Insular aurochs (Mammalia, Bovidae) from the Pleistocene of Kythera Island, Greece

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ABSTRACT

Islands are renowned for their remarkable biotas and have been widely recognised as natural laboratories for the study of evolution, speciation, and extinction. Large mammals in insular environments typically evolve to dwarfs and small ones to giants, a trend known as the island rule. Despite their dominance in the continental European mammal faunas of Middle-Late Pleistocene, *Bison* and *Bos* are usually lacking from the neighbouring endemic insular assemblages. Here, we report the first insular bovin from the Late Pleistocene of Kythera Island, Greece and we carry out a detailed morphometrical analysis with emphasis on its adaptations and palaeogeographic implications. Based on both dental and postcranial qualitative and quantitative comparisons, we attribute the studied material from Kythera to *Bos primigenius*. Significant differences from both its continental Pleistocene relative and the endemic bovins from Mediterranean islands, allow us to recognize it as a new subspecies, *Bos primigenius thrinacius* n. ssp., the third known insular dwarf of this taxon in Europe. Our main hypothesis is that the gradual disconnection of Kythera Island from the neighbouring Peloponnese peninsula just after MIS 6 (late Middle Pleistocene, ~180 ka) resulted in the isolation of a mainland *Bos primigenius* population in the rocky and predator free environment of palaeo-Kythera Island. Under these particular conditions the population underwent some remarkable changes and gained some peculiar features, especially on metapodials. The timing and reasons of *Bos primigenius thrinacius* extinction remain unknown.

KEY WORDS

Bovinae, Pleistocene, Island Evolution, Dwarfism, Body Size, Europe, Quaternary

1. Introduction

1.1. European Pleistocene Bovinae

From the Early Pleistocene onwards, bovins (subfamily Bovinae; tribe Bovini) and caprins (subfamily Antilopinae; tribe Caprini) gradually become the dominant artiodactyls in the European continental mammal faunas. Both groups' diversity decreases during the Pleistocene due to environmental and anthropogenic factors but bovin assemblage was further simplified during the late Middle to Late Pleistocene, monopolised by the species *Bison priscus* Bojanus, 1827 and *Bos primigenius* Bojanus, 1827.

A significant number of *Bison* remains has been discovered over the past century from many Eurasian Quaternary sites, expanding significantly the spatial and temporal distribution of this genus (Tong et al., 2017; Maniakas and Kostopoulos, 2017; Kostopoulos et al., 2018; Sorbelli et al., 2021, 2023 and references therein). The well-known steppe bison, *Bison priscus*, first appeared in eastern Eurasia by the mid-Middle Pleistocene (Schertz, 1936; Sala, 1986; Sher, 1997; Kahlke, 1999 and references therein). The taxon quickly expanded across the whole Holarctic, invading North America through Beringia, where it gave rise to the American bison lineages, as demonstrated by both molecular and fossil evidence (Shapiro et al., 2004; Froese et al., 2017; Sorbelli et al., 2023). *Bison priscus* was a massive species displayed large head with long horns and stout limbs, but overall, extremely polymorphic across its geographic and chronostratigraphic range (Kahlke, 1999; Maniakas and Kostopoulos, 2017; Sorbelli et al., 2023).

The hypothesis of an Asian ancestry indicates *Bos acutifrons* Lydekker, 1878 from the Early Pleistocene of Siwalik Hills, northern India as the possible forerunner of *Bos primigenius* (Pilgrim, 1947; Groves, 1981). An alternative hypothesis suggests that

Middle Pleistocene *Bos* probably evolved in Africa from the Late Pliocene - Early Pleistocene large sized Olduvai 'buffalo' *Pelorovis* Reck, 1928 (Martínez-Navarro et al., 2007; Martínez-Navarro and Rabinovich, 2011). In Europe, the oldest evidence of *Bos primigenius* comes from the sites of Venosa-Notarchirico, and GRA Km 2 (Rome), Italy, dated at 0.5–0.6 Ma (Caloi and Palombo, 1979; Cassoli et al., 1999; Martínez-Navarro et al., 2010; Pandolfi et al., 2011; Masini et al., 2013). *Bos primigenius*, the auroch, is characterised by a highly derived cranial anatomy, large size and a robust postcranial skeleton (Martínez-Navarro et al., 2007), and it is generally accepted as the extinct ancestor of modern domesticated cattle (Poplin, 1983; Chaix, 1994; Clutton-Brock, 1999). Aurochs has been shown to have a flexible feeding strategy within a range of generally open, flat, low-altitude areas from swamps and swamp forests along river valleys to grasslands and steppe-like environments (Clutton-Brock, 1999; Van Vuure, 2005; Schulz and Kaiser, 2007; Hall, 2008; Bocherens et al., 2015; Rivals and Lister, 2016).

Despite their dominance in the continental Middle-Late Pleistocene European mammal faunas, *Bos* and *Bison* are strikingly lacking from neighbouring endemic insular assemblages as opposed to other herbivore large mammals, such as proboscideans and deer (Van der Geer et al., 2010) or other places of the world, where insular bovins are quite common (e.g., the Indonesian buffaloes). The only insular European bovins known so far have been reported from the Late Pleistocene deposits of Sicily, i.e., *Bos primigenius siciliae* Pohlig, 1911 and *Bison priscus siciliae* Pohlig, 1911 (Brugal, 1987; Bonfiglio et al., 2008; Masini et al., 2008), and have been also claimed for Malta (*Bos* sp., likely *Bos primigenius*; Hunt and Schembri, 1999) and Pianosa (*Bos primigenius bubaloides* De Stefano, 1913) (Van der Geer et al., 2010 and references therein; Rozzi and Palombo, 2014).

Both *Bison priscus* and *Bos primigenius* are well known from numerous Greek mainland fossil sites, but again never described from an insular context (Kostopoulos, 2006, 2022 and references therein), in contrast to other large mammals. Here, we report the first insular bovin from the Late Pleistocene of Kythera Island, Greece and we discuss in detail its morphometrical adaptations in comparison with other continental and insular relatives of Europe, as well as its palaeogeographic implications.

1.2. Geography, Geology, and Palaeontology of Kythera Island

The island of Kythera is located in the southern part of Greece between Crete Island and the Peloponnese peninsula (Fig. 1a,b). It is separated from the latter by an 8.5 km wide and 200 m deep sea strait. The island has an area of approximately 280 km^2 with a coastline length of 52 km and it is characterised as rocky plateau with an east and a west sierras and steep coasts due to faults (Fig. 1c).

The pre-Alpine metamorphic crystalline basement of Kythera is composed of barely exposed marbles (Mani Unit), as well as plyllites and quarzites that dominate the northern part of the island (Arna Unit). The Jurassic-Eocene limestones, dolomites and flysch of Tripolis geotectonic Zone overthrust this basement, whereas Cretaceous-Early Cenozoic limestones and flysch of the Olonos-Pindos Zone overthrust both previous units (Manolessos, 1955; Theodoropoulos, 1973; Meulenkamp et al., 1977; Papanikolaou and Danamos, 1991 and references therein). Post-Alpine sedimentation starts at Tortonian (Late Miocene) and Neogene-Quaternary deposits, crop out mainly in the central-eastern and southern part of the island, unconformably overlie the Hellenic nappes (Meulenkamp et al., 1977; Papanikolaou and Danamos, 1991). Neogene sediments are primarily marine with intercalations of fluvial and lacustrine deposits. A shark tooth, a lower rhinocerotid jaw and parts of cetacean skeletons are reported from the Upper Neogene deposits of Kythera (Theodoropoulos 1973; Bartsiokas, 1998).

Quaternary sediments are largely terrestrial and scattered around the island; they often represent by-products of the extensive karstic process recorded (Gaki-Papanastassiou et al., 2011; Lazaridis, 2011). Karstic landforms (caves, fissures etc.) are particularly common, especially along the shoreline. The numerous caves of variable origin are open mainly in the limestones of Tripolis Zone (west and southern part of the island), but also in the carbonates of Olonos - Pindos Zone, and a few though, in the Neogene formations (Lazaridis, 2011; Trantalidou et al., 2019).

Major glacial and interglacial stages during the Middle and Late Pleistocene created great differences between the lowest and highest sea level stands in the Aegean region in respect to the present-day state (Lykousis, 2009 and references therein). The intense Quaternary eustatic events along with the extensive fault tectonism and the variable local lithology (limestones, marls, conglomerates) have mostly controlled the coastal and fluvial evolution of the island of Kythera (Fig. 1d) and its palaeogeographic history (Theodoropoulos, 1973; Meulenkamp et al., 1977; Papanikolaou and Danamos, 1991; Lykousis, 2009; Gaki-Papanastassiou et al., 2011; Sakellariou and Galanidou, 2017).

Although known for two centuries, the Pleistocene vertebrate fossils of Kythera Island are rather scattered and little studied. According to Sen (2017) the Italian naturalist L. Spallanzani was the first to mention fossil bones from the so called '"montagna delle ossa'" in the southern part of Kythera. Spallanzani (1786) reported among the collected fossils human and animal remains but, unfortunately, he did not provide further details of his finds (Sen, 2017).

Travelers, naturalists, archaeologists, and geologists of the 19th century who passed through the island (summarised in Bartsiokas, 1998), briefly refer to fossil findings from various sites of Kythera but without properly describing them. Pleistocene fossil remains, mostly mammals, are usually found into highly consolidate calcified clayey or brecciated fissure fillings, making them vulnerable to damage and difficult to recover (Athanassiou et al., 2019; Bartsiokas per. obs.). Petrochilos (1938) and Manolessos (1955) mentioned, and Kuss (1967, 1973) studied deer and elephant fossil remains from the island, the latter recently overviewed by Sen (2017) and Athanassiou et al. (2019).

FIGURE 1 (around here)

2. Materials and Methods

The material under study comes from the north-west coast of Kythera Island, west of Logothetianika village, and south of Lykodimou Beach. There, on the north side of a small promontory called Trachelas, is a small cave we named Mikelis 1 (MKL; Fig. 1), whereas on the south side, at a place called “Kakos Potamos”, another cave that we named Mikelis 2 occurs. The names come from I. Mikelis who was the first to record Mikelis 1 in a manuscript dated on September 5th, 1824, and first published in a series of articles in a local newspaper (Mikelis, 1898-1899). Although Mikelis 2 is very poor in fossil remains, which are, additionally, heavily brecciated, Mikelis 1 provided a significant fossil assemblage.

Mikelis 1 cave is opened on thin-bedded limestones of Tripolis Zone and its present-day mouth is about 7 m above the current sea level on a steep seaside slope (Fig. 1d, e), hence subject to winter seawater erosion. A couple of meters after the entrance, the cave is divided into two uneven sub-chambers less than eight meters in length each, and tapering in height and width at their ends. A detailed geological-speleological study is pending. The fossil material from Mikelis 1 was intermittently collected from the surface layer of the cave (Fig. 1f) between 1976 and 1998 by Professor Emeritus A. Bartsiokas at the request of the Society of Kytherian Studies (Bartsiokas, 1998). The collection was donated by A.B. to the Museum of Geology-Palaeontology-Palaeoanthropology of the Aristotle University of Thessaloniki (LGPUT) in 2020 for study and curation, where it is currently housed.

Field observations by A.B. and an exhaustive lab examination of the collection at LGPUT revealed neither human skeletal remains, nor any artefacts, nor any traces of charcoal, nor any evidence of bone surface modifications on animal bones that might be explicitly attributed to human presence. Instead, the fossil collection shows that it represents a rather eclectic assemblage including skeletal elements (craniodental and postcranials) almost exclusively of a single bovid taxon (98.5%); a few additional specimens (n<10) belong to a large-sized cervid, and three postcranial remains to a tortoise, attributed by Vlachos (2015) to *Testudo marginata*. In total, 723 identifiable bovid specimens are registered so far; 136 represent craniodental and 587 postcranial elements (Table A.1). All studied specimens are catalogued using the prefix “MKL” and then a serial number. Two attempts with radiocarbon dating of bone and dental samples were failed as laboratory processes could not yield a separable collagen fraction, likely due to hydrolysis by seawater.

Petrous bone description and discriminant features are based on Guadelli (1999) and Galindo-Pellicena et al. (2019). The dental terminology is according to Gentry (1992), Bärmann and Rössner (2011) and Cherin et al. (2019). Postcranial descriptions follow Sala (1986), Masini, (1989), and Sher (1997).

A comparative morphological study of both dental and postcranial features focuses on similarities/dissimilarities with *Bos* and *Bison*. A morphometric distinction between these genera and their Middle-Late Pleistocene representatives is not always straightforward and largely discussed on the literature. Dental discrimination is based mostly on features recorded by Sala (1986) and Slott-Moller (1990), whereas postcranials are examined through 65 discriminant characters selected from an expanded literature (Bibikova, 1958; Olsen, 1960; Stampfli, 1963; Brugal, 1983; Sala, 1986; Martin, 1987; McCuaig-Blackwill and Cumbaa, 1992; Gee, 1993) (Table A.2). Measurements were taken with a digital calliper to the nearest 0.1 mm. Dental measurement include: Length (L) and Width (W) of the occlusal surface, and maximum Height (H) if available; we preferred occlusal than basal crown measurements of both L and W as better embracing the maximum size range due to ontogenetic age in our sample. The Relative Hypsodonty index is calculated as the height of the crown at the paracone (for the upper unworn molars) or the metaconid (for the lower unworn molars) divided by the occlusal length of the tooth (Fortelius et al., 2002). Postcranial measurements follow von den Driesch (1976) as modified by Sorbelli et al. (2021: fig. 2), but for the metapodials, we preferred to follow Scott (2004) and Scott and Barr (2014) as applied by Maniakas and Kostopoulos (2017: fig. 2). When the transition from the diaphysis to the distal epiphysis (i.e., on the distal metaphysis) of the metapodials is abrupt (i.e., forming distinct 'shoulders' in anterior or posterior view; 'claret bottle' shaped according to Gee, 1993) is described as "kinked"; otherwise as smooth ('burgundy bottle' shaped according to Gee, 1993). Measurement abbreviations are explained in Table B.1; dental and postcranial measurements are provided in Tables B.4–B.24. Body mass estimations are provided from a set of equations available in the literature and applied to different postcranial and dental elements (Table B.2).

Although *Bos* and *Bison* show important differences in their cranial and postcranial anatomy, their hybridization is possible (Polziehn et al., 1995). Thus, their relationships are debatable and taxonomic decisions on genus level depend largely on the type of evidence applied (e.g., Brugal, 1985; Moyà-Solà, 1987; Hassanin et al., 2013; Massilani et al., 2016). Here we follow the traditional morphological concept of two distinct genera (e.g., Kostopoulos et al., 2018; Sorbelli et al., 2021, 2023).

Comparative data considering the endemic bovins *Bison priscus siciliae and Bos primigenius siciliae*, currently housed in Museum of Geology "G. G. Gemmellaro" (Sicily, Italy) were obtained by RZ (for details on Sicilian sites and their finds see Burgio et al., 1983; Brugal, 1987; Bonfiglio et al., 2001, 2008; Ferretti, 2008). *Bos* data from the Italian locality Avetrana and other Italian sites are provided by Dr. L. Pandolfi. Other comparative data from Greece and European Pleistocene sites were taken from: Sala (1986), Brugal (1985, 1987), Prat et al. (2003), Vercoutère and Guérin (2010), Pandolfi et al. (2011), Wright (2013), Maniakas and Kostopoulos (2017), Uzunidis-Boutillier (2017), Maniakas (2019) and Samartzidou et al. (2021). Table A.3 summarizes data of comparative samples of Pleistocene mainland and insular populations of *Bos* and *Bison* used in this study. Bivariate plots of length (L) against width (W) of upper and lower premolars and molars in several *Bos* and *Bison* species were carried out. To assess the stoutness of metapodials, bivariate plots of MLEN against IDML/MLEN % (maximum length against distal robusticity index; see Table B.1 for abbreviations) are employed. Because short metapodials are not necessarily stout and vice versa, we also calculate the response variable associated with 'low gear' locomotion following Rozzi et al. (2020), i.e., the average shortening index (SI) for metacarpals (SI Mc;

length of metacarpal/length of radius) and metatarsals (SI Mt; length of metatarsal/length of tibia).

