Mt) Metatarsal; (Ph) Phalanx.

For measurements, we used the following abbreviations (mainly after VON DEN DRIESCH 1976): Vertebrae, cervical: GLPa: Greatest length from processus articulares craniales to processus articulares caudales, lumbar: PL: physiological length of the body; BF (cr): Greatest breadth of facies terminalis cranialis. Scapula: SLC: Smallest length of collum; LG: Length of glenoid cavity. Humerus: BT: Greatest breadth of trochlea. Radius: Bp: Greatest breadth proximal; BFp: Greatest breadth of facies articularis proximalis (humeral); SD: Smallest breadth of diaphysis. Ulna: DPA: Depth across processus anconaeus. Metacarpus (Mc III+IV): Bp: Greatest breadth proximal. Tibia: SD: Smallest breadth of diaphysis; Bd: Greatest breadth distal. Metatarsus (Mt III+IV): Bd: Greatest breadth distal. Astragalus: GLl: Greatest length of the lateral half; GLm: Greatest length of the medial half; Dl: Greatest depth of the lateral half; Dm: Greatest depth of medial half; Bd: Greatest breadth distal. Proximal phalanx (Ph I): Glpe: Greatest length of the peripheral (abaxial) half; Bp: Greatest breadth proximal; SD: Smallest breadth of diaphysis; Bd: Greatest breadth distal. Intermediate phalanx (Ph II): GL: Greatest length; Bp: Greatest breadth proximal; SD: Smallest breadth of diaphysis; Bd: Greatest breadth distal. Distal phalanx (Ph III): MBS: Middle breadth of sole. Patella: GL: Greatest length; GB: Greatest breadth. Ossa Capitato-trapezoideum, Triquetrum, Lunare, Hamatum, Scaphoideum, Cubonavicular: GB: Greatest breadth. Teeth: L: Length; B: Breadth.

The abbreviations NCSR is used for the National Centre for Scientific Research “Demokritos”.

For dating samples, bone fragments (tibiae, humeri and ribs) from a uniform layer were subjected to radiocarbon dating at the Laboratory of Archaeometry (NCSR). The laboratory uses the Gas Proportional Counting technique (GPC). Details for the sample treatment and measurement protocols used by the laboratory can be found in MANIATIS et al. (2016). The methodology used for the treatment of this particular sample and the radiocarbon age obtained ( $19,752 \pm 100$  BP) are reported in STOULOS et al. (2018). However, a new radiocarbon calibration curve was released in 2020 which exhibits certain differences in the date period of interest compared to the previous version of 2013. Hence the radiocarbon age was recalibrated here using the program OxCal v.4.4.4 with the new dataset `intcal20` (REIMER et al.

2020). The age of ribs and tibiae fragments was also estimated using the U-series geochronology and the methods and dates obtained were also reported in STOULOS et al. (2018).