Principal component analyses (PCAs) were performed based on various log-transformed variables of the postcranial bones, to explore the main metric differences among different populations of *Bos* and *Bison* species and the Kytherian bovin. To investigate respective shape similarities/ dissimilarities an extra analytic approach has been followed based on shape-transformed variables calculated after Scott and Barr (2014): each measurement is adjusted as the log-transformed ratio between the linear measurement and Scott's (2004) metapodial global size variable (MGSV) (Table B.3).

In order to investigate body size change in the Kytherian bovin and discuss it in light of the island rule, we estimated the insular body size divergence index (Si) sensu Lomolino (1985, 2005). Si is calculated as the mean mass of individuals from an insular population divided by the body mass of individuals of the mainland or ancestral form (M). Values of Si < 1.0 indicate evolution towards dwarfism, while values > 1.0 indicate evolution towards gigantism. *Bos primigenius* from Petralona Cave, Greece is used here as the mainland putative relative.

Both *Bos* and *Bison* are well-known as sexually dimorphic (e.g., Brugal, 1985; Sala, 1986; Sher, 1997; Brugal and Fosse, 2005; Kostopoulos et al., 2018; Sorbelli et al., 2021). Here, we investigate sexual bimodality in the most informative and rather well-represented in our sample adult metacarpal bones following methodology and suggestions by Lewis et al. (2005 and references therein): adult metacarpals (n=9) are recognised as males (n=5) or females (n=4) based on the results of a PCA analysis on the four most discriminative parameters, i.e., PAP, PML, MML, and IDML (see Table B.1 for abbreviations). Then the average of each metrical parameter plus MLEN (total length) per subgroup (male/female) is calculated and the % difference between the obtained values is provided as an estimation of the sex difference in the population in comparison with data by Brugal (1985) and Maniakas (2019). All the statistical analyses and plots were performed on PAST 4.03 software (Hammer et al., 2001). The main text includes descriptions and comparison of cranio-dentognathic material, metapodials, and astragali only; additional descriptions and comparisons are provided in Appendix C. Juvenile specimens are not included in the metric analyses.

3. Systematic Palaeontology

Order Artiodactyla Owen, 1841 Owen, 1841

Family Bovidae Gray, 1821 Gray, 1821

Subfamily Bovinae Gray, 1821 Gray, 1821

Genus *Bos* Linnaeus, 1758 Linnaeus, 1758

Bos primigenius Bojanus,1827 Bojanus, 1827

Bos primigenius thrinacius n. ssp.

(Figs. 2-5)

Holotype: left mandibular ramus with p3-m3, MKL571

Paratypes: right mandibular ramus with m1-m3 and alveoli of p2-p4, MKL585; right male metacarpal, MKL142; left male metatarsal, MKL54.

Referred material studied: 136 craniodental and 587 postcranial specimens (Table A.1).

Origin of the name: from Thrinacia (or Thrinakia, Θρινακία, "Θρινακίην", meaning three edges), the island where the god Sun (Helios) kept his cows in Odyssey [Book 12), [126-127]: "… And thou wilt come to the isle Thrinacia. There in great numbers feed the cows of Helios and his goodly flocks, seven herds of cows and as many fair flocks of sheep ... [260-265] ... we came to the goodly island of the god, where were the fair cows, broad of brow, and the many goodly flocks of Helios Hyperion. Then while I was still out at sea in my black ship, I heard the lowing of the cattle that were being stalled and the bleating of the sheep ...". Kythera island has been suggested as the ancient Thrinacia by Bartsiokas (2009).

Type Locality: MKL cavity, NW Kythera Island, Greece

Age: Late Pleistocene (MIS 6 – ?MIS 2)

Diagnosis: A dwarf insular subspecies of *Bos primigenius* characterised by: (I) small size (average Body Mass= 380 kg); (II) decreased sexual bimodality; (III) the presence of a strong incisure on the caudal crest of petrous bone at the orifice of the cochlear canal; (IV) derived hypsodonty (Hypsodonty index ≥1.7); (V) tendency to lose p2; (VI) short metapodials with expanded proximal and "kinked" (*Bison*-like) distal metaphysis.

3.1. Descriptions

3.1.1. Cranial remains

Unfortunately, very few and fragmented parts of the cranium are preserved. MKL580 is a left part of the frontal of a calf bearing the horncore (I-S stage of Skinner and Kaisen, 1947). The incipient horncore (anteroposterior basal diameter: 23.3 mm; dorsoventral diameter: 16.2 mm; length ~30 mm) is inserted well behind the orbit, its dorsal surface lays almost on the same level with the frontals and with a clear posterolateral direction.

FIGURE 2 (around here)

Specimens MKL691, and MKL689 represent the exoccipital-basioccipital and basisphenoid respectively, whereas MKL690, and MKL688 are sphenoids; most likely specimens represent part of at least two crania of different ontogenetic age. The bicondylar width is 83.6 mm and the width of the basioccipital at the posterior tuberosities is about 48 mm. The state of preservation does not allow the recognition of important morphological features.

Eleven petrous bones are preserved (7 left, 3 right and one that cannot be referred to either side). On the rostral face the Fallopian hiatus opens directly downwards (Fig. 2), and it is not associated by a groove. On the medial face, the trigeminal nerve impression is slightly concave (Fig. 2); the petrosal crest is weak; the internal acoustic meatus is oval shaped (length/width ration ~1.5); the cerebellar fossa is well-shaped, round and deep (Fig. 2); the anteroinferior apex is weak, crenulated; and the caudal crest presents a strong incisure at the orifice of the cochlear canal (Fig. 2).

3.1.2. Dentognathic remains

The studied specimens include a large number of isolated teeth and a few fragmentary mandibles and maxillae (Table A.1).

Twelve isolated upper deciduous teeth are preserved. All have the typical Bovini morphology (e.g., Sala, 1986). In addition, the DP2 have a much more developed parastyle and protocone compared to the distal part of the tooth. The mesial lobe of DP3 is wider than the distal one and square shaped. The DP4 have a strong and thick parastyle, well developed entostyle, and thin meso- and metastyles.

Four isolated P4 are preserved. In mesial view, the lingual and labial edges are subparallel and not converging towards the base. The parastyle is well developed; the paracone pillar is acute and placed close to the metastyle; the paracone is stronger and protrudes more labially than the para- and metastyle; the metastyle is inclined mesially and lingually. In occlusal view, the central fossette has weak spurs (when present) and tend to have a reverse Greek “Π” -shape. The right P4 MKL681 in moderate wear stage shows a small semicircular isolated column in the mesio-lingual corner. The worn P4 MKL687 has a quite odd structure with greater mesial than distal wear due to taphonomic agents (under study).

Nine isolated M1 are preserved; all but one representing individuals in full maturity. Eleven isolated M2 are also preserved; six are in a moderate to advanced wear stage, three in initial stage, and two are unworn. Two maxillaries with only M2 (MKL674 and MKL675) represent elderly individuals, and the surface is almost flat due to the advanced wear. Two more maxillae with M1 and M2 are also preserved; in MKL721 the M1 is just rising and the M2 is still within the alveolus. Six isolated M3 in a moderate to advanced wear stage, suggest they all belong to adult individuals.

All the upper molars (Fig. 3a-c) have a columnar appearance and are quite hypsodont. Hypsodonty index is estimated at 1.94 based on the M2 MKL625. Cement cover is generally thin restricted to the lower two third of the crown and in several cases stronger along the entostyle. The entostyle is strong and mainly attached on the hypocone; the paracone and the metacone are well-developed; the parastyle, mesostyle and metastyle are also pronounced. In M1, the mesostyle is less strong than the para- and metastyle. In M2, all styles are more or less equally developed. In M3 (Fig. 3c), the metastyle is stronger and thicker than the other two styles. In occlusal view, the protocone is strong, but shorter and more lingually shifted compared to the hypocone. A weak constriction appears on the protocone indicative of tightening. The shape of the protocone and hypocone pillars is straight, and columnar without thickening at the cervix. The fossettes have a rectangular reverse Greek "Π" shape with a complicated folding. The cavities become more crescent-shaped with wear. The right M3 MKL601 and the left M3 MKL605 probably of the same individual, both are more worn anteriorly than posteriorly, a feature of taphonomic interest but beyond the scope of this study. An enamel fold on the disto-lingual corner of the posterior fossette of the molars (i.e., hypoconal spur) occurs. The hypoconal spur appears in 5 out of 9 M1 (55.5%), in 6 out of 11 M2 (54.5%) and in 6 out of 6 M3 (100%). A central islet is present in various stages of wear; it is present in 6 out of 9 M1 (66.6%), in 4 out of 11 M2 (36.4%) and in 6 out of 6 M3 (100%).

FIGURE 3 (around here)

Two mandibles with dp3-dp4 (MKL708 and MKL710), two with dp3-m1 (MKL588 and MKL722) and an isolated worn dp4 (MKL626) are preserved. The dp3 has a much thicker paraconid than parastylid, directed perpendicular to the mesiodistal axis of the tooth; the metaconid is long and directs distolingually. The dp4 bears a thin but distinct entostylid and two strong labial stylids between the second and the third lobe, respectively.

No complete adult mandible or hemimandible is preserved. Combining features from the best-preserved specimens it appears that the anterior edge of the ascending ramus steeps abruptly compared to the alveolar level (Fig. 4b); the horizontal ramus is deep below m2-m3 and narrows quickly rostrally forming a characteristically raising ventral edge (Fig. 4b,c,d); the angle of the mandible is smoothly convex with slightly concave posterior edge of the ascending ramus and a strong wide demarcation at the ventral junction with the horizontal ramus marked rostrally by an acme (Fig. 4b); the mandibular tuberosity is strong prolonged posteroventrally by a crest; the neck to the mandibular condyle is short and not projecting caudally; the coronoid process is rather strong (Fig. 4b). Only five mandibles preserve part of full permanent toothrow. Apart from m1-m3, the mandible MKL585 has the alveoli for p3-p4, a diastema and then the alveolus for p2 (Fig. 4b). Similarly, the partial mandible MKL671 with one left p3, shows a diastema before the alveolus for p2. In contrast, MKL586 possesses the alveoli for p3-m1, but not for p2 (Fig. 4c). On MKL571 with m3-p3, the p2 seems also to be missing naturally, but between m1 and p4 appears a diastema with a narrow alveolus, possibly suggesting an individual abnormality (Fig. 4d). The length p3-m3 ranges from 133.8 mm (m3 just erupted) to 130.0 mm (m3 worn), whereas the length m1-m3 ranges from 85 mm to 90 mm (n=3).

FIGURE 4 (around here)

Four isolated p3 are available, all representing individuals in full maturity or senile. The overall shape of p3 is quite narrow; the parastylid and the paraconid are fused from the very initial wear stages, forming a strong and thick mesial stylid that is lingually shifted. The first valley (between paraconid-parastylid) is open only in unworn teeth. In occlusal view, the metaconid, is well developed, narrow and directs distolingually. The second valley, between the paraconid and the metaconid, is largely open but closes well above the base of the crown. The third valley, between the metaconid and the entoconid, is narrower than the second one, but still quite open. The entostylid and the entoconid are fused quickly each other, forming a strong distal stylid, and the posterior (fourth) valley does not exist in worn teeth. The parastylid is more developed than the entostylid; the hypoconid and the protoconid are separated by a shallow labial groove and the hypoconid is narrow and directs distobucally. In worn teeth, there is a distal fossette formed from the fusion of the metaconid with the distal stylid (entostylid + entoconid).

Five isolated p4 are available; four are in initial to moderate stage of wear and one in advanced, representing a senile individual. The p4 (Fig. 3d) is morphologically similar to the p3, but larger; the metaconid is stronger than in p3 and in occlusal view projects distolingually forming a Greek “Γ” shape, which with wear becomes more curved. The second valley is narrower and deeper than in p3, while the hypoconid is much more developed in p4 than in p3. A distal fossette is formed in moderate wear stage but tends to close later in wear. A left isolated p4 (MKL677), which is in initial stage of wear, shows a thin parastylid, weakly distinguished from the paraconid.

From the 18 preserved isolated lower molars eight are m1, five m2 and five m3. From the eight m1, three are in initial wear stage, three in moderate and two in advanced wear stage. From the five m2 three are in moderate to advanced wear stage and two are unworn, while from the five m3, three are in a moderate wear stage and two unworn.

The lower molars (Fig. 3e-g) are fairly hypsodont; the hypsodonty index is estimated at 1.78 and 1.86 based on the m2 specimens MKL636 and MKL678, respectively and at 1.73 for a single m3 (MKL660). The m1 and m2 have a columnar appearance, rather than compressed mesio-distally. Cement cover is moderately developed in the lower half of the crown, more on m3 than on m1-2 and increases with age. The parastylid is strongly projecting; the endostylid is well developed, but less than the parastylid; the metastylid is weak and appears only in unworn teeth; the ectostylid is strong, high, attached to the mesial lobe and it is much stronger in m3 than in the rest of the molars. The metaconid and the endoconid pillars are well developed, project more than the stylids and they are separated by a wide "U" shaped valley. The protoconid and the hypoconid are straight, and columnar. On the m1 and m2 (Fig. 3e-f) the hypoconid is much narrower than the protoconid, with signs of a labial constriction. In occlusal view, the shape of the fossettes is simple without spurs, and the cavities become more crescent-shaped with wear. The third lobe of m3 (Fig. 3g) is forming a continuity in the lingual side of the tooth and a largely open angle with the labial side of the first two lobes. The labial re-entrant valley between the hypoconid and the hypoconulid is rounded, rather than angular. In mesial view, the third lobe widens from the crown towards the collar and in occlusal view, the third lobe is semi-circular shaped with a strong distal stylid. An additional labial stylid between the second and the third lobe is absent. The unworn m3 MKL660 and the moderate worn MKL650, both appear with a second, less strong stylid, in the distolingual side of the hypoconulid. The third lobe of the m3 on the mandibles MKL586 and MKL719 both have a central circular fossette, but it seems to close quickly with wear.

3.1.3. Metapodials

A total number of 19 metacarpals III+IV are preserved representing at least nine individuals. Seven of them are almost complete (Fig. 5a-g), six of them have damages mainly in the distal part of the bone and four preserve only the diaphysis.

In proximal view, the articular surface displays a D-shaped outline (Fig. C.1c). The lateral facet for *os hamatum* (carpal IV) is triangular with rounded corners and located on a lower plane than the medial articular facet for the capitotrapezoid (carpal V), being separated from it by a high crest oriented anteroposteriorly. The capitotrapezoid facet is larger and quadrangular shaped with straight anterior internal edge. The depression medial to the posteromedian tubercle is well defined and variably sized. The articulation for the fifth metacarpal is well pronounced, while the median tubercle is completely fused to the main bone. In anterior view, the proximal and distal epiphyses have almost the same width, and the distal part of the bone displays a “kinked” transition from the diaphysis to the distal epiphysis (i.e, on the distal metaphysis). The vascular groove on the distal portion of the diaphysis is variable, from narrow and shallow to wide and deep.

From a total of 21 preserved metatarsals III+IV over the half are lacking the distal epiphysis and most of them are damaged. Only two specimens are complete (MKL35 and MKL54), both belong to adult individuals (Fig. 5h-j). As for the metacarpals, the distal part of the metatarsals shows a similarly “kinked” distal metaphysis. The anterior side of the bone is characterised by the well-marked and deep vascular groove. On the proximal surface of the metatarsal (Fig. C.1h), the medial articular facet for the large cuneiform (tarsal II+III) is posteriorly concave; the lateral facet for the naviculo-cuboid (tarsal IV) is higher and relatively flat. A narrow sharp ridge separates these articular facets, but they tend to form a gap between them. The large proximal foramen is located inside a deep synovial fossa, distal to the posterior margin of the proximal epiphysis. The proximal articular surface of the small cuneiform (tarsal I) and the posterior surface for the naviculo-cuboid are clearly separated. A small tubercle is visible on the posteromedial corner of the facet for the large cuneiform.