## Results

### Systematics

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Genus *Bos* Linnaeus, 1758

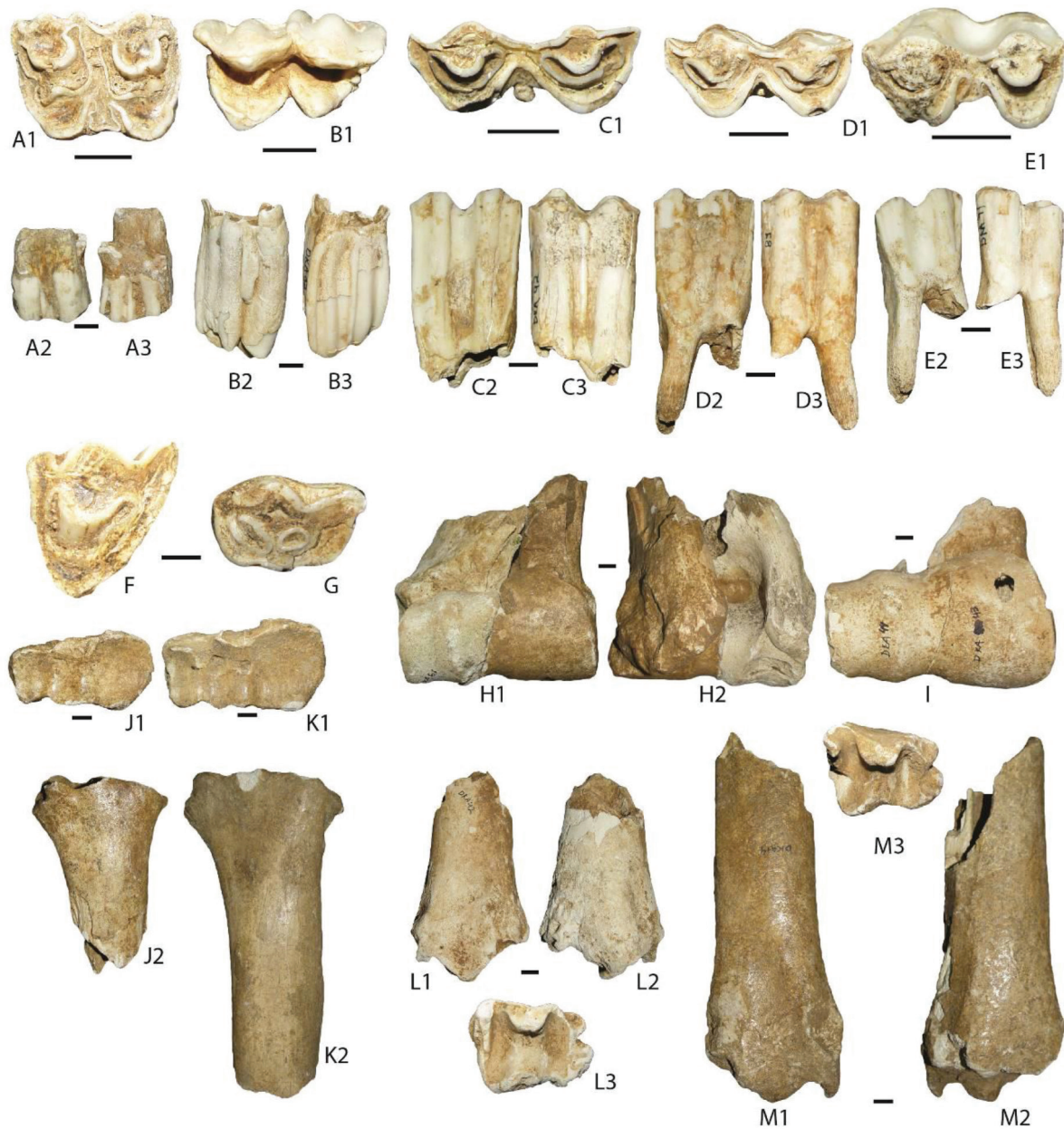
*Bos primigenius* Bojanus, 1827

The fossil bones belonged to the extinct species *Bos primigenius* Bojanus, 1827. Visual comparison with a modern reference collection of *Bos taurus* Linnaeus, 1758 bones as well as identification atlases of the related species *Bison priscus* Bojanus, 1827 and measurements of the bones under study led to the identification. The distinction from *Bison priscus* was based on the following characteristic bones (GEE 1993): radius, metacarpus, tibia, astragalus, metatarsus. In detail, the following criteria were used: (a) in proximal radius, the corresponding depth and prominence of the articular groove to receive the ulnar joint is deeper and sharper in *Bos* but shallower in *Bison* (see BIBIKOVA 1958, STAMPFLI 1963, BRUGAL 1983, HIDDINGH 1984); (b) in distal radius, the shape of the scaphoid articulation has converging and longer edges in *Bison* (see OLSEN 1960, STAMPFLI 1963, BRUGAL 1983); (c) in proximal Mc III+IV, the articular facet for the vestigial 5<sup>th</sup> metacarpus is more pronounced in *Bos* than *Bison* (see BRUGAL 1983); (d) in distal tibia, the shape and layout of the malleolar facets are different in the two species, i.e. the anterior facet is raised, circular and separate from the posterior facet in *Bison* but narrow, flat and confluent with the posterior facet in *Bos* (see BIBIKOVA 1958, STAMPFLI 1963, BRUGAL 1983); (e) in the distal posterior surface of the astragalus, in *Bison*, there is a prominent laterally directed flange on the posterior lateral edge of the bone, which curves medially and distally around the posterior nutrient foramen; in *Bos*, this flange is reduced or absent and the nutrient foramen opens directly outwards, posteriorly (BIBIKOVA 1958, GEE 1991). It must be noted that the primitive bison (*Bison priscus*) is referred together with *Bos primigenius* in the Middle-Late Pleistocene open sites of Megalopolis and Haliakmon basin (MELENTIS 1965, 1966) and in the Middle Pleistocene Petralona cave (TSOUKALA 1989), whereas the younger *Bison* sp. is referred in the Late Pleistocene Vraona cave (Attika) (RABEDER 1995).