FIGURE 5 (around here)

3.2. Morphological comparison

The general morphological characters of both dental and postcranial (see also Appendix C) remains from Kythera are typical of Bovini and consistent with those of both *Bison* and *Bos* from the European Pleistocene. The petrous bone morphology as described above matches better *Bos* than *Bison* in the absence of groove associated with Fallopian hiatus, which opens directly downwards, the slightly concave trigeminal nerve impression, the low length to width ratio of internal acoustic meatus, and the weak anteroinferior apex (Guadelli, 1999; Galindo-Pellicena et al., 2019). The strong incisure on the caudal crest differentiates the Kytherian taxon from both continental *Bos primigenius* and *Bison priscus*.

The upper premolars of MKL sample have subparallel lingual and labial edges as in *Bos* and not converge towards the base as in *Bison* (Slott-Moller, 1990). The MKL upper molars have a more columnar and hypsodont appearance, rather than a distinctly swollen just above the cervix, as often in *Bison* (Sala, 1986). Moreover, they have a strong entostyle on the lingual face between the protocone and the hypocone, mainly attached to the hypocone, a character reported as typical for the genus *Bos* (Sala, 1986). The fossettes have a rectangular reverse Greek “Π” shape with a complicated folding as in *Bos* species, rather than a more rounded, “U” shape with simpler enamel folds as in *Bison* (Rütimeyer, 1861; Sala, 1986). The presence of the hypoconal spur in the MKL upper molars is a feature considered typical of the species of the genus *Bos*, but less marked than in *Pelorovis* (Martínez-Navarro et al., 2007). The presence of an enamel islet on the upper molars between the protocone and the hypocone is a character more frequently observed on *Bos* (Brugal, 1987); the MKL sample displays this character in almost all teeth in a medium to advanced wear stage.

As opposed to *Bison*, the shape of the mandible from Kythera is certainly more *Bos*-like in the degree of development and caudal projection of the mandibular angle, the strong demarcation of the ventral edge between the ascending and horizontal rami, the more vertical ascending ramus, and the stronger shallowing of the horizontal ramus towards the rostrum that makes the pre-cheek teeth part of the jaw appear raising. Regarding the lower dentition, MKL molars have a greatly hypsodont appearance, a character that according to Slott-Moller (1990) seems to be one of the most reliable and most constant for both upper and lower teeth of *Bos*. The overall morphology of the m3 shows that the third lobe widens from the crown towards the collar as in *Bos*, whereas in *Bison* its width is almost constant or narrows towards the collar. The ectostylid is strong, high, attached to the mesial lobe and it is much stronger in m3 than in the rest of the molars, as often in *Bos* (Sala, 1986; Slott-Moller, 1990). The protoconid and the hypoconid are straight, and columnar as in *Bos* species (Moullé, 1992). Moreover, the third lobe of m3 seems to be in line with the longitudinal axis of the tooth, a feature that is more common in the genus *Bos* than in *Bison* (Brugal, 1995). The MKL m3 displays a largely open angle with the labial side of the first two lobes, while the labial re-entrant valley between the hypoconid and the hypoconulid is rounded, as often in *Bos*; in *Bison* this open angle is rather asymmetrical and twisted, while the re-entrant valley is angular (Sala, 1986; Slott-Moller, 1990). An additional labial stylid between the second and the third lobe, a character mentioned as typical of *Bison* species, is absent from the MKL sample (Stampfli, 1963).

As in MKL sample, the molars of *Bos primigenius siciliae* from Puntali Cave, Italy, are straight and columnar, not swollen above the cervix; the upper molars bear a strong entostyle, mainly attached on the hypocone; M2 and M3 show a clear enamel islet; and the third lobe of m3 is in line with the longitudinal axis of the tooth. The upper isolated molar M1 (ST153) of *Bos primigenius siciliae* from San Teodoro Cave, presents an enamel fold on the distolingual part of the posterior fossette (=hypoconal spur), similarly to the MKL upper molars, whereas on the isolated m3 (i.e., ST312, ST149I) a labial stylid between the second and the third lobe is absent. The only mandible (ST145) of *Bos primigenius siciliae* from San Teodoro Cave, displays a partial m3, the alveoli for m2-p4 and p3, while the alveolus for p2 is naturally missing, just like in the specimens MKL586 and MKL571. On the contrary, four mandibles of *Bos primigenius siciliae* from Puntali Cave retain the p2 alveolus. The only specimen of *Bison priscus siciliae* from Puntali Cave (PA282) is a mandible with the third molar displayed. Unlike MKL, a labial stylid between the second and the third lobe is present, and all the alveoli for m2-p2 are present too.

The metacarpal is one of the best and most preserved bones, and taxonomically one of the most useful in the systematics of Bovini (e.g., Brugal, 1983; Sher, 1997). The overall shape of the metacarpals in *Bos* is rather long and narrow, while it is wider and slightly shorter in *Bison* (Table A.2). Overall, the MKL metacarpals are displaying *Bos* characters (Table 1; Table A.2), including: the articular facet for the fifth metacarpal, which is more pronounced in *Bos* than in *Bison* (Brugal, 1983); the large contact between the tubercle and main bone on the proximal surface, which in *Bos* is completely fused, whereas in *Bison* exists a noticeable gap (McCuaig-Blackwill and

Cumbaa, 1992); the depression medial to the posterior median tubercle that is better defined in *Bos* than in *Bison* (Gee, 1993); the anterior internal edge of the capito-trapezoid facet that is curved in *Bison* and straight in *Bos* (Olsen, 1960; Brugal, 1983). However, MKL metacarpals also exhibit features approximating *Bison* (Table 1). At first the shape of the lateral proximal facet for the hamatum is triangular, as often in that genus, instead of quadrant shaped in *Bos* (Bibikova, 1958; Gee, 1993). Furthermore, the shape of the distal epiphyses of MKL metacarpals is certainly closer to the "kinked" pattern seen in *Bison*, in contrast to the smoother transition seen in *Bos* species (Bibikova, 1958; Olsen, 1960; Brugal, 1983; McCuaig-Blackwill and Cumbaa, 1992; Gee, 1993) (Fig. 3). However, this feature was found by Gee (1993) to be much less reliable than previously assumed.

Among the Sicilian metacarpals, four belong to *Bos primigenius siciliae* from San Teodoro Cave and four to *Bison priscus siciliae* from Puntali Cave. All the Puntali specimens show the typical *Bison* characters (Table 1; Table A.2), including the less pronounced articular facet for the fifth metacarpal; the noticeable gap between the tubercle and main bone on proximal surface; the less defined depression medial to the posterior median tubercle; the rounded anterior internal edge of the medial facet for the capito-trapezoid, and the triangular shape of the lateral proximal facet for the hamatum. However, the overall shape is quite slender, except one specimen (Puntali 2), which is clearly short and wide. *Bison priscus siciliae* metacarpals show the typical for the genus "kinked" transition from diaphysis to epiphysis, similarly with MKL specimens, but in one (PA244), the transition is quite smooth, and closer to *Bos*. According to Brugal (1987), *B. primigenius siciliae* closely resembles the respective continental ancestor in morphology, slightly reduced in size though (about 20%).

On the contrary, the San Teodoro specimens, display the typical *Bos* features including (Table 1; Table A.2): the well pronounced articular facet for the fifth metacarpal; the well-defined depression medial to the posterior median tubercle; the fused tubercle with main bone on the proximal surface; the almost straight anterior internal edge of the medial facet for capito-trapezoid; and the quadrant shape of the lateral proximal facet for the hamatum (Gee, 1993). It is notable that some San Teodoro specimens demonstrate a more “kinked” transition from diaphysis to epiphysis, just like the MKL metacarpals and *Bison*; in particular ST169, has an overall short and quite wide appearance.

Generally, metatarsals of *Bos* and *Bison* are less easily distinguished each other than metacarpals. Overall, MKL metatarsals display some *Bison* or *Bison*-like characters (Table 1; Table A.2), such as: confluent proximal facets; and a quite noticeable small tubercle on the posteromedial corner of the facet for the large cuneiform. The proximal facets are well separated by a channel in *Bos*, whereas they are clearly confluent in *Bison*, demarcated only by a small ridge (Brugal, 1983; Gee, 1993). Moreover, the presence of a small medial tubercle on the posteromedial corner of the facet for the large cuneiform is reported as missing in *Bos*, but Gee (1993) marks high inconsistencies on the expression of this feature. Nevertheless, the major difference in metatarsal morphology between *Bos* and *Bison* lies at the distal half of the bone. As for the metacarpals, the MKL metatarsals display a *Bison*-like morphology, i.e., a “kinked” distal metaphysis (Gee, 1993) (Fig. 5h-j).

Five metatarsals from Sicily are preserved; one of *Bison priscus siciliae* form Puntali Cave and four of *Bos primigenius siciliae* form San Teodoro Cave. The *Bison* specimen shows all the typical *Bison* characters, including (Table 1): the “kinked” distal metaphysis; the clearly confluent proximal facets that are demarcated by a small ridge;

the presence of a small medial tubercle on the posteriomedial corner of the facet for the large cuneiform; and the narrow neck that joins the two proximal articular facets for the small cuneiform and the naviculo-cuboid. On the contrary, the San Teodoro Cave specimens display all the typical *Bos* features (Table 1; Table A.2). Nevertheless, one specimen (ST168) shows a “kinked” transition from the diaphysis to distal epiphysis, just like the MKL sample and *Bison*.

TABLE 1 (around here)

3.3 Biometric comparison

Quantitative comparisons include *Bos primigenius* and *Bison priscus* populations from several Pleistocene continental sites of Greece and Europe, as well as the two endemic samples from Sicily (Table A.3). Upper and lower dental dimensions show that the analysed MKL bovin has overall smaller teeth compared to continental representatives of either *Bison* or *Bos*. The average lower molar row length from Kythera (~87 mm; n=3) appears 15-20% shorter than that of *Bison priscus* from Habarra (~103 mm; n=6), and Romain-la-Roche (109.5 mm; n=7) (Prat et al., 2003; Vercoutère and Guérin, 2010), and 20-22% shorter than in *Bos primigenius* from the Late Pleistocene to Holocene of Denmark (~110.5 mm; n=21; Degerbøl and Fredskild, 1970) or Romain-la-Roche (112.4; n=6; Vercoutère and Guérin, 2010).

The proportions of the fourth upper premolar, P4 (Fig. 6a) indicate that the Kytherian taxon is significantly smaller in both length and width than those of *Bison priscus* and *Bos primigenius* from Romain-la-Roche, France. Regarding the proportions of the fourth lower premolar, p4 from Kythera appears shorter compared to continental representatives of *Bos* and *Bison*. Despite the small length dimensions, the MKL p4s have a quite expanded width range with maximum values reaching the minimum ones of continental *Bison*/*Bos* populations.

FIGURE 6 (around here)

The proportions of the second upper molar, M2, indicate that the MKL taxon is smaller than the continental representatives of *Bos* and especially *Bison* (Fig. 6b), but of comparable width with *B. primigenius* from Megalopolis. Compared to the *Bos primigenius* populations from Biache-Saint-Vaast and Bau de l'Aubesier, the dimensions of MKL are significantly smaller, but closer to the length dimensions of latter population (Fig. 6b).

The second lower molars (m2) of the MKL bovin are metrically shorter and slightly narrower than the continental populations of *Bos* and *Bison* (Fig. 6c). They are identical in size to those of *Bos primigenius siciliae* from Puntali Cave and from Carburangeli Cave, but shorter than the same taxon from San Teodoro Cave (Fig. 6c). The MKL sample shows a quite expanded width range with maximum values reaching the minimum ones for continental *Bison*/*Bos* population.

The proportions of the third lower molars (m3) of the MKL bovin are metrically identical to those of *Bos primigenius siciliae* from Puntali Cave and very close to those of *Bos primigenius siciliae* from San Teodoro Cave (Fig. 6d). The Kytherian taxon shows narrower and shorter on the average m3 than continental representatives of *Bos* and *Bison*.

MKL metacarpals are characterised as short and robust (Fig. 7a), clearly distinguished from any other taxon/population in comparison. The insular *Bos primigenius siciliae* has similarly short but rather less stout metacarpals (judging from the single available specimen), while *Bison priscus siciliae* shows slightly longer and appreciably less stout metacarpals. Interestingly metacarpals of the Sicilian *Bison* show IDML/MLEN % values comparable to those of continental *Bos*, whereas MKL metacarpal values are comparable to those of continental *Bison*. The bivariate plot of maximum length (MLEN) against midshaft mediolateral (transverse) diameter (MML) (Fig. 7c) and the maximum length (MLEN) against distal epiphysis anteroposterior diameter (DEAP) (Fig. 7e) for the metacarpals indicates that the canon bone of the Kytherian bovin has similar values to *Bos primigenius bubaloides* from Pianosa, but is much shorter, with narrower diaphysis and relatively deeper distal epiphysis, compared to continental populations of *Bos primigenius* and *Bison priscus*. An analysis of metacarpal static allometry based on the same dataset as in Fig. 7c, revealed that the allometric coefficient ‘a’ is about 1 in continental *Bos* (n=44), slightly less in continental *Bison* (a=0.7; n=26) and about 1.5 in the Kytherian bovin (n=7), suggesting a high degree of metacarpal shortening.

FIGURE 7 (around here)

A PCA analysis of metacarpal proportions based on seven log-transformed variables is given in Fig. 8a. PC1 (90.1 % of variance) is positively affected by the overall size and mostly by the large diaphysis (MAP, MML) and proximal epiphysis (PAP, PML), separating metacarpals with wide diaphysis and massive proximal epiphysis from the those with narrow diaphysis and slender proximal epiphysis. PC2 (5.4 % of variance) is positively correlated with length (MLEN), and negatively influenced by DEAP, distinguishing longer metacarpals with shallow distal epiphysis (positive scores) from shorter and deeper ones (negative scores). MKL and in a similar degree *Bos primigenius siciliae* and *Bos primigenius bubaloides* are negative for both PC1 and PC2 separated from all continental samples of *Bos* and *Bison*; they exhibit rather short metacarpals with narrow diaphysis, slender proximal epiphysis and relatively deep distal epiphysis. *Bison priscus siciliae* metacarpals are comparable in proportions, but longer (Fig. 8a).

A PCA based on six shape-transformed variables (not including DEAP), shows that PC1 (74.1 % of variance) is driven principally by the stoutness of the shaft (ReMAP and ReMML) and to a lesser extent by the shape of the proximal epiphysis (RePML and RePAP) (Fig. 8b). Hence, PC1 separates metacarpals with slender proximal epiphysis and narrow diaphysis toward the negative values, from metacarpals with wide diaphysis and robust proximal epiphysis at the opposite end of the spectrum. In turn, PC2 (15.2% of variance) is mostly influenced by ReMLEN and distinguishes longer metacarpals from shorter ones. The MKL sample displays negative scores for both PC1 and PC2, and is, thus, characterised by short metacarpals with slender proximal epiphysis and narrow diaphysis. Regarding its metacarpal shape it distinguishes from both the Sicilian taxa and that from Pianosa, approaching the much larger continental populations of *Bison priscus* from Habarra and Filo Cave (Fig. 8b).

FIGURE 8 (around here)

Regarding the amount of stoutness, the metatarsals of MKL sample are significantly shorter than those of continental *Bos* and *Bison* populations and as stout as large-sized continental morphotypes from Filo Cave and Habarra (Fig. 7b). *Bison priscus siciliae* shows similarly short and even stouter metatarsals (but judging from a single complete specimen), while *Bos primigenius siciliae* displays more elongated and slenderer on the average metatarsals than the MKL taxon.

A PCA based on six log-transformed variables (not including length) for the metatarsals is given in Fig. 9a. PC1 (80.7% of variance) is principally driven by MAP and secondarily by the dimensions of the proximal epiphysis, PML and PAP. Thus, it separates metatarsals with wide diaphysis and robust proximal epiphysis (positive scores) from metatarsals with a narrow diaphysis and slender proximal epiphysis (negative scores). In turn, PC2 (17.5% of variance) is positively influenced by DEAP, but negatively by MML. Hence, it distinguishes metatarsals with small dimensions of diaphysis and massive distal epiphysis (positive scores), from those characterised by large diaphysis and narrow distal epiphysis (negative scores). The MKL bovin gets negative scores for PC1 and positive for PC2 and is, thus, characterised by metatarsals with a narrow diaphysis, slender proximal and stout distal epiphysis. These features distinguish it from any other sample/population in comparison, including the Sicilian bovins that are characterised by slenderer distal epiphysis.

The bivariate plot of MLEN against MML (Fig. 7d) and MLEN against DEAP (Fig. 7f) for the metatarsals indicates that the MKL bovin is significantly shorter, with narrower diaphysis and relatively deeper distal epiphysis compared to the continental populations of *Bos* and *Bison*. The populations of Romain-la-Roche and *Bos primigenius* from Petralona Cave display the most elongated metatarsals with wide diaphysis.

FIGURE 9 (around here)

A PCA based on six shape-transformed variables (not including length) for the metatarsals, shows that PC1 (51% of variance) is driven principally by the stoutness of the shaft (ReMAP and ReMML) and to a lesser extent by the negative loading for ReDEAP (Fig. 9b). Hence, PC1 separates metatarsals with narrow diaphysis and deep distal epiphysis (negative scores), from metatarsals with wide diaphysis and shallow distal epiphysis (positive scores). In turn, PC2 (42% of variance) is influenced by the shape of the proximal epiphysis (RePML and RePAP) and distinguishes metatarsals with massive proximal epiphysis (positive scores) from those with slender proximal epiphysis (negative scores). The MKL sample displays negative scores for PC1 and positive for PC2, and thus characterised by metatarsals with narrow diaphysis, deep distal epiphysis and massive proximal epiphysis. By their shape MKL metatarsals are distinguished from both Sicilian taxa; *Bos primigenius siciliae* displays metatarsals with wide diaphysis, shallow distal and slender proximal epiphysis, while *Bison priscus siciliae* shows metatarsals with narrow diaphysis, deep distal and slender proximal epiphysis.

The body mass estimations for the MKL bovin provide values ranging between 251 and 593 kg (Fig.10; Table B.27) and an average weight of 380 kg, based on the five most highly correlated with body mass postcranial elements (Scott, 1983; Damuth, 1990; Janis, 1990). The lowest predicted average weight has been provided from the equations based on the tibia (326 kg), while the largest one on metacarpals estimations (404 kg). Based on dental equations the mean body mass prediction for the MKL bovin is at 425 kg ranging widely between 104 to 833 kg. However, estimations based on teeth are considered less credible compared to those based on postcranials, as the latter carry the weight of an animal (Janis, 1990; Mendoza et al., 2006). Based on the same postcranial bones and equations, the endemic *Bos primigenius siciliae* from San Teodoro Cave has an average weight of 430 kg, whereas the other endemic taxon, *Bison priscus siciliae* from Puntali Cave is estimated at 480 kg (Fig. 10).

Comparative data from the literature (Sala, 1986; Prat et al., 2003; Vercoutère and Guérin, 2010; Wright, 2013; Maniakas, 2019) highlight the high difference in weight between the main European populations of *Bison priscus* and *Bos primigenius* and the MKL bovin. The Middle-Late Pleistocene *Bison priscus* from Romain-La-Roche stands at 1000 kg, while the remarkably huge Taubach bison weighs more than 1 tonne. The isochronous *Bison priscus* from Cave Filo and Habarra have an estimated body mass of 649-1230 kg and 691-1062 kg, respectively, while *Bison priscus* from Petralona Cave has an average weight of 900 kg. The huge *Bos primigenius* from Ilford stands between 974 and 1300 kg, while the auroch from Petralona Cave is estimated at 704-1191 kg. The Romain-la-Roche *Bos primigenius* has an average weight of 950 kg, that from Lunel Viel of 990 kg, whereas the Italian *Bos primigenius* from Avetrana stands between 837-949 kg. *Bos primigenius* from Paglicci Cave weights around 850 kg.

FIGURE 10 (around here)

The estimated insular index Si for the MKL bovin is 0.48, lower than that for *Bos primigenius siciliae* (0.51), and *Bison priscus siciliae* (0.58) (Table 2; see also Rozzi, 2018). Regarding the shortening SI indices for the metapodials, both are calculated at 0.681 for the Kytherian taxon, reflecting a less extreme shortening of the metacarpals and metatarsals, compared to the two Sicilian bovids (Table 2; Table B.28). However, the SI Mt is based on only one tibia and two metatarsals, since the majority of the MKL specimens are fragmentary and lack the length measurement.

TABLE 2 (around here)

Among the 17 partially of fully preserved metacarpals from Kythera, two represent calfs, 6 young individuals lacking the distal epiphysis, and nine individuals in full maturity to seniles (Fig.11). The PCA analysis of the last group based on the four selected metrical parameters according to Lewis et al. (2005) indicted two subgroups representing females (four metacarpals; MKL235, 48, 44, 45) and males (five metacarpals; MKL142, 46, 40, 36, 50). The % difference between average values for the four metrical parameters plus total length are given in Table 3 in comparison with that of European *Bos* and *Bison* populations/samples. The Kytherian bovin shows comparable sexual bimodality in total length with both continental *Bos primigenius* and *Bison priscus*, but generally milder on the proximal epiphysis, middle diaphysis and distal epiphysis transverse diameters. Available data on island bovins are much less (three complete metacarpals from Pianosa and four from Puntali Cave) and therefore of lower credibility. Here again, however, the Kytherian taxon appears less dimorphic in proximal, diaphyseal and distal dimensions than *Bison priscus siciliae,* and *Bos primigenious bubaloides* (Table 3), the latter showing instead, a seemingly great difference in total length (MLEN) between males and females.

TABLE 3 (around here)

4. Discussion

4.1. Taxonomy and island evolution

The Kytherian bovin shares 13 out of 15 (87%) cranio-dental morphological features with *Bos*, one with *Bison*, whereas another one is autapomorphic (the tendency of losing p2). Out of 65 postcranial morphological features, the Kytherian bovin shares 42 with *Bos* (65%) and 14 with *Bison* (21.5%), whereas 9 more characters (17.5%) appear mixed or autapomorphic. We, therefore, ascribe the Kytherian taxon to *Bos.*

A reduction in body size and associated skeletal modifications is a well-known process during domestication for several mammals, including bovins (Grigson, 1969; Uerpmann, 1978; Meadow, 1989; Morey, 1994; Hongo & Meadow, 1998; Albarella et al., 2006). Several studies showed that *Bos taurus* is indeed smaller than *Bos primigenius* but size overlap between larger domestic cattle and smaller aurochs does exist (e.g., Grigson, 1978) and several hypotheses have been suggested to explain this (e.g., Grigson, 1969; Degerbøl and Fredskild, 1970; Rowley-Conwy, 1995; Viner, 2010). Nevertheless, the MKL *Bos* is markedly smaller (~52%) than the mainland wild form and appreciably smaller (25-30%) than its domestic varieties (based on data from Ballarin et al., 2016), staying well outside the ranges of size reduction due to domestication in this genus, at least compared to what is known from a continental context. On the other hand, an *in situ* (island) domestication is highly unlikely and there is no known case of bovin domestication in an island environment (A. van der Geer, pers. com. 2023). Skeletal features also inconsistent with a scenario of domestication for the Kytherian taxon. Although MKL *Bos* and domestic cattle exhibit several *Bison*-like morphological postcranial characters (e.g., proximal features of femur), several features shared by *B. taurus* and *B. primigenius* are expressed differently in the MKL bovin (e.g., the shape of the scaphoid articulation; the shape and layout of the malleolar facets; see also Table A.2), whereas others have been transformed into more *Bison*-like (e.g., the shape of metapodial’s metaphysis; see also Table A.2). These data, combined with the absence of human presence from the taphonomic context of the findings, certainly remove the possibility that the MKL *Bos* is domesticated. Instead, both dental and postcranial qualitative and quantitative data suggest that the studied material from Kythera belongs to *Bos primigenius.*

FIGURE 11 (around here)

MKL *Bos* differs from continental populations of *Bos primigenius* in: (i) the overall smaller size (Si= 0.48; average Body Mass= 380 kg); (ii) weakened sexual bimodality; (iii) the presence of a strong incisure on the caudal crest of petrous bone at the orifice of the cochlear canal; (iv) the advanced hypsodonty (Hypsodonty index ≥1.7); (v) a tendency to loose p2; (vi) the shorter metapodials (SI Mc= SI Mt= 0.68) with “kinked” (*Bison*-like) distal metaphysis; (vii) the triangular shaped (*Bison*-like) proximal facet for the hamatum on metacarpals; (viii) the confluent (*Bison*-like) proximal articular facets on the metatarsals; (ix) the presence of a small tubercle on the postero-medial corner of the facet for the large cuneiform on metatarsals; (x) the nearly vertical and relatively long (*Bison*-like) neck from the femoral head to the trochanter minor and the resulted residual trochanteric fossa; (xi) the shape and layout of the malleolar facets on tibia;

and (xii) the slenderer astragalus with elongated (Bison-like) articular facet for the calcaneum. In both metric and morphological features, the MKL bovin matches and overlaps to a greater or lesser extent with insular samples of *Bos primigenius* from Sicily and Pianosa islands (Figs. 6-9), whose particular combination of characters has been explained in the light of island endemism (e.g., Azzaroli, 1978; Brugal, 1987; Rozzi, 2018).

Bos primigenius siciliae from San Teodoro Cave, Sicily differs from the MKL *Bos* in: the larger size, the similarly short but rather less stout metacarpals and more elongated and slenderer on the average metatarsals, both, however, are shorter compared to the zeugopodium and with smooth distal metaphyses. *Bos primigenius siciliae* retains more typically *Bos* postcranial morphological features, although some metapodials (e.g., ST168, ST169) exhibit a “kinked” transition from diaphysis to distal epiphysis, just like the MKL taxon.

Bos primigenius bubaloides from the Pleistocene of Pianosa Island, Italy (Azzaroli, 1978), is known by a few dental and postcranial remains found in bone-breccias, and caves eroded by the sea. Azzaroli (1978) and Brugal (1987) suggested for the Pianosa taxon a height at the withers of about 100-120 cm, and an overall reduction of 17-20% compared to the continental relative. Caloi and Palombo (1994) implied that several limb modifications probably represent adaptations for movement on hard grounds, but not all the data agreed on this point. Rozzi et al. (2020) estimated the body mass of the Pianosa taxon at 418 kg and a Si index of 0.42, supporting a great level of endemism. According to the limited available metrical and morphological data provided by Azzaroli (1978) and Brugal (1987) the Pianosa small auroch differs from the Kytherian taxon in the overall greater size, wider distally humerus, larger astragalus, and slightly longer metacarpals with smoother distal metaphysis and lower distal robusticity index (IDML/MLEN%: 31.7-33.5; n=3).

Thus, according to our knowledge the Kythera *Bos primigenius* does not match any other mainland or island population of this species and we, therefore, ascribe it to a new subspecies, *Bos primigenius thrinacius* n. ssp. As for the Sicilian and Pianosa island aurochs, several of the morphometric features seen on Kythera *Bos primigenius* are consistent with insular endemicity.

The degree of hypsodonty is the best-known indicator linked to both habitat type and diet of the ungulates, regardless of body size (e.g., Janis and Fortelius, 1988; Fortelius et al., 2002; Mendoza et al., 2002). *Bos primigenius thrinacius* n. ssp. exhibits a relatively high hypsodonty (>1.2; Fortelius et al., 2002) with an estimated hypsodonty index at 1.82 (1.78-1.86) for m2, at 1.73 for m3 and at 1.94 for M2. The continental population of *Bos primigenius* from Petralona Cave provide an hypsodonty index around 1.5 for the lower and around 1.6 for the upper molars (Maniakas, 2019); similar values were obtained for *Bos primigenius* from Fontana Ranuccio, Italy (~1.5; Strani et al., 2018). Thus, the Kytherian bovin shows a greater degree of hypsodonty, compared to the hypothetical mainland form. An increase in molar crown height is a quite common morphological trend in insular artiodactyls and is shared by most insular bovids (Rozzi et al., 2013), because of the expansion of their dietary niche under resource limitation, and as an adaptation for eating more abrasive plants (Van der Geer et al., 2010; Damuth and Janis, 2011; Winkler et al., 2013).

Insular artiodactyls under dwarfism are common to lose their lower premolars (e.g., the second premolar in *Myotragus* and anoas; Van der Geer et al., 2010; Rozzi, 2017). *Bos primigenius thrinacius* n. ssp. also displays a loss of the second lower premolar or a clear tendency to it. Similarly, the single available mandible of *Bos primigenius siciliae* from San Teodoro Cave, seems to naturally missing its p2, but the rest of *B. primigenius siciliae* mandibles from Puntali Cave retain the alveolus for the p2, implying that the loose of tooth in a single mandible may be just an individual abnormality.

The majority of the comparative continental populations of *Bos* and *Bison* show a significant degree of sexual dimorphism, especially as expressed on their metacarpal bones (Brugal and Fosse, 2005; Lewis et al., 2005 and references therein). Although sexual segregation does exist on the Kytherian taxon (Table 3; Fig.11), it is milder compared to continental relatives. In a similar manner, living insular bovids do not exhibit significant sexual dimorphism (Jass and Mead, 2004; Rozzi and Palombo, 2014; Rozzi, 2017 and references therein).

Body size alterations are frequently observed in the mammal fossil record and are the most striking changes undergone by island settlers (De Vos et al., 2007; Lomolino et al., 2013; Lomolino, 2016; Rozzi and Lomolino, 2017). The majority of island bovids, as large mammals, do follow the main prediction of the island rule, showing a body size reduction (Van Valen, 1973; Lomolino, 2005; Rozzi, 2018). The tremendous reduction in body mass (at average 52.5% less compared to continental representatives of *Bos primigenius*) and the low Si value calculated for *Bos primigenius thrinacius* n. ssp. (Si=0.48; Table 2), suggest that this taxon was an island dwarf. The endemic population of *Bos primigenius siciliae* from Sicily has a Si value of 0.51, (Table 2; Rozzi, 2018) and remains 12% heavier than the Kytherian taxon, whereas *Bos primigenius bubaloides* from Pianosa has Si=0.42 and remains 9% larger than the Kythera auroch based on their body masses. This last observation confirms previous ones that congeneric bovid species on different islands (e.g., *Bubalus mindorensis* and *Bubalus depressicornis*) as well as on the same island (*Bubalus depressicornis* and *Bubalus quarlesi*) may show different degrees of body size reduction, even though they originate from the same continental ancestor (Rozzi and Palombo, 2014). Time in isolation seems to play a crucial role here, since body size decrease for bovids becomes more pronounced with longer residence times on the islands (Rozzi and Palombo, 2014; Rozzi, 2018 and references therein). Unfortunately, the absence of accurate chronological data for both the Kytherian and the Italian insular taxa cannot allow a safe comparison of their size decrease to isolation relationships. The area per se version of the resource limitation hypothesis by McNab (2002) also suggests that body mass of insular species would be directly affected by the total space available (Lomolino et al., 2012). However, this hypothesis finds limited support with no significant relationships between the insular body size and the area of the palaeo-islands (Lomolino, 2000; Van der Geer et al., 2016a; Rozzi, 2018). According to Rozzi (2018), the evolution of insular bovids is affected more by the ecological interactions than by the island area *per se*. This is consistent with the so-called ecological hypothesis for body size evolution (Palombo, 2009; Lomolino et al., 2012), in which the direction and degree of body size changes depends on the size and the trophic strategies of both the focal species and those species with which they interact. Contra, for instance, to insular proboscideans where competitive release appears to be the central force influencing their body mass changes (Palombo, 2007; Van der Geer et al., 2016a, 2016b), the major factor in driving the body size evolution of insular bovids is predator diversity /predatory release (Rozzi, 2018). In fact, the number of competitors and/or predators that can be found on an island is largely controlled by the island isolation that generally influences the species richness; more isolated islands tend to have less predators and competitors (Van der Geer et al., 2016b; Simaiakis et al., 2017; Rozzi, 2018). Bovids and other ruminants are among the most common prey of large carnivores, both now and in the past, so the relative importance of the ecological release from predators or competitors in triggering island dwarfism may vary for different taxonomic groups of large mammals (Rozzi, 2018).