**Material examined:** Total 99 identified specimens: 2 cranium fragments DKA 87, DKA 95; 2 mandible fragments DKA 81 right (condylus) DKA 106 left; 9 teeth P2 DKA 39 right; M1,2 DKA 150 right; M3 DKA 93 left; p2 DKA 40 left; 5 M/1,2 DKA 89, DKA 94 left, DKA 90, DKA 91, DKA 92 right; atlas DKA 86; 3 cervical vertebrae DKA 7, DKA 63, DKA 64; 3 thoracic vertebrae DKA 75, DKA 80, DKA 83; rib fragment DKA 70; lumbar vertebrae DKA 9; 2 caudal vertebrae DKA 84, DKA 85; 8 vertebrae fragments DKA 72, DKA 73, DKA 74, DKA 76, DKA 77, DKA 78, DKA 79, DKA 109; 4 scapulae DKA 47 glenoid, DKA 48, DKA 49 glenoid right, DKA 105 left; 3 distal humeri DKA 11+61, DKA 43+44, DKA 45+46, right; 3 distal femori DKA 6 condylus, DKA 20 condylus left, DKA 68 condylus right, DKA 60 caput femori; patella DKA 96 right; 9 radii proximal DKA 29, DKA 67 left, DKA 34 distal epiphysis, DKA 65 left, proximal DKA 12, DKA 21, DKA 66 right, distal DKA 1, DKA 19 epiphysis juv. right; proximal ulna DKA 50+51 right; 5 tibiae DKA 41 diaphysis left, 4 distal DKA 14 right, DKA 15 left, DKA 42 left, DKA 71 left; unciform DKA 36 left; lunare DKA 99 right; triquetrum DKA 97 right; capitato-trapezoideum DKA 98 right; scaphoid DKA 35 left; 3 astragali DKA 10, DKA 53 right, DKA 107 left; calcaneus DKA 5 right; 2 cubonavicular DKA 16, DKA 28 left; 5 Mc III+IV proximal DKA 2 left, DKA 54, DKA 55 right, distal DKA 26 (trochlea), DKA 33; 2 Mt III+IV distal DKA 13 right, DKA 25 left; 3 metapodia trochleae DKA 27, DKA 57, DKA 58; Phalanges: 8 proximal phalanges (Ph I) DKA 4, DKA 8, DKA 23, DKA 31 proximal fragment, DKA 32 distal fragment, DKA 52, DKA 56, DKA 62 proximal; 4 intermediate phalanges (Ph II) DKA 22, DKA 24, DKA 30, DKA 59; 3 distal phalanges (Ph III) DKA 17, DKA 18, DKA 88 artic.; and additionally 56 identified bone fragments (Table S3).

### Taphonomy, NISP, MNI, age and sex-ratio:

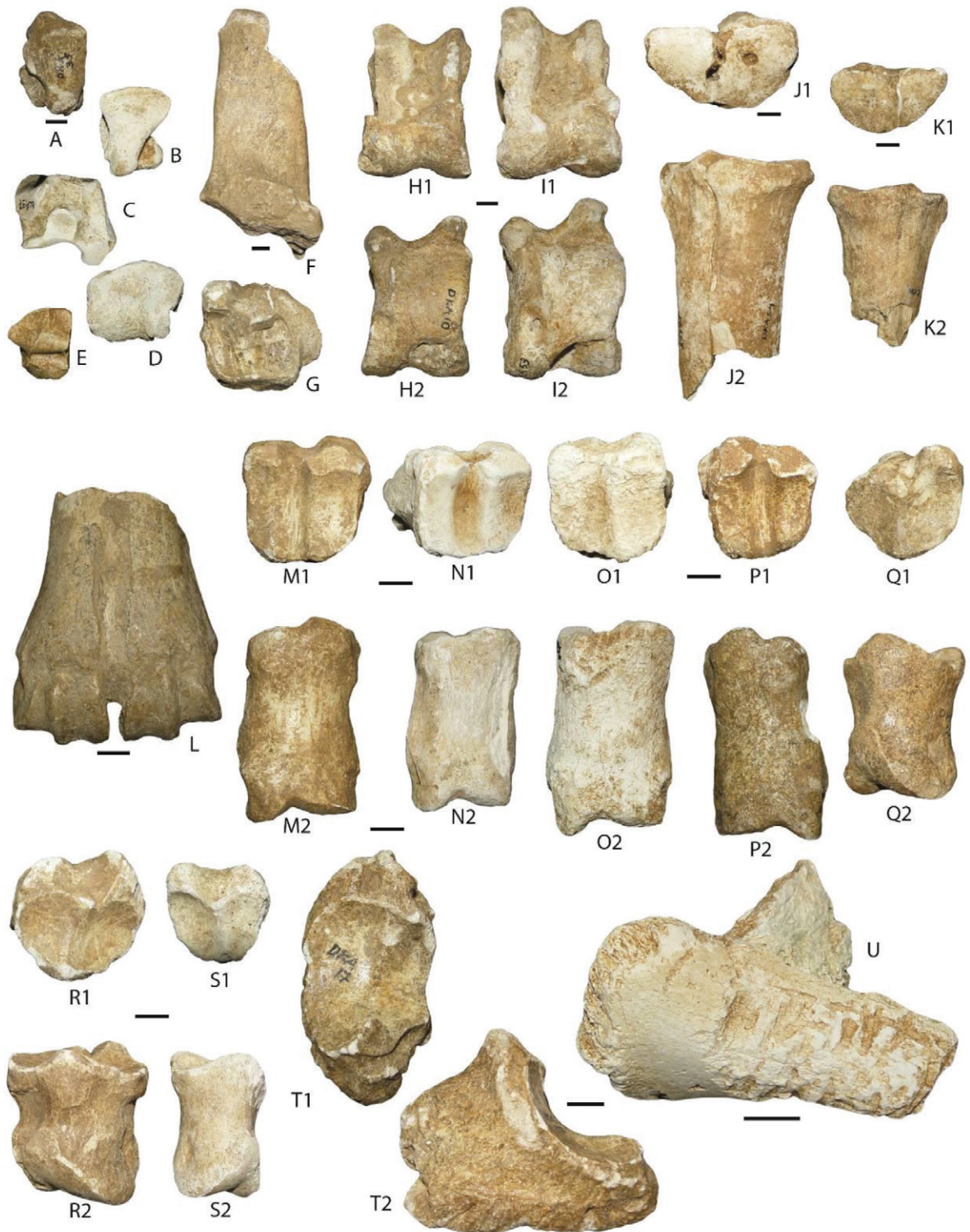
Various parts of the skeletons of the aurochs are present (Figs 2, 3, Table S3), but not in expected numbers, as normally found in intact skeletons; the individuals found are partly represented (Fig. 4). The majority of the specimens have a beige-yellowish color (N=127). Only a minority presents white-yellowish and white color (N=29), probably due to their exposure for some time to open air conditions. The percent completeness of the bones varies (Tab. S3, Fig. S1). Some specimens are almost intact (N=31, 20%), whereas in most cases only a small part of the original bone is preserved (N=107). Phalanges, carpals and tarsals are preserved almost intact, as they are more compact bones, whereas hu-