Insular ruminants often gain a peculiar structure of their limbs including the shortening of the long bones, most markedly the metapodials, the increasing of the robustness, and at times the development of bone fusions (Sondaar, 1977; Bover et al., 2010; Rozzi and Palombo, 2014; Rozzi et al., 2020). This has been described as ‘low gear’ modifications of locomotion (Sondaar, 1977), a repeated phenomenon believed to increase stability, especially on rocky and uneven grounds, and often in a carnivore-free environment (Bover et al., 2010). Nonetheless, this combination of features is not regarded as a “common trait”; exceptions can be found in some taxa as a result of the special environmental context they were adapted to (e.g., the quite long metapodials seen in *Nesogoral* and *Duboisia santeng*; (Palombo et al., 2013; Rozzi et al., 2013; Rozzi and Palombo, 2014). The quite elongated limbs and the slenderness of metapodials characterizing some insular bovids suggest a cursorial ability, in agreement with the presence of predators on the respective islands (Palombo et al., 2013; Rozzi et al., 2013). On the other hand, bovids that evolved in predator-free and species-poor islands, such as *M. balearicus* and *Bubalus mindorensis*, invest in increasing their stability and acquire morphological traits related to ‘low-gear’ locomotion (e.g., shortened and stout metapodials) (Rozzi et al., 2020).

The shortening of *Bos primigenius thrinacius* n. ssp. long bones from Kythera is not uniform (see Table B.29). The Kythera femur shortening is the lowest and that of the humerus the highest, in comparison to the other bone length reductions (see Table A.5). The slight lateral curvature observed on both the radius and tibia from Kythera (see Appendix C and Fig. C.1b, e), may also be an alternative way of the same compaction process for the zygopodium. While we lack intact femora of the Sicilian and Pianosa aurochs, *Bison priscus siciliae* demonstrates an extreme reduction of 49% of femur length when compared to continental *Bison priscus* populations. These differences of the limb shortening between *Bos primigenius thrinacius* n. ssp. and *Bison priscus siciliae* may probably be related to the different evolutionary paths that *Bison* and *Bos* follow in insular environments.

The metacarpals of Kythera sample are significantly short and stout (Fig. 7a, 8, 11; Table A.1); 32% shorter, compared to the continental *Bos* representatives from Petralona Cave, and 35% in comparison with various European *Bos primigenius* populations (Table B.29). The Sicilian *Bos* displays 28% total length decrease in comparison to the continental Italian auroch population. Furthermore, the metacarpals of the Kytherian bovin are on average 9% shorter than the Sicilian and 13% than the Pianosa *Bos primigenius* metacarpals. Nevertheless, the estimated shortening indexes (SI) for the metapodials (Table 2) indicate that the Kytherian taxon has not so extremely shortened metacarpals relative to radius, and metatarsals relative to tibia, in contrast to the two Sicilian taxa that show more markedly relative shortening of the their metapodials (Table 2; see also Rozzi et al., 2020). Overall, the metacarpals of *Bos primigenius thrinacius* n. ssp. are displaying *Bos* characters, but the shape of the distal metaphysis is certainly more *Bison*-like. In a similar way, some *Bos primigenius siciliae* specimens, also display a “kinked” distal metaphysis, suggesting some convergent similarity. Additionally, in insular populations the distinction between the two morphotypes (*Bos*-like and *Bison*-like) may be not as clear as in continental forms.

Proportionally, the Kythera metatarsals are quite short and stout (Fig. 5b, 9; Table 1), displaying 30% length reduction compared to the continental *Bos primigenius* from

Petralona Cave (Fig.12) and 34% in comparison with various European *Bos primigenius* populations (see Table B.29). In comparison, the metatarsals of the Sicilian auroch appears only 19% shorter than the continental Italian *Bos* populations, and 18% longer than those of *Bos primigenius thrinacius* n. ssp. The Kythera metatarsals display more *Bison* or *Bison*-like characters, and similarly with the metacarpals the major difference at the “kinked” transition from the diaphysis to distal epiphysis (Fig.12). Regarding the Sicilian population, one specimen of *Bos primigenius siciliae* also displays a shorter and more “kinked” appearance; according to Brugal (1987) this specimen corresponds to a male, so the difference may be due to or accentuated by the sex, but data are inadequate for certain conclusions.

FIGURE 12 (around here)

The marked shortening of the *Bos primigenius thrinacius* n. ssp. long bones and the increased stoutness of the metapodials, especially the metacarpals seem to fall within the typical ‘low-gear’ locomotion path that appears more marked in the Kytherian than in the Sicilian bovins, but not as extreme as in *Myotragus* and extant dwarf Indonesian buffaloes. Following Rozzi et al. (2020) these data suggest that Kythera would represent at that time a species-poor island where the local auroch evolved in a competitive released and predator-free environment. The Sicilian bovids have also evolved this type of locomotion, but less strongly, since they were co-occurring with several predators and competitors (Rozzi and Palombo, 2014).

Strong metapodial changes in insular bovids appear also to be significantly influenced by the amount of ragged terrain present on each island (Rozzi et al., 2020). The *Bos* from Kythera does not show any bone fusions, but exhibits some particular morphological trait, such as the *Bison*-like shape of many articulations of the long bones (i.e., the shape of the radioulnar articulation and the distal scaphoid articulation of radius, the orientation of the cranial articular surface and the shape of the caput femoris, the shape and layout of the malleolar facets, and the elongated articular facet for the calcaneum of the astragalus; see Appendix C). These modifications may reflect particularly morphofunctional adaptations to the unique environment this taxon was living. The *Bison*-like "kinked" distal metaphysis of *Bos primigenius thrinacius* n. ssp. metapodials, along with their increased robusticity, may also have provided more stability in the rocky landscape of this island and boosted the species' survivability by lowering the chance of traumatic injuries (Rozzi et al., 2020 and references therein).

4.2. Palaeogeographic implications

During the Pleistocene, the Aegean coastal palaeogeography underwent dramatic changes due to important sea-level fluctuations resulted from the combination of eustatic, isostatic and tectonic contributions (Lambeck, 1995; Lykousis, 2009; Sakellariou and Galanidou, 2017). Differences between the lowest and highest sea-level stands, reaching −120 m and +10 m, respectively compared to the present-day sea level (Lykousis, 2009; Grant et al., 2014; Spratt and Lisiecki, 2016). These changes led to successive isolations – reconnections of present-day islands with each other or mainly with the main body of the nearby mainland, drastically affecting their faunal content. Long-time insular isolation led the indigenous fauna to endemism, whereas secondary colonisations were common too (Van der Geer et al., 2010; Lyras et al., 2022 and references therein).

Kythera, as a small palaeo-peninsular island located in the southern part of Peloponnese between continental Greece and Crete may provide an ideal geographic setting for the evolution of endemic species (Simaiakis et al., 2017 and references therein). The present-day sea-channel between Kythera and Peloponnese is less than 9 km wide and 200 m deep (Fig. 1b). During Middle-Late Pleistocene periods of low sea level stands (especially MIS 12, MIS 10, MIS 8, and MIS 6) the surface area of the palaeo-island increased up to twice than today, Kythera was connected to both the Peloponnese and Antikythera Island by presumably exposed shallow submerged landmasses and shelves, and the sea strait separating this land from Crete was restricted to 3–5 km (Fig.1g) (Lykousis, 2009; Sakellariou and Galanidou, 2017; Athanassiou et al., 2019; Radacovic, 2021). This palaeogeographic model seems to agree with the results by Van der Geer et al. (2010), and Lyras et al. (2022), who, based on the sparse and taxonomically impoverished known Pleistocene large mammal fossils from Kythera, suggested that recurrent immigrations did not permit the island populations to evolve into endemic forms. Although cervid remains from Kythera Island (Kuss, 1967, 1973) are inadequate to address this issue, elephant remains are better known and more informative; opinions on the dwarfism of the Kythera elephant, however, vary widely among researchers (see Athanassiou et al., 2019 for an overview). In the most recent reviews, Sen (2017) cannot disprove and Athanassiou et al. (2019) cannot confirm the Kythera *Palaeoloxodon* as an island dwarf.

The new data provided here feed the discussion of the paleogeographical history of Kythera Island with new evidence. The abundant studied material of 723 bovid remains from more than 10 individuals (based on metacarpals) including calfs, juveniles, adults and elders depicts with sufficient completeness a fully established local population. On the other hand, both the strong body mass reduction *Bos primigenius thrinacius* n. ssp. underwent and the craniodental-postcranial changes it gained compared to the respective continental relative, can only be explained by a relatively prolonged time of insular isolation and a local evolution in a rather predator-free context. The clear island dwarfism detected in the bovin from Mikeli 1 cave is probably combined with the ‘gigantism’ observed by Vlachos (2015) in the postcranials of *Testudo marginata* from the same site (i.e., ~50% larger than mainland representtives; E. Vlachos pers. com. 2023) although the latter data are not sufficient to draw firm conclusions.

Obviously, *Bos primigenius thrinacius* n. ssp. originates from a continental *Bos primigenius* population, most likely from the Peloponnese peninsula, that reached the island or originally expanded its range till there, and at some later time isolated and became fully endemic. Although this picture seems to contradict that derived from the study of *Palaeoloxodon*, it is not taking into account the timing of the events, as both elephant and bovin remains from Kythera Island are not chronostratigraphically controlled. Based on the well-supported palaeogeographic data by Lykousis (2009) and Sakellariou and Galanidou (2017 and references therein), we suggest that both elephant remains from Kythera, as well as the parental population of *Bos primigenius,* predate MIS 6 (180-130 ka), when the island repeatedly and over relatively long periods of time connected (partially or fully) to the mainland of the Peloponnese. Both *Palaeoloxodon antiquus* and *Bos primigenius* took part in the rich fauna developed around the swamps and lakes of Megalopolis in the central part of the Peloponnese during MIS 19 - MIS 12 (Melentis, 1965; Konidaris et al., 2018 and references therein). Data from both west and east of the Peloponnese indicate that from MIS 6 to MIS 2 relative land mass subsidence ranged from 0.34 m/ka to 0.70 m/ka (Lykousis, 2009;

Zavitsanou et al., 2015) indicating a relative sea-level increase of 40-75 m over 128 ka. Despite, therefore, the absence of absolute chronology, we suggest based on geological evidence that during this period the island of Kythera started to permanently disconnect from the Peloponnese peninsula, allowing the local *Bos* population to be isolated. The fact that island artiodactyls may decrease their body mass at 25–50% compared to their mainland ancestors in just a few millennia (Rozzi and Lomolino, 2017), may reinforce this hypothesis. Species stranded early on palaeo-peninsular islands may have been better adapted to insular conditions but also less resilient to area reduction (Simaiakis et al., 2017 and references therein).

The accurate time and causes for the extinction of *Bos primigenius thrinacius* n. ssp. remain unknown for the moment. Competition and predation-release, area reduction and habitat destruction, diseases, and hunting, are common causes proposed for the extinction of numerous endemic insular taxa (MacPhee, 2009; Van der Geer et al., 2010; Rozzi et al., 2023). According to the study by Simaiakis et al. (2017) Kythera shows low area (and rate of area) loss, and medium distance increase from the mainland at low rates starting from the Last Glacial Maximum (LGM) onwards. As the island remained fully isolated from the mainland after the LGM untill today (Lykousis, 2009; Sakellariou and Galanidou, 2017; Simaiakis et al., 2017), introduced predators/competitors during the LMG or previous low sea level stands might be possible reasons for the extinction of *Bos primigenius thrinacius* n. ssp., not substantiated by the present data though. Anthropogenic causes are also highly unlikely as they are currently not supported by other local evidence. An analysis of the postmortem osteological modifications observed in the material (in progress) together with a full multidisciplinary investigation of the site, potentially will shed more light on the causes of rise and fall of the enigmatic Kytherian bovin.

5. Conclusions

Based on both qualitative and quantitative features, the described bovin from Kythera is attributed to a new, insular subspecies of *Bos primigenius*, *B. p. thrinacius* n. ssp., distinct from both its mainland European Pleistocene relative taxon and endemic aurochs from other Mediterranean islands. Morphological and biometrical data suggest a significant reduction in body size, decrease in the size of the dentition, tendency to lose the second lower premolar, markedly shortening of the long bones and great stoutness of the metapodials, which all together indicate that the Kythera auroch was an island dwarf. Based on indirect evidence, we propose that the gradual disconnection of Kythera Island from the neighbouring Peloponnese peninsula just after MIS 6 (late Middle Pleistocene, ~180 ka) allowed the isolation of a mainland *Bos primigenius* population in a restricted rocky and predator-free context. Under the new conditions, the population underwent some remarkable changes that follow the island rule and gained some marked postcranial *Bison*-like features to meet a 'low-gear' locomotion. The rapid and rather easy shift from *Bos-* to *Bison*-like features under the peculiar conditions in an island environment may be another example of the tight phylogenetic proximity of the two genera. We assume that the extinction of *Bos primigenius thrinacius* n. ssp. likely occurred during the LGM but the exact timing and causes that led to the special thanatocoenosis within Mikelis 1 Cave require further multidisciplinary studies.

Author contributions

S.S. and D.S.K, conceptualization and writing of the paper; S.S, data curation and formal analysis; B.A. and R.R, resources, review and editing; D.S.K., supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Datasets related to this article are included in the online Appendices A-C. Additional data are available on request.

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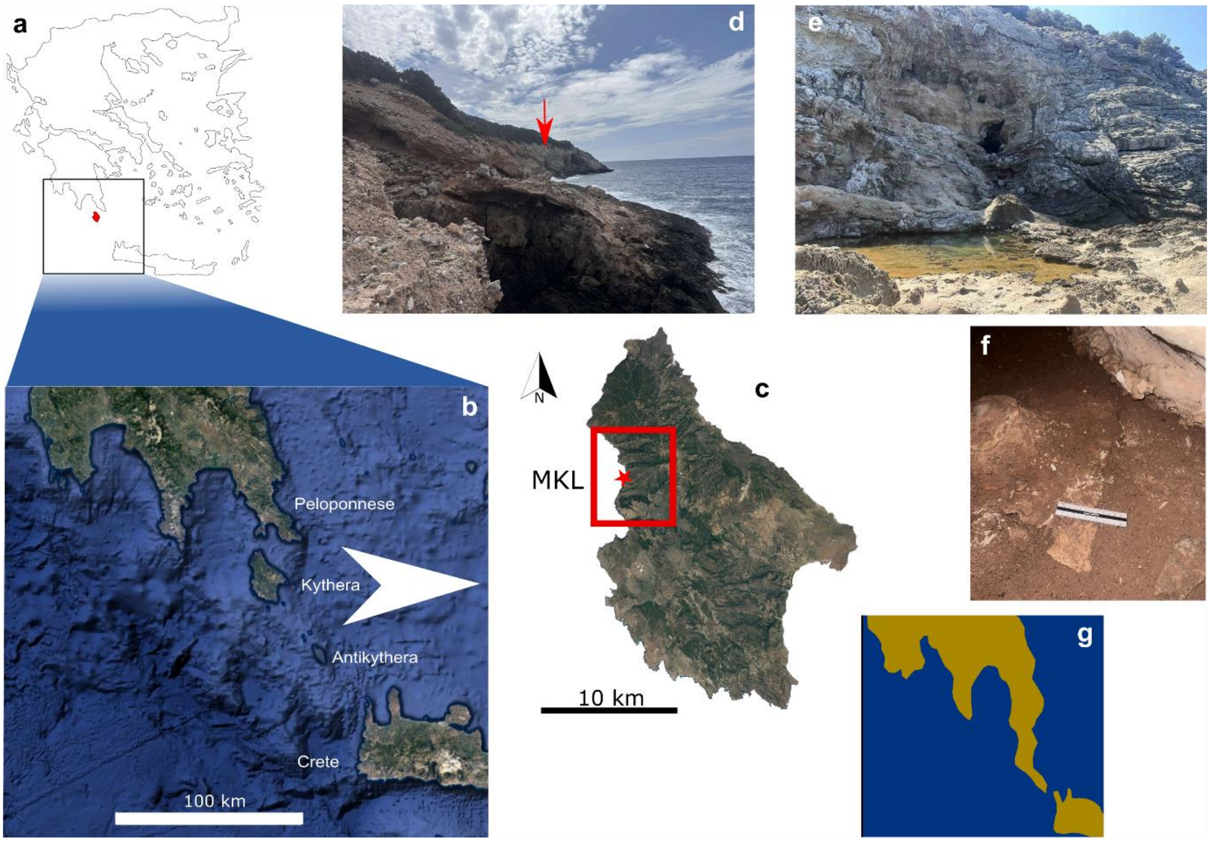

Figure 1. a) Map of Greece; the island of Kythera is marked in red; b) placement of Kythera Island in comparison with mainland and neighboring islands; c) topography of Kythera Island and area of discovery (red star); d) general view of the shoreline SW of Lykodimou Beach; the arrow indicates the Mikelis 1 cave; e) the entrance of the Mikelis 1 cave within the Tripolis limestones; f) image of the cave floor where crusts and bone fragments can be seen; g) simplified palaeogeography of the area during Pleistocene low sea level stands (modified from Sakellariou and Galanidou, 2017). Satellite images from Google Earth.

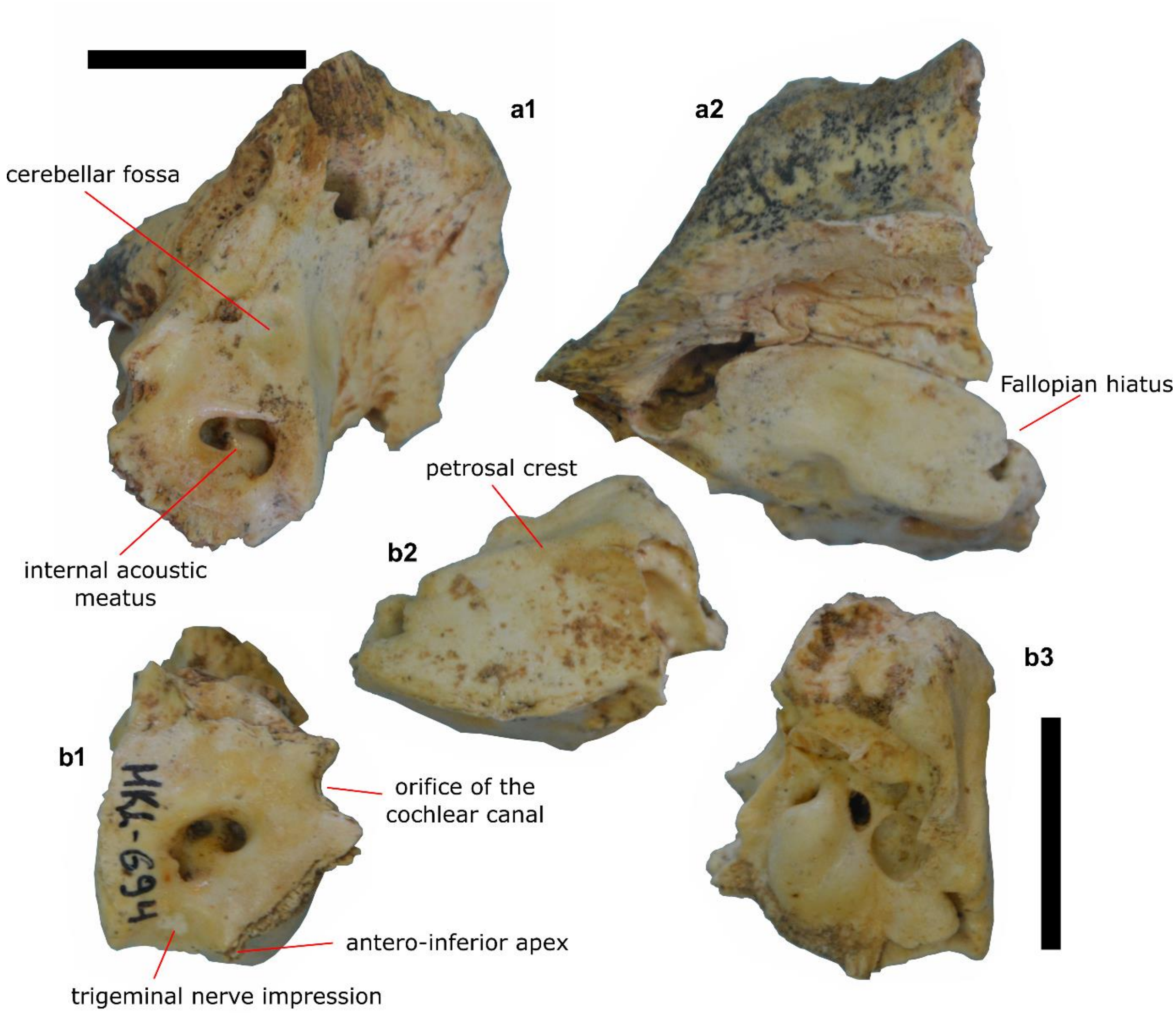

Figure 2. *Bos primigenius thrinacius* n. ssp. petrous bone remains from Kythera Island: a, right petrous bone MKL694 in medial (1) and rostral (2) views; b, left petrous bone MKL695 in medial (1), rostral (2) and lateral (3) views; Scale bar: 20 mm.

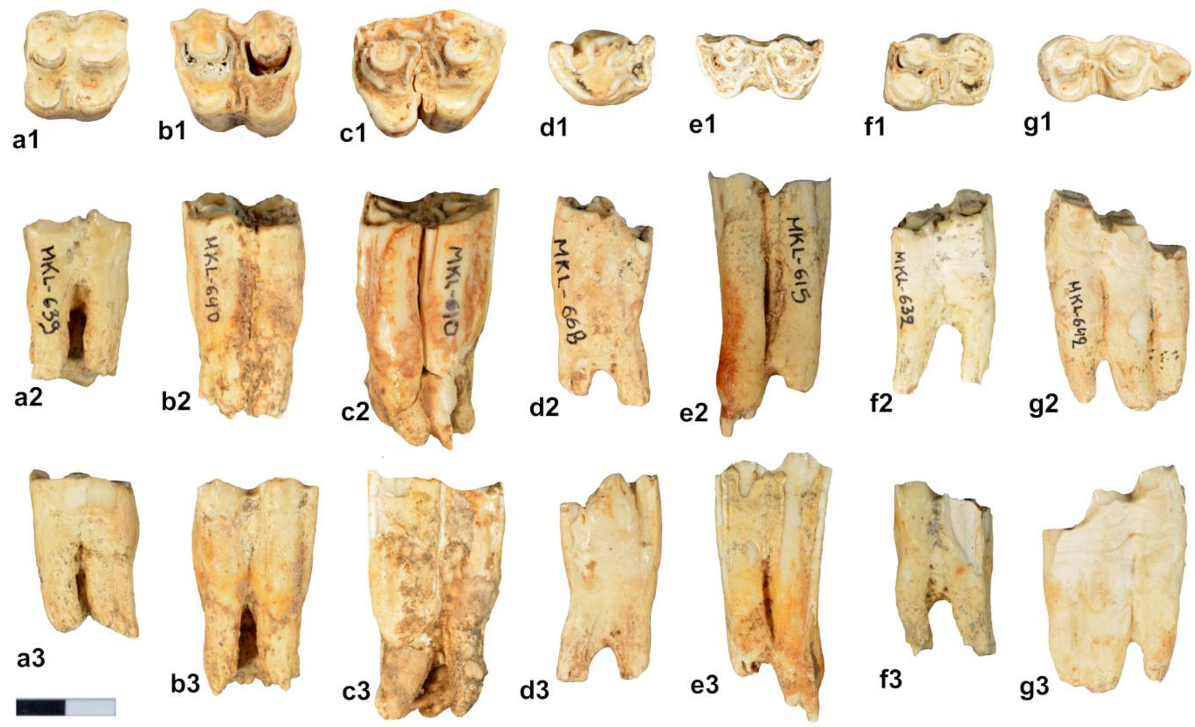

Figure 3. *Bos primigenius thrinacius* n. ssp. dental remains from Kythera Island: a, left M1, MKL639 in occlusal (1), lingual (2) and buccal (3) views; b, right M2, MKL640 in occlusal (1), lingual (2) and buccal (3) views; c, left M3, MKL610 in occlusal (1), lingual (2) and buccal (3) views; d, left p4, MKL668 in occlusal (1), lingual (2) and buccal (3) views; e, left m1, MKL615 in occlusal (1), lingual (2) and buccal (3) views; f, left m2, MKL632 in occlusal (1), lingual (2) and buccal (3) views; g, left m3 MKL642 in occlusal (1), lingual (2) and buccal (3) views. Scale bar: 20 mm.

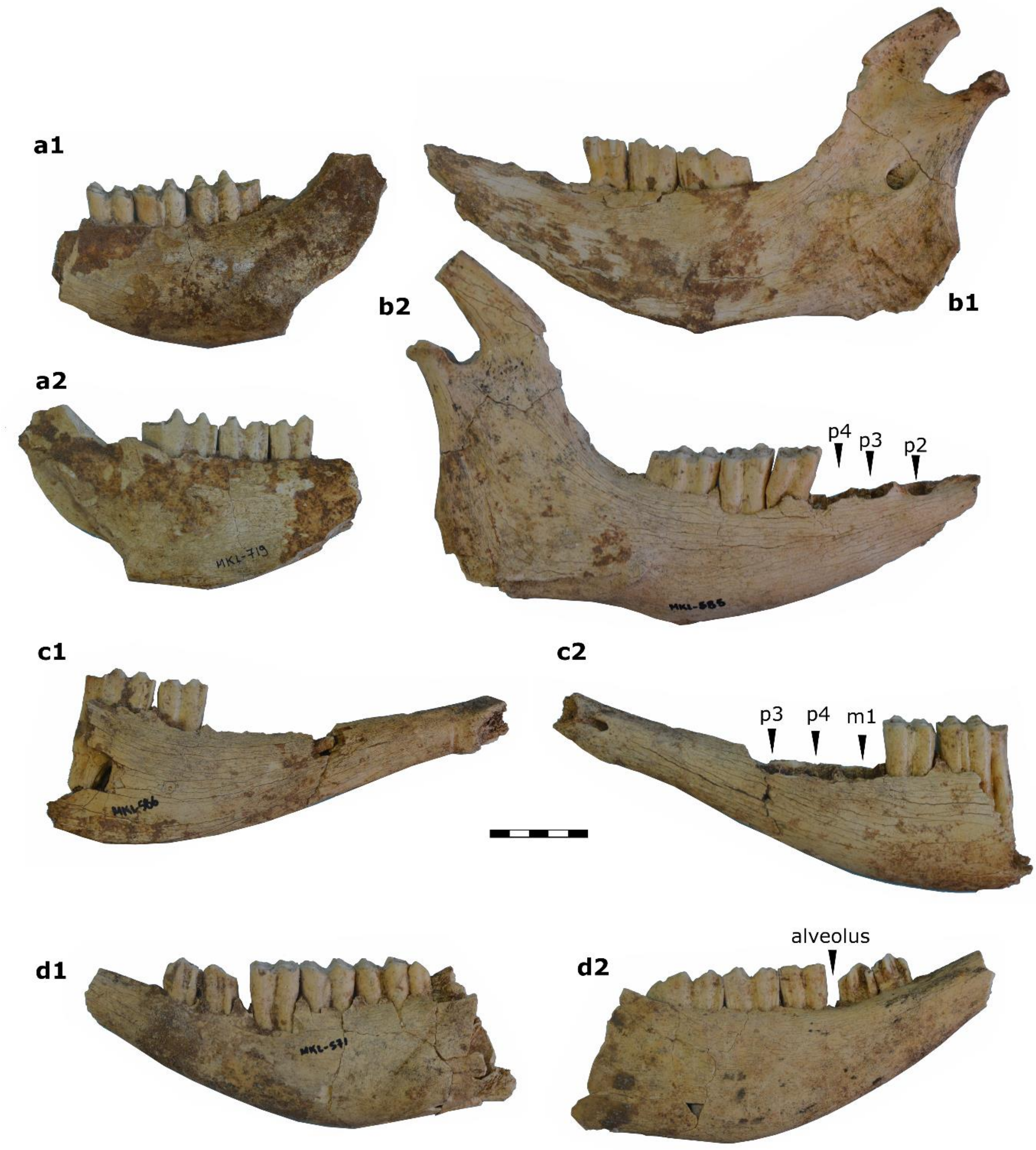

Figure 4. *Bos primigenius thrinacius* n. ssp. mandibular remains from Kythera Island: a, partial left hemimandible, MKL719 in buccal (1) and lingual (2) views; b, paratype partial right hemimandible, MKL585 in lingual (1) and buccal (2) views; c, partial left hemimandible, MKL586 in lingual (1) and buccal (2) views; d, holotype left partial hemimandible, MKL571 in buccal (1) and lingual (2) views. Scale bar: 50 mm.

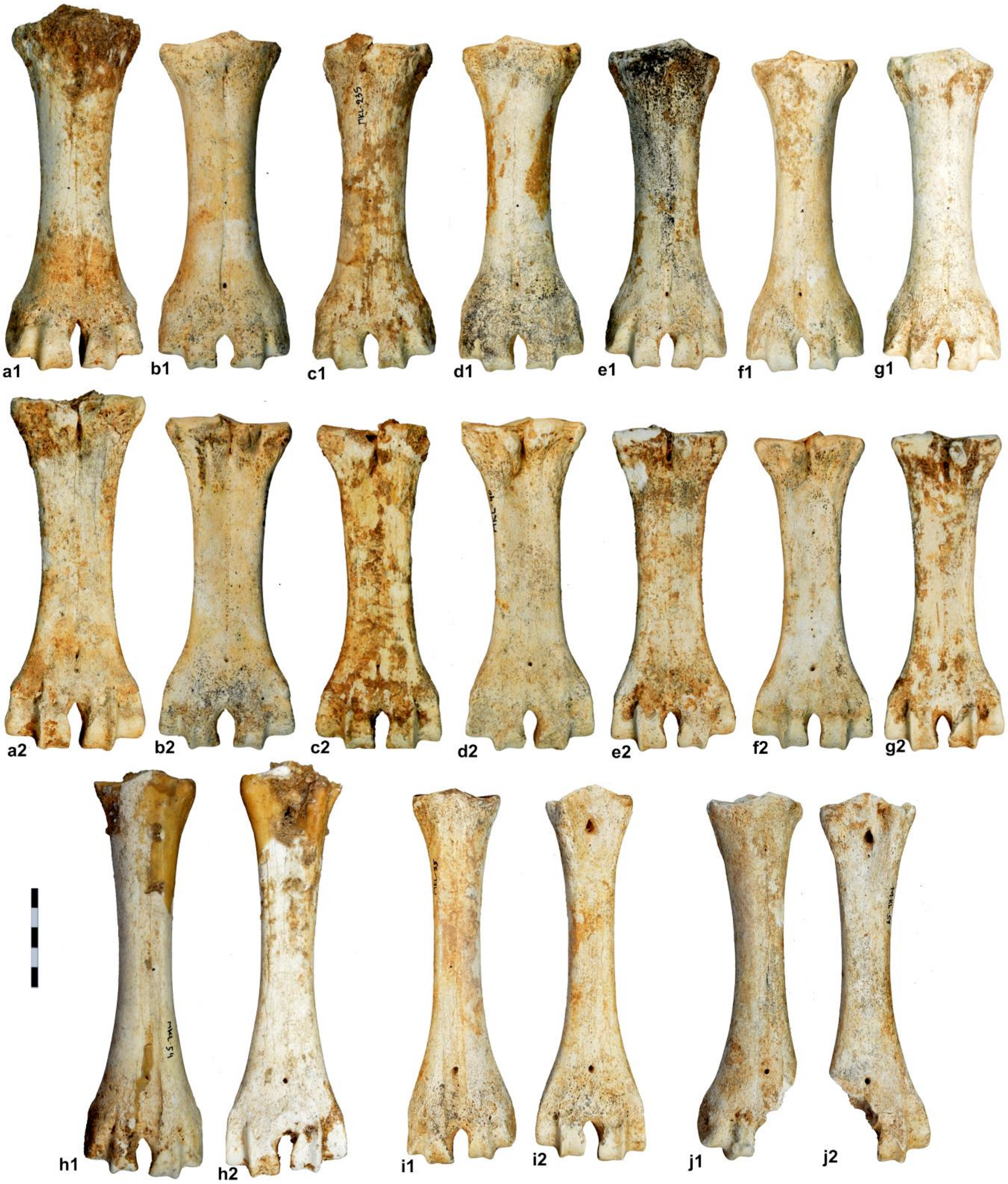

Figure 5. *Bos primigenius thrinacius* n. ssp. metapodials from Kythera Island: a, right male metacarpal, MKL142 (paratype) in anterior (1) and posterior (2) views; b, left male metacarpal, MKL46 in anterior (1) and posterior (2) views; c, left female metacarpal, MKL45 in anterior (1) and posterior (2) views; d, right female metacarpal, MKL48 in anterior (1) and posterior (2) views; e, right femle metacarpal, MKL235 in anterior (1) and posterior (2) views; f, right male metacarpal, MKL40 in

anterior (1) and posterior (2) views; g, left female metacarpal, MKL44 in anterior (1) and posterior (2) views; h, left male metatarsal, MKL54 (paratype) in anterior (1) and posterior (2) views; i, right female (?) metatarsal, MKL35 in anterior (1) and posterior (2) views; j, left female (?) metatarsal, MKL51 in anterior (1) and posterior (2) views. Scale bar: 50 mm.