**Fig. 2.** Kataphyto *Bos primigenius*, teeth and bones. A. M1,2 DKA150 right, 1. occlusal, 2. labial, 3. lingual view; B. M3 DKA 93 left, 1. occlusal, 2. lingual, 2. labial view; C. M/1,2 DKA 92 right, 1. occlusal, 2. lingual, 3. labial view; D. M/1,2 DKA 89 left, 1. occlusal, 2. lingual, 3. labial view; E. M/1,2 DKA 91, right, 1. occlusal, 2. lingual, 3. labial view. F. P2 DKA 39 right, occlusal view; G. p2 DKA 40 left, occlusal view; H. Humerus distal DKA 61+11 right, 1. anterior, 2. posterior view; I. Humerus distal DKA 43+44 right, anterior view; J. Radius proximal DKA 12 and K. DKA 21 right, 1. proximal, 2. anterior view; L, M. Tibia distal: L. DKA 42 left, M. DKA 14 right, 1. anterior, 2. posterior, 3. distal view. Scale bar: 10 mm.

merus, radius and tibia are mostly broken. In most cases, the bones' outer surface is well preserved. Most of the bones show characteristic signs of root etching (N=89), which is probably the result of their deposition close to the surface layer. Forty-five bones were recorded as bearing the characteristic cracks of weather erosion, an outcome of their exposure to open air conditions for a long time before

their final burial. In addition, in some cases (N=18) root etching and weathering are present in the same specimens denoting that weathering followed during a secondary exposure of the bones to open air conditions. Five out of nine gnawed specimens have signs of gnawing by carnivores (bite marks), which corresponds only to 3% of the total number of specimens. This coupled with the general morphology of



**Fig. 3.** Kataphyto *Bos primigenius*, bones. A. Scaphoid DKA 35 left, proximal view; B. Lunare DKA 99 right, proximal view; C. Triquetrum DKA 97 right, medial view; D. Capitato-trapezoideum DKA 98 right, proximal view; E. Unciform DKA 36 left, proximal view; F. Calcaneus DKA 5 right, medial view; G. Cubonavicular DKA 16 left, proximal view; H. Astragalus DKA 10 right, 1. anterior, 2. posterior view; I. Astragalus DKA 53 right, 1. anterior, 2. posterior view; J. Mc III+IV proximal DKA 54+55 right, 1. proximal, 2. anterior view, K. Mc III+IV DKA 2 left, 1. proximal, 2. anterior view. L. DKA 8 right Mt III+IV, anterior view; M,N,O,P proximal phalanges: M. DKA 13, N. DKA 56,; O. DKA 52 and P. DKA 4, 1. proximal, 2. anterior view; Q,R,S intermediate phalanges: Q. DKA 22, R. DKA 24, S. DKA 59, 1. proximal, 2. anterior view; T. Distal phalanx DKA 17, 1. proximal, 2. lateral view; U. Mandible fragment (condyles), with gnawing marks DKA 81 right, posterior view. Scale bar: 10 mm.

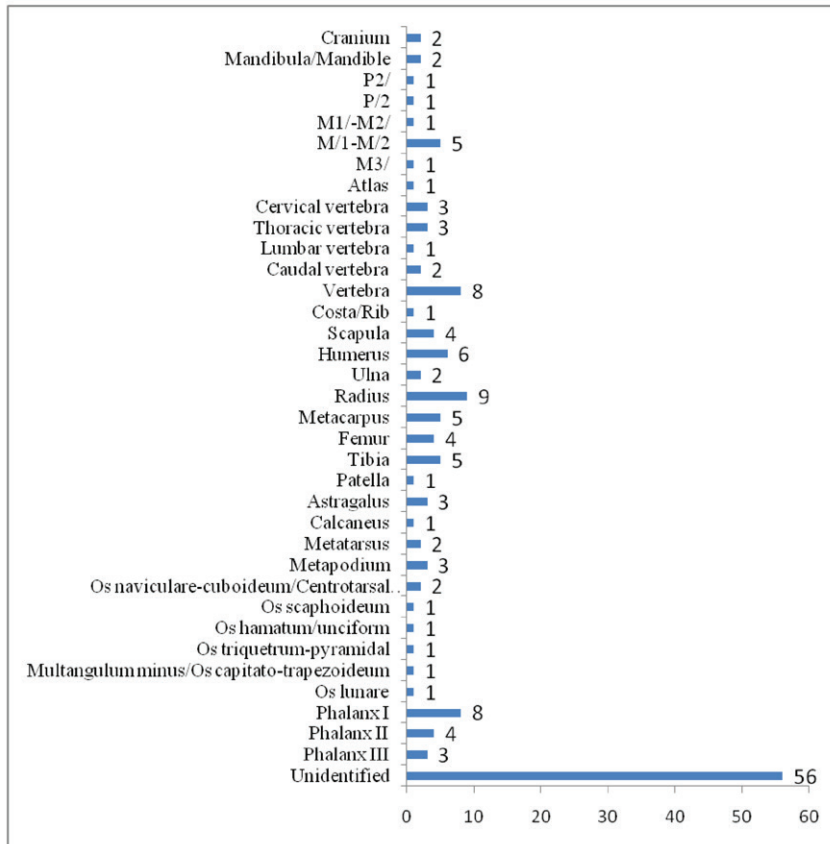


Fig. 4. Kataphyto *Bos primigenius*, bones: Number of Identified Specimens (NISP, N=155).

the specimens, i.e. absence of cylinders and splinters (as scavengers' attack results in the production of bones, which have the form of "cylinders" or "shaft splinters", BINFORD 1981) implies that the assemblage was not formed by scavengers (Fig. S2). Furthermore, one specimen showed gnawing by a rodent. In general, Kataphyto assemblage seems to be a natural accumulation formed after the transportation of the specimens from another close location, where they were originally deposited (weathering, gnawing marks, accumulation of disarticulated skeletons partly represented in the assemblage).

A total of 155 specimens comprise the osteological sample from Kataphyto (Fig. 4, Table S3) according to NISP, whereas according to MNI (based on counts of left distal tibiae), at least four adult individuals are represented in the sample. Out of the 155 specimens, 56 could not be identified to species level. The sex ratio of the sample (based on Mc: Bp measurement) suggests the presence of at least one female and one male individuals (Fig. S3), whereas the presence of 2-3 males is evidenced according to the measurements of Ph I, which is in accordance with the robustness index (Fig. S4, see relative section: related literature and methods). All the bones belong to adults (at least 3-4 years old). Unfused

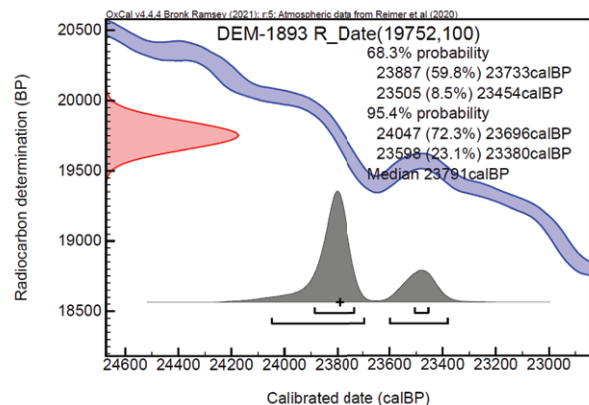


Fig. 5. The calibration plot using the program OxCal v.4.2.4 (BRONK RAMSEY 2021) with the most recent dataset *IntCal20* (REIMER et al. 2020).

epiphyses were noticed only in the case of two distal radii, which fuse in the age of 2-3 years and two distal femori, which fuse in the age of 3-4 years (Fig. S5, Tables S3 and S4).

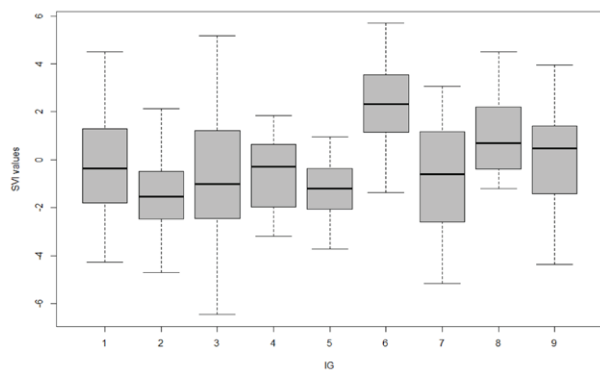
**Dating results:** The radiocarbon dating provided a  $^{14}\text{C}$  age of  $19,752 \pm 100$  BP. When this is calibrated with the latest calibration curve using the program OxCal v.4.4.4 with the latest dataset *IntCal20* (REIMER et al. 2020) it gives an overall calibrated

BP range of 24,047-23,380 calBP with probability 95.4%. Due to a winkle in the new calibration curve this range splits into two subranges: 24,047-23,696 calBP (72.3%) and 23,598-23,380 calBP (23.1%) (Fig. 5, Table 2). The first range has the highest probability to be the true age of the sample however one cannot exclude the second one. The median date of the overall 94.5% range is 23,791 calBP which is very close to the peak date of the 72.3% probability subrange (Fig. 5). We can therefore accept a most probable date for the Katapyto *Bos* sample of about 23,800 calBP. It is also interesting to note the  $\delta^{13}\text{C}$  value of -19.16 ‰. This value is similar to bovine and goat/sheep values of much later periods, e.g.