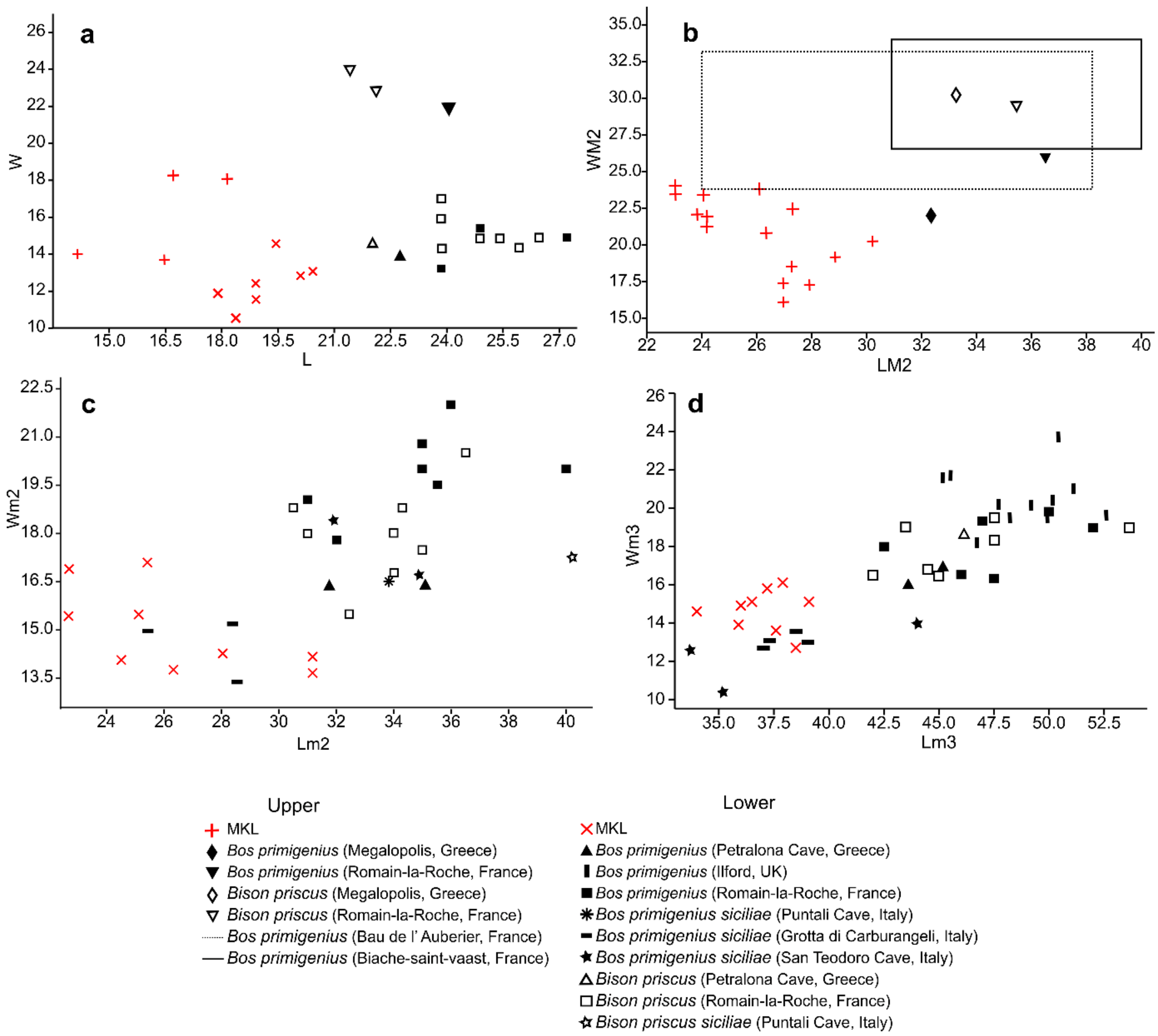

Figure 6. Bivariate plots of occlusal length (L) against width (W) of the fourth upper and lower premolars (a); second upper molar, M2 (b); second lower molar, m2 (c); and third lower molar, m3 (d) of Kythera taxon, compared with European samples/populations of *Bos* and *Bison*. Data from: Vercoutère and Guérin (2010), Wright (2013), Uzunidis-Boutillier (2017) and Maniakas (2019).

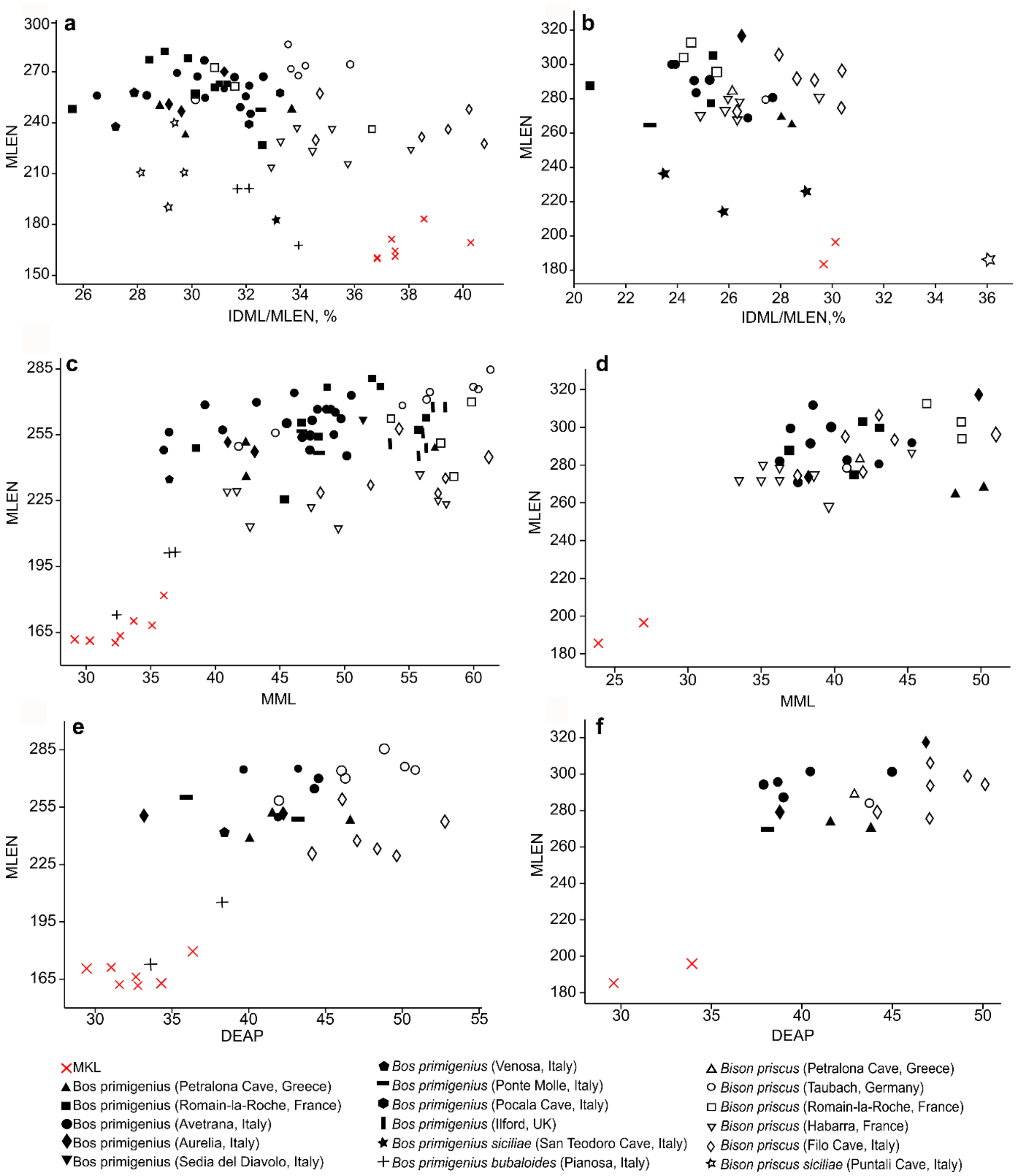

Figure 7. Bivariate plot of maximum length (MLEN) against index IDML/MLEN% (mediolateral diameter of distal epiphysis/maximum length %) to evaluate stoutness of Kythera *Bos* metacarpals (a), and metatarsals (b); MLEN against midshaft mediolateral (transverse) diameter (MML) of metacarpals (c), and metatarsals (d); and of MLEN against anteroposterior diameter (DEAP) of distal epiphysis of

metacarpals (e), and metatarsals (f), compared with the European specimens of *Bos primigenius* and *Bison priscus* from various localities. Data from: Sala (1986), Brugal (1987), Prat et al. (2003), Vercoutère and Guérin (2010), Pandolfi et al. (2011), Wright (2013), Maniakas and Kostopoulos (2017), Maniakas (2019) and Pandolfi (pers. data).

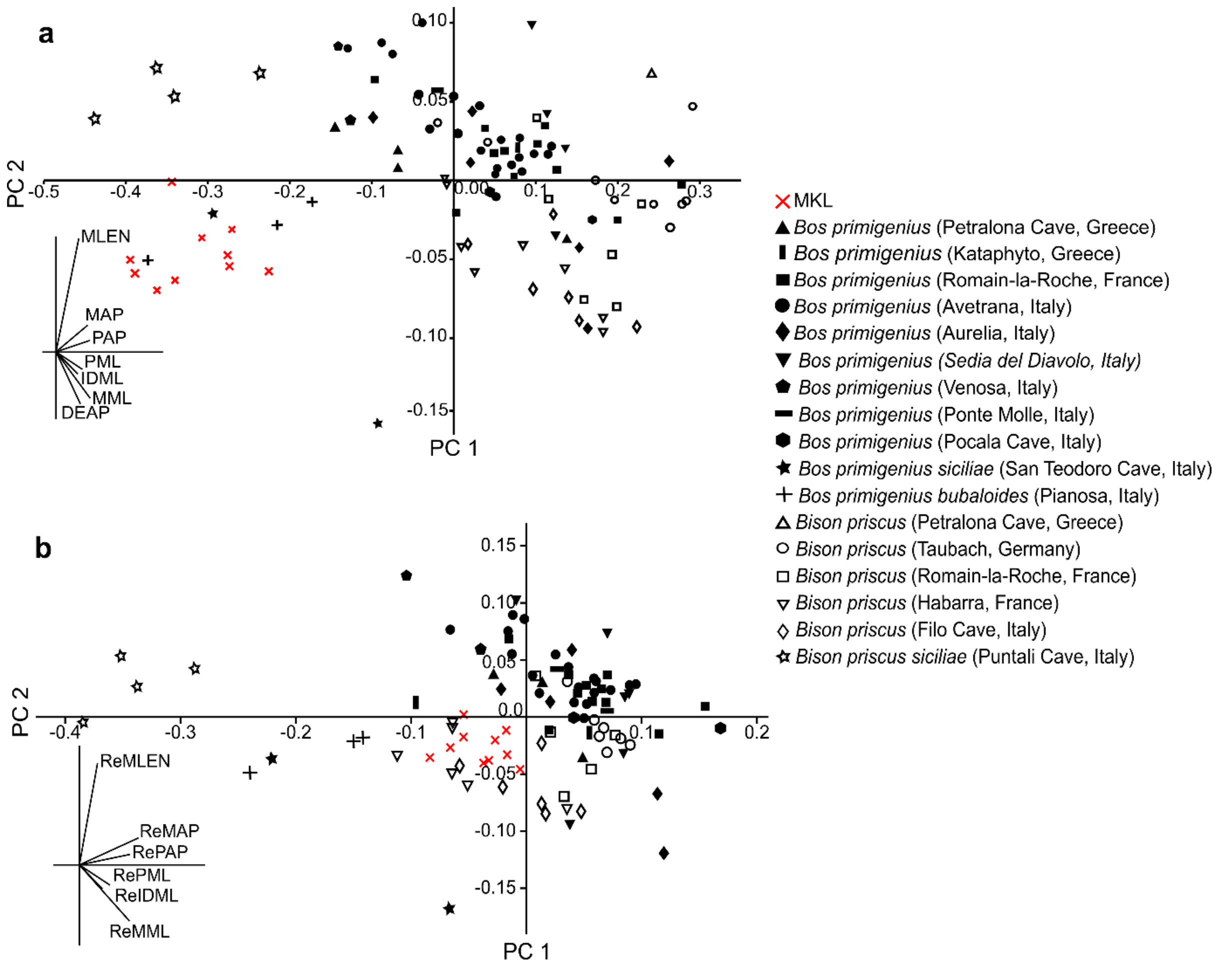

Figure 8. Bivariate plots of the first two principal component (PC) scores resulting from principal components analyses of metacarpal, based on seven log-transformed variables (a) and six MGSV variables following Scott and Barr (2014) (b). Abbreviations as in Table B.1. Data from: Sala (1986), Brugal (1987), Prat et al. (2003), Vercoutère and Guérin (2010), Pandolfi et al. (2011), Maniakas and Kostopoulos (2017), Maniakas (2019) Samartzidou et al. (2021) and Pandolfi (pers. data).