Bronze age in mainland Greece and the islands (MANIATIS & ARVANITI 2015) indicating a diet based on similar C3 plants and similar animal metabolism, although a different range of flora would be expected in the colder and drier climate around 24,000 calBP (see e.g. ADAMS et al. 1999). However, for a more complete tracing of the plant baseline of that period and area the  $\delta^{15}\text{N}$  isotopic value would be needed which was not measured as the purpose here was to correct for fractionation of the radiocarbon date using the  $\delta^{13}\text{C}$  value.

Additional evidence for the age was obtained from the ribs and tibiae fragments of the *Bos* using U-series geochronology. The specific results have already been published and gave an age from 21,000 to 25,000 BP with the  $^{231}\text{Pa}/^{230}\text{Th}$  and  $^{235}\text{U}$ -methods respectively and 21,000 to 31,000 with the  $^{238}\text{U}$ -series method (STOULOS et al. 2018).

**Body size variation of *Bos primigenius* in Greek Pleistocene and Holocene sites:** In general, the measurements of Katapyto bones (Table S5), when compared with individual values from other *Bos primigenius* remains from Pleistocene and Holocene sites of Greece (Neolithic and Bronze Age; Table S6) reveal that in some cases there is an overlap in size, i.e. in Ph I GLpe (with Petralona, Pefkasia, Argissa). In other cases DKA values are higher, i.e. in Mt III+IV Bd (Katapyto has higher values in



**Fig. 6.** Box-plot of the SVI index. 1-9, groups represented by populations of aurochs of similar age (Tables 2 and 3).

**Table 1.** Descriptive table of the considered groups with sample size, median values, maximal and minimal values, mean values and standard deviation (SD).

Group	Sample size	Median	Max	Min	Mean	SD
1 (Middle-Late Bronze Age/Early Helladic III-Middle Helladic)	77	-0.360	4.51	-18.4	-0.447	2.77
2 (Early Helladic II/Early Bronze Age-Middle Bronze Age)	57	-1.55	14.2	-9.51	-1.19	2.92
3 (Middle Neolithic-Early Bronze Age)	56	-1.01	7.91	-6.46	-0.644	2.87
4 (Middle-Final Neolithic)	7	-0.288	1.85	-3.18	-0.608	1.88
5 (Early-Middle Neolithic)	18	-1.21	0.952	-4.77	-1.36	1.47
6 (Late Pleistocene/Agios Georgios)	54	2.31	5.69	-1.38	2.24	1.58
7 (Late Pleistocene/Katapyto)	48	-0.607	3.06	-13.9	-0.756	2.90
8 (Late Pleistocene)	31	0.697	4.51	-1.20	0.932	1.54
9 (Middle-Late Pleistocene)	52	0.472	3.96	-4.37	0.0180	1.92

**Table 2.** Katapyto. Radiocarbon dating of *Bos primigenius* bone sample (NCSR Demokritos).

Laboratory Code	Sample	Material	Age $^{14}\text{C}$ (BP)	$\delta^{13}\text{C}$ (‰)	Calibrated date (calBP)	Probability
DEM – 1893	DKA: From a single uniform strata-layer Depth: 20-80 cm from surface	Bones (ribs and tibiae) of <i>Bos primigenius</i> )	19752 ± 100	-19.16	24,047 – 23,380 calBP 24,047 – 23,696 calBP 23,598 – 23,380 calBP	(95.4%) (72.3%) (23.1%)
Median of full range: <b>23,791 calBP</b> Peak of 72.3% probability range: <b>23,800 calBP</b>						

**Table 3.** Results of the pairwise permuted ANOVA, p-values corrected using “Holm” correction (Megalo Nisi Galanis: GREENFIELD & FOWLER 2005; Platia Magula Zarkou: BECKER 1991; Magula Pefkakia: JORDAN 1975, AMBERGER 1979).

Locality	Petralona	Pencios	Kataphyto	Agios Georgios	Lerna I+II, Argissa EN, Lerna I	Megalo Nisi Galanis, Argissa MN, Lerna II, Platia Magula Zarkou MN	Sitagroi, Magula Pefkakia LN	Magula Pefkakia EBA-MBA, Lerna III, Magula Pefkakia EBA	Magula Pefkakia LBA, Argissa MBA, Lerna V, Magula Pefkakia MBA, Lerna IV+V
Group	9	8	7	6	5	4	3	2	1
9	NA	0.499	1	0.035	0.160	1	1	0.149	1
8	NA	NA	0.051	0.035	0.035	0.482	0.149	0.035	0.219
7	NA	NA	NA	0.035	1	1	1	1	1
6	NA	NA	NA	NA	0.035	0.035	0.035	0.035	0.035
5	NA	NA	NA	NA	NA	1	1	1	1
4	NA	NA	NA	NA	NA	NA	1	1	1
3	NA	NA	NA	NA	NA	NA	NA	1	1
2	NA	NA	NA	NA	NA	NA	NA	NA	1
1	NA	NA	NA	NA	NA	NA	NA	NA	NA

comparison to most sites with the exception of Agios Georgios), while in other cases Kataphyto measurements present lower values, i.e. astragalus GLI in comparison to Stavroupoli and Sitagroi. A general observation is that the bones of Agios Georgios are larger than those of the other sites.

The SVI indexes were calculated from the linear measurements of aurochs bones and grouped on the basis of their ages (Table S7) in order to investigate possible trends in body size variations of the aurochs populations in Greece. Fig. 6 shows the variations of the SVI for each age group whereas the values of sample size, median, minimal and maximal values, mean and standard deviation of SVI for each group are reported in Table 1. It is evident that the median values are different from the mean values; the latter are indeed influenced by the minimal and maximal values (outliers) which could represent large males or very young individuals. The group 6, represented by Agios Georgios Cave, is different from all the other groups by means of pwpANOVA (Table 3). Groups 5, 3 and 2 are also significantly different from group 8. The groups 9, 8 and 7 are not statistically different from each other and group 1 is not statistically different from groups 5, 4, 3 and 2. A non-significant variation in SVI has been detected between Middle Pleistocene populations (groups 9 and 8) and that from Kataphyto (group 7; around 24,000 BP). A significant variation in SVI is detected during the Late Pleistocene, in particular from group 6 (Agios Georgios; around 12,000 BP) and, partially, during the beginning of the Holocene

(group 5; around 8000 BP). Especially, the population from group 6 displays a statistically significant increase in SVI values in respect to older groups, because it is particularly larger in size (Figs. 6-7). The Mann-Whitney U Test provided a non-significant difference between group 9 and 8 ( $p$ -value = 0.056), between group 5 and 4 ( $p$ -value=0.49), between group 4 and 3 ( $p$ -value=0.8), and between group 3 and 2 ( $p$ -value=0.31), and a significant difference between group 8 and 7 ( $p$ -value=0.0045), between group 7 and 6 ( $p$ -value=2.792e-09), between group 6 and 5 ( $p$ -value=1.274e-08), and between group 2 and 1 ( $p$ -value=0.002), thus confirming the above-mentioned observations.

## Discussion

Late Pleistocene remains in Drama (eastern Macedonia) are rare. They were recovered in Kataphyto, Kapnophyto cave (TRANTALIDOU 1996) and Angitis cave (TRANTALIDOU 2013). The Kataphyto remains are dated at 23,800 calBP. Measurements were taken in 38 cases and compared with those from other *Bos primigenius* individuals from Pleistocene and Holocene sites of Greece (Neolithic and Bronze Age; Tables S5, S6) revealed that there are similarities in size, but in many cases, also, outliers. Only in Agios Georgios cave (Late Pleistocene), bone measurements of *Bos primigenius* seem to have much higher values than those of the remaining sites. These results are confirmed by a statistical approach and considering the SVI as a body size proxy. PANDOLFI

et al. (2011) recognised an evolutionary trend in the size of Italian aurochs, which is characterised by five stages connected to climatic fluctuations and species competition (*Bos primigenius* versus *Bison* and *Homo*).

Aurochs populations in Italy were small-sized (~650-500 ka, Middle Pleistocene, MIS 16-14) during cool temperate climates. In the second stage, during late Middle Pleistocene (480-300 ka), aurochs present an increase in size, which can be related to warm temperate climate and the decrease of bison populations. In the third stage, during the Middle Pleistocene (300-200 ka), aurochs are represented by very large-sized specimens, probably due to the optimum climate stage. In the fourth stage, there is a decrease in size, connected, probably, with climatic deterioration of the late Late Pleistocene (75-20 ka), the migration of *Bison priscus* in southern Europe and human presence. Lastly, during the fifth stage (Holocene), aurochs populations are similar in size to those of Middle Pleistocene, i.e. small.

Nevertheless, these variations need to be tested by means of modern statistically approaches and by comparison with other southern European populations. Several studies have been recently devoted to the investigation of body size of large artiodactyls throughout the Pleistocene in Europe (PANDOLFI et al. 2011, 2013, 2015, MADE et al. 2014, DI STEFANO et al. 2015, WRIGHT & VINER-DANIELS 2015, RIVALS & LISTER 2016, SAARINEN et al. 2016, MANIAKAS & KOSTOPOULOS 2017) using different approaches and different scales of investigations, at regional and continental levels.

Recent studies on trends in body size of southern European mammals revealed fluctuations but a non-significant correlation between body size and climatic changes (PANDOLFI et al. 2015, SANSALONE et al. 2015). The study of TEPLITSKY & MILLIEN (2014) argued that Bergmann's rule is too simplistic and body size varied not only in response to temperature. Besides, GOHLI & VOJE (2016) concluded that Bergmann's rule is not an important interspecific phenomenon in mammals. Moreover, YOM-TOV & GEFFEN (2011) argued that in some species, body size may not be related to a climatic variable per se, but instead to a biological phenomenon such as temporal availability of an abundant food source.