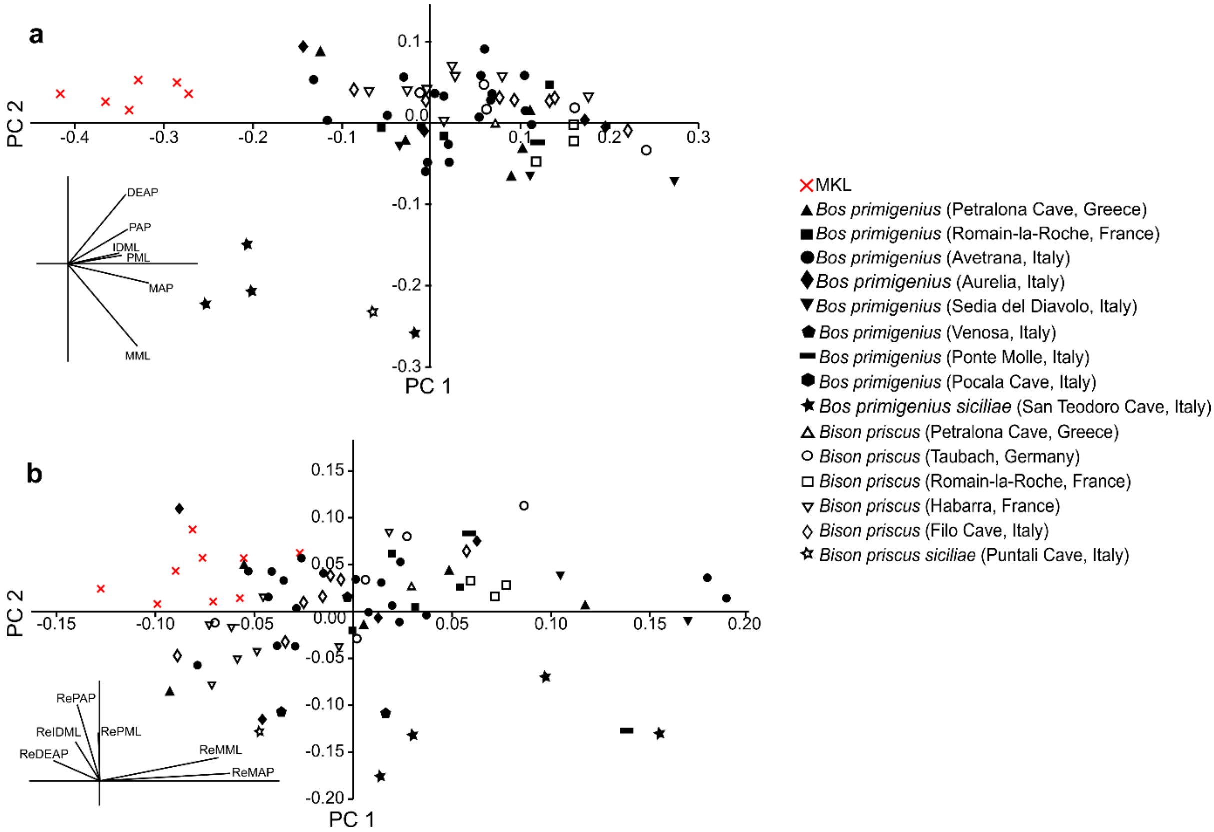

Figure 9. Bivariate plots of the first two principal component (PC) scores resulting from principal components analyses of metatarsal, based on six log-transformed variables (a) and six MSGV variables following Scott and Barr (2014) (b). Abbreviations as in Table B.1. Data from: Sala (1986), Prat et al. (2003), Vercoutère and Guérin (2010), Pandolfi et al. (2011), Maniakas and Kostopoulos (2017), Maniakas (2019) and Pandolfi (pers. data).

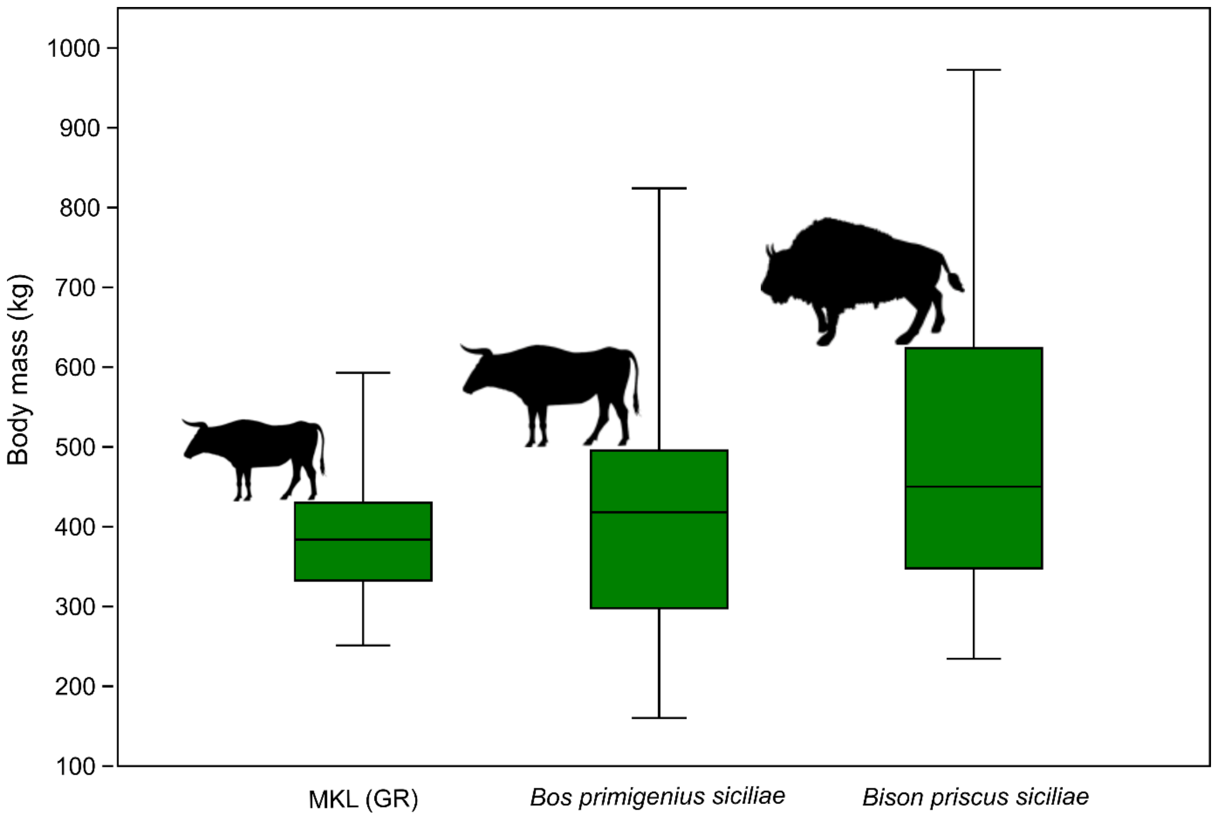

Figure 10. Box plots of Body Mass (BM) estimations based on five postcranial elements (Humerus, Radius, Tibia, Metacarpal and Metatarsal) following the 13 equations by Scott (1983). Weight values are in kg. MKL: Kythera, Greece (n=34 specimens), *Bos primigenius siciliae*, San Teodoro Cave, Italy (n=18 specimens), and *Bison priscus siciliae*, Puntali Cave, Italy (n=14 specimens).

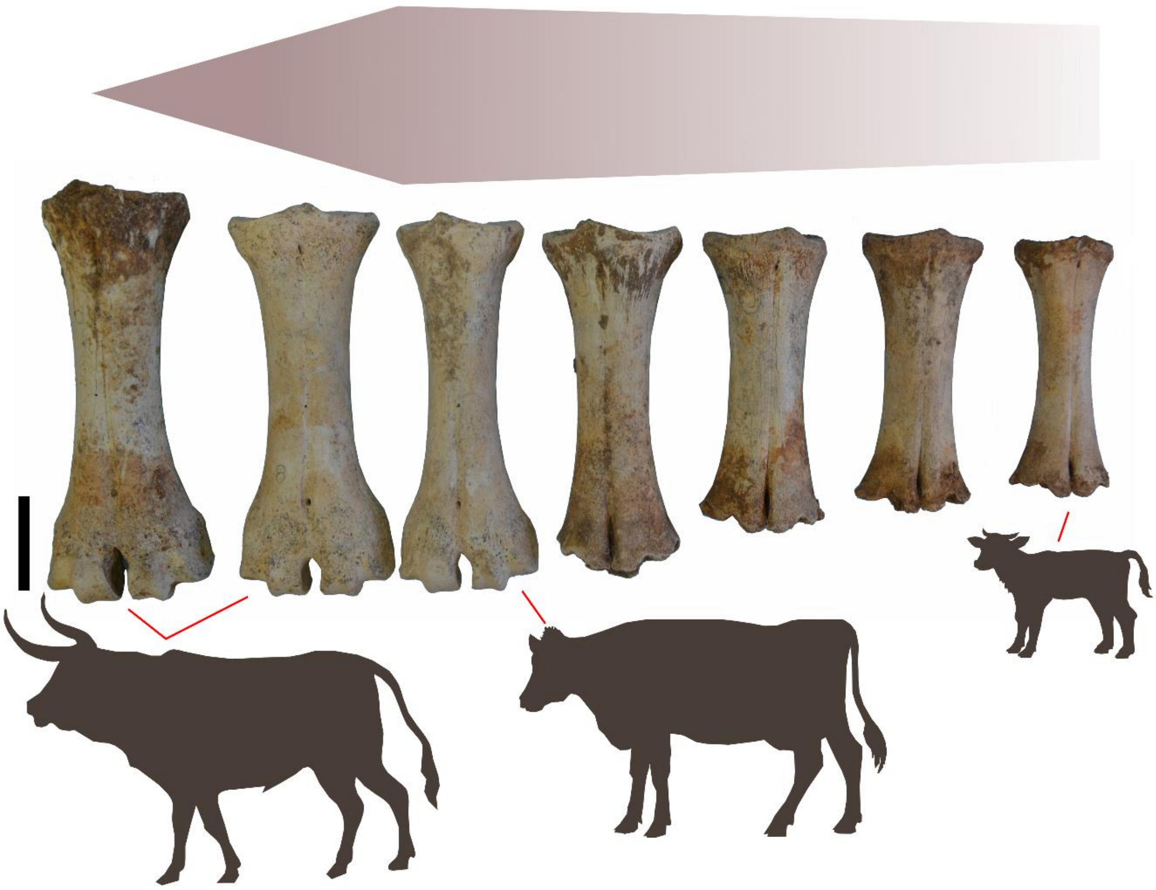

Figure 11. Morphometric changes of metacarpal bones of *Bos primigenius thrinacius* n. ssp. according to age and sex (from right to left: MKL235, MKL138, MKL137, MKL38, MKL48, MKL46, MKL142). Figurines represent calf, female and male individual of the taxon. Scale bar: 40 mm.

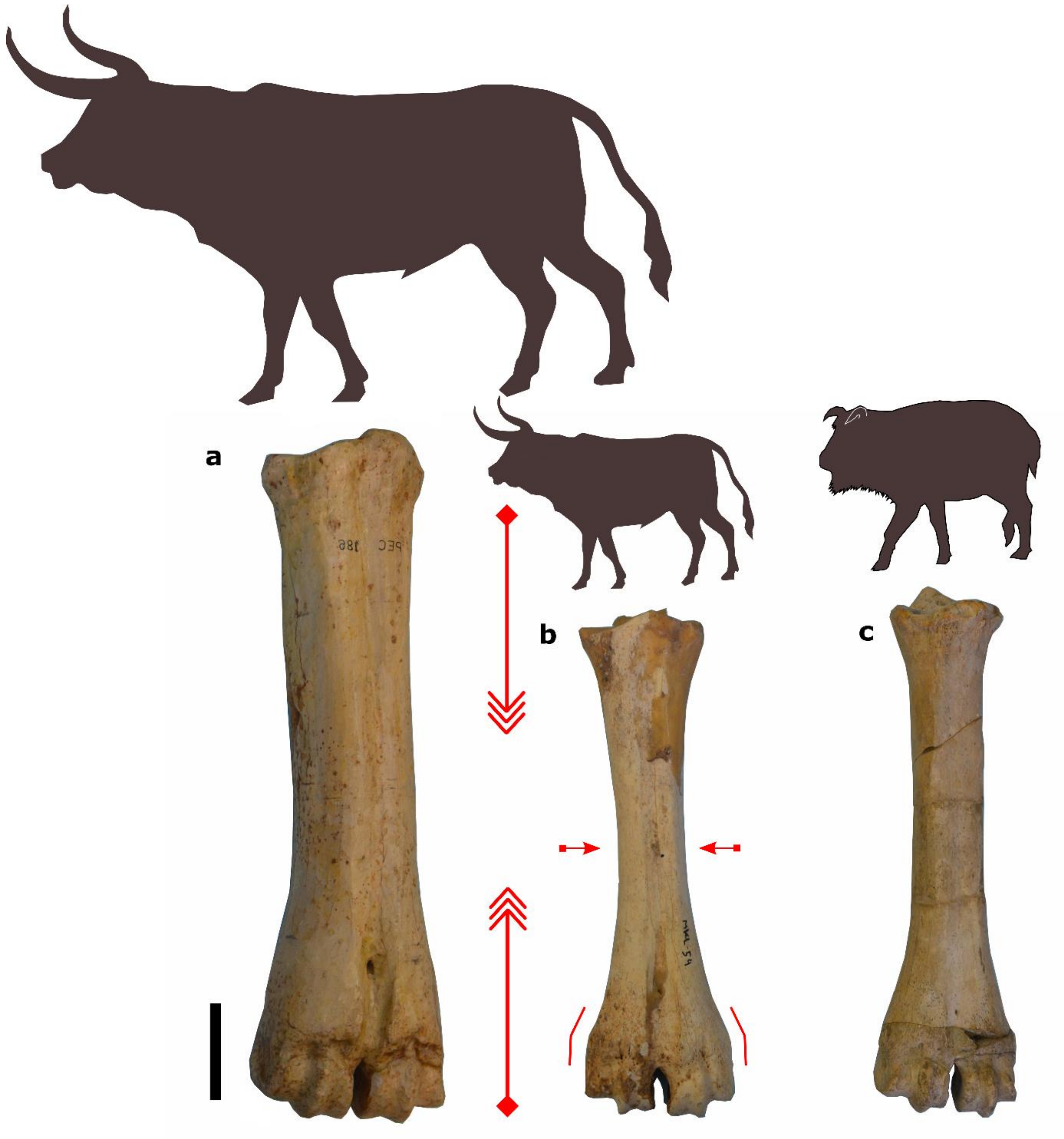

Figure 12. Basic transformations of (b) *Bos primigenius thrinacius* n. ssp. metatarsal (MKL54, left, anterior view) in comparison with (a) continental *Bos primigenius* from Petralona Cave (LGPUT PEC186, right-reversed); the degree of transformations is highlighted by contrasting the metatarsal of Petralona and Kythera *Bos* with that of the ovibovine *Soergelia* (c) from the lower Pleistocene site of Apollonia (APL58, left). Animal figurines depict body size difference between taxa. Scale bar: 40 mm.

Table 1. Summary of main morphological differences between *Bos* and *Bison* metapodials in comparison with Kythera and the two Sicilian bovins; extract from Table A.2 based on the postcranial discriminant characters by Bibikova (1958), Olsen (1960), Brugal (1983), McCuaig-Blackwill and Cumbaa, (1992) and Gee (1993).

Element	**Character**	***Bos***	***Bison***	**MKL**	***Bos primigenius siciliae***	***Bison priscus siciliae***
Metacarpal	Overall shape	Long and narrow	Wide and short	*Bison*-like	*Bos*	*Bison*
	Shape of distal metaphysis	Smooth	“Kinked”	*Bison*	*Bos*-like	*Bison*-like
	hamatum (lateral proximal) facet	Quadrant shaped	Triangular – rounded corners	*Bison*-like	*Bos*	*Bison*

	Shape of the distal metaphysis	Smoothly curving	“Kinked”	*Bison*	*Bos*	*Bison*
Metatarsal	State of fusion of the proximal facets	Well separated by a channel	Clearly confluent	*Bison*-like	*Bos*	*Bison*
	Tubercle on the posteromedial corner of the large cuneiform	Neither as strong nor as often	Strong	*Bison*	*Bos*	*Bison*

Table 2. Hindlimb and forelimb shortening indexes SI and insular body size divergence (Si) of MKL (see Table B.28) and Sicilian bovids (Rozzi, 2018; Rozzi et al., 2020).

Taxon	**Island**	**S_i**	**SI Mc**	**SI Mt**
Kytherian bovin	Kythera	0.48	0.681	0.681
Bos primigenius siciliae	Sicily	0.51	0.605	0.559
Bison priscus siciliae	Sicily	0.58	0.586	0.667

Table 3. The percentage (%) difference between male/female of Kytherian taxon, *Bos primigenius* and *Bison priscus* continental populations, as well as two Italian inslular bovins based on the average values of the five measurements of metacarpals. Measurement abbreviations as in Table B.1. Comparative data from Brugal (1987) and (Maniakas, 2019).

Taxon	**MLEN**	**PAP**	**PML**	**MML**	**IDML**
Kytherian bovin	5.7	9	10	10	8.5
Bos primigenius bubaloides (Pianosa island, Italy)	15.5	-	14.7	13	11.2
Bison priscus siciliae (Puntali Cave, Italy)	6.3	-4	18.8	-	16
Bos primigenius (MIS7 UK)	2.6	15	12	17	14.5
Bos primigenius (Romain-la-Roche, France)	6	9	11	14	11
Bos primigenius (Avetrava, Italy)	1	9.5	11	14	8
Bos primigenius (Lunel Viel, France)	3	16	16.5	23	16.5
Bison priscus (several sites)	2.5-6.5	11.5-17.5	13.5-16.5	17-21	12-15