In extant mammals, the seasonality and food availability influence the total body mass (e.g. SUZUKI et al. 2001, YOKOYAMA et al. 2001). However, body length, shoulder height and hind-foot length are parameters that are strictly related with the age of the animal even if the total body mass changes during different seasons and food availability (SU-

ZUKI et al. 2001, YOKOYAMA et al. 2001). A recent study on body mass of fossil North American bison demonstrates an inverse correlation between increasing global temperatures and body size over the last 40000 years, which is probably the result of persistent effects on the growth of the animal (MARTIN et al. 2018) and its seasonal mass gain (MARTIN & BARBOZA 2019). LEWIS et al. (2007) suggest that the spread of C4 grasses between 8000 to 7500 BP explains both the size reduction and the gracilization of the late Quaternary North American bison.

Some authors remarked different trends of aurochs through time in several areas (PANDOLFI et al. 2011, 2013, WRIGHT & VINER-DANIELS 2015, SAARINEN et al. 2016) but considering different set of data. SAARINEN et al. (2016) analyzed British and German Pleistocene ungulates and reported relatively small size for early Holocene aurochs population of Star Carr compared to those from the Pleistocene. However, they did not find connection between aurochs' body size and florae whereas fossil European *Bison* displayed on average smaller mean size in more open ecosystems. WRIGHT & VINER-DANIELS (2015) considered *Bos primigenius* samples from several localities across Europe and recorded some differences among the considered localities and time spans. Nevertheless, they did not include the large amount of data from Pleistocene and Holocene localities reported in some published papers (e.g., PANDOLFI et al. 2011, 2013 and references therein) which suggested a more complex framework at regional scale. On the contrary, the Greek aurochs populations are relatively constant in size during the Middle Pleistocene, reaching a large size only during the end of the Pleistocene. PANDOLFI et al. (2011) considered the Holocene Italian populations as belonging to a single sample, thus it is not possible to investigate if there are fluctuations during that time span as instead recorded in the present work. WRIGHT & VINER-DANIELS (2015) did not include populations from Greece and they did not include Late Pleistocene samples (WRIGHT & VINER-DANIELS 2015: table 1). Therefore, it is not possible to verify if they recognized an increase in size during that time span. Nevertheless, the authors suggested a North to South cline, with populations from southern Europe (Italy and Spain) smaller than central and northern European populations, at least during the Middle Pleistocene and early Holocene.

The early Holocene sample is difficult to compare with that from WRIGHT & VINER-DANIELS (2015), in particular due to the different methods of sampling. In the present study, only localities with the same or very similar chronology were grouped

together in order to avoid the loss of punctual variations through time and space. The comparison of the measurements (in particular those from astragali) from some early Holocene Greek localities with the data reported by WRIGHT & VINER-DANIELS (2015) reveals that some specimens (e.g. Lerna; see Table S6) are included within the variability of southern European populations.

The data on Greek aurochs reveal different trends in body-size variation in respect to those recorded from Italy, with populations from the latest Pleistocene statistically larger than the Middle and Late Pleistocene ones. The population from Kataphyto, dated at 24,047-23,380 calBP (which is close to the peak of the Heinrich-event 1) is not as large in size as that from Agios Georgios. The variations here identified depict a much more complex framework than that reported till now in the literature.

The variations are not statistically significant during the middle and late Holocene suggesting a homogeneity in aurochs size. This effect could be related with domestication which would be responsible for an increase in variation of body size (WRIGHT & VINER-DANIELS 2015). This is particularly clear in Fig. 6 which shows the mean values for every considered anatomical element of each population and the 95 % interval of confidence for each group. The Holocene sample (groups 1-5) does not display a statistical difference, as revealed by test in Table 3. Body size fluctuations in aurochs during the Pleistocene can be affected by several regional factors and population dynamics (as recorded for red deer and wolf; PANDOLFI et al. 2015, SANSALONE et al. 2015). Further investigation is required and the data here provided might be useful in order to investigate body size variations of auroch populations in other areas of Europe. This will allow punctual time-calibrated comparisons in order to verify regional variations in time and space at different scales of observation.

## Conclusions

Kataphyto aurochs assemblage from the northernmost part of Greece, represents one of the few records of *Bos primigenius* Bojanus, 1827, is revised here. The 155 specimens from Kataphyto date to 24,047-23,380 calBP and provide information on its dispersal in Greece. Kataphyto individuals are similar in size with those recorded in Middle Pleistocene (Petralona), Late Pleistocene (Peneios, Larissa), and later Holocene faunal assemblages from Greece (similarities statistically supported; Table 3). In addition, the statistical analysis of the measurements

of aurochs from Kataphyto and many other Greek Pleistocene-Holocene sites show that the Greek aurochs have a different trend in body-size variation overtime in respect to those recorded for the same period in Italy. In Greece, populations from the end of the Late Pleistocene are statistically significantly larger than those of the Middle and Late Pleistocene. In the light of this research, further studies should be planned in order to better detect the change in body-size through time of this species and to understand the factors that have led to its body-size variation considering regionally environmental and anthropogenic factors.

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**Supplementary material:** <http://www.acta-zoologica-bulgaria.eu/2022/002552-suppl>

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