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Proboscideans from the upper Miocene localities of Thermopigi, Neokaisareia and Platania (Northern Greece)

Proboscidiens des localités du Miocène supérieur de Thermopigi, Neokaisareia, et Platania (Grèce du Nord)

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ABSTRACT

In the present article, we study the proboscidean remains from three upper Miocene localities of Northern Greece: Thermopigi (Serres), Neokaisareia (Pieria) and Platania (Drama). The material from the Turolian locality of Thermopigi includes only postcranial specimens. The morphological features of the scapula indicate the presence of the deinotheriid *Deinotherium* sp., whereas most of the other specimens are morphologically distinct from *Deinotherium* and can be referred to Elephantimorpha indet. The material from Neokaisareia consists of a partial skeleton of a single individual and is attributed to the mammutid *Mammut* sp. (*M. obliquelophus*?). This taxon is known in Greece from the early–middle Turolian. The Platania proboscidean belongs to the tetralophodont amebelodontid *Konobelodon* cf. *atticus*. The genus *Konobelodon* was already present during the Vallesian of the wider area, but the lower tusk of the Platania shovel-tusker presents some morphological and metrical differences from the Vallesian representative, yet it has also smaller dimensions in its deciduous dentition than the morphologically similar Turolian specimens. The type locality of *K. atticus* is Pikermi (Attica, Greece), correlated to the middle Turolian, but the known biostratigraphic range of this species covers the entire Turolian. Platania is possibly correlated close to the Vallesian/Turolian boundary and the possible record of this species could document one of its earliest occurrences.

Keywords: Proboscidea, late Miocene, Turolian, *Mammut*, *Konobelodon*

RÉSUMÉ

Dans le présent article, nous étudions les proboscidiens fossiles de trois localités du Miocène supérieur de la Grèce du Nord: Thermopigi (Serres), Neokaisareia (Pieria) et Platania (Drama). Le matériel de la localité turolienne de Thermopigi ne comprend que des spécimens postcrâniens. Les caractéristiques morphologiques de l'omoplate indiquent la présence de la déinotheriide *Deinotherium* sp., tandis que la plupart des autres spécimens sont morphologiquement distincts de *Deinotherium* et peuvent être référés à Elephantimorpha indet.

Le matériel de Neokaisareia consiste en un squelette partiel d'un seul individu et est attribué au mammutide *Mammut* sp. (*M. obliquelophus*?). Ce taxon est connu en Grèce depuis le Turolien ancien–moyen. Le Platania proboscidean appartient au tétralophodonte amebelodontid *Konobelodon* cf. *atticus*. Le genre *Konobelodon* était déjà présent pendant le Vallésien de la région, mais la défense inférieure de l'amebelodontid de Platania présente quelques différences morphologiques et métriques par rapport au représentant de Vallésien, toutefois sa dentition à feuilles caduques présente également des dimensions plus petites que celles des spécimens Turolien de morphologie similaire. La localité type de *K. atticus* est Pikermi (Attique, Grèce), corrélée au Turolien moyen, mais son aire de répartition biostratigraphique connue couvre l'ensemble du Turolien. Il existe probablement une corrélation entre Platania et la limite Vallésien/Turolien, et le possible enregistrement de cette espèce pourrait documenter l'une de ses premières occurrences.

Mots clés: Proboscidea, Miocène supérieur, Turolien, *Mammut, Konobelodon*

1. Introduction - Fossiliferous localities

The palaeontological research and excavations carried out during the last years in upper Miocene sediments of Northern Greece led to the discovery of three fossiliferous localities – Thermopigi, Neokaisareia and Platania– and brought into light a great number of fossil vertebrates. Among them, proboscideans are represented by few but important specimens, which are described in the present article, aiming to add new taxonomical and biostratigraphical information, and contribute to improving our knowledge of this mammal group.

1.1. Thermopigi

The site of Thermopigi (Serres; SIT: Sidirokastro Thermopigi; Fig. 1a, b; N 41°17'16.0", E 23°21'51.0") yielded at least 1500 catalogued specimens unearthed from consolidated reddish sandstones. Paleontological research began in 1998 and the systematic excavations were initiated in 1999. In 2011, research continued with the collaboration of the University of Vienna (Prof. D. Nagel) until 2015. The fossils are often deformed and cracked due to post-depositional tectonic activity. The SIT fossils are stored at the municipal Palaeontological Museum in Thermopigi village. Preliminary faunal list includes *Pristifelis attica*, *Paramachairodus* sp., *Amphimachairodus* sp., *Adcrocuta eximia*, *Deinotherium* sp., Elephantimorpha indet., *Hipparion* cf. *dietrichi*, *Hipparion* cf. *matthewi*, *Ancylotherium pentelicum*, *Dihoplus pikermiensis*, *Microstonyx major*, *Propotamochoerus* cf. *hysudricus*, *Bohlinia* cf. *attica*, cf. *Palaeotragus rouenii*, *Helladotherium duvernoyi*, *Tragoportax* cf. *amalthea*, *Palaeoreas lindermayeri* and *Gazella* sp., and indicates a Turolian age for the locality (Geraads et al., 2007; Tsoukala, 2018; this study).

Figure 1.

1.2. Neokaisareia

Systematic excavations carried out at the site of Neokaisareia (Katerini, Pieria; NKP; Fig. 1a; N 40°16'14.7", E 22°25'22.1", elevation 143 m a.s.l.) were conducted in 2014 and 2016, and headed by Prof. D. S. Kostopoulos (University of Thessaloniki) and one of the authors (ET). Approximately 50 fossils, predominantly proboscidean remains, including both dental and post-cranial elements, were recovered disarticulated and belong to the same individual. Only a single right lower molar (NKP-6) of a small bovid, and an almost complete left tibia (NKP-16) and a proximal fragment of left ulna (NKP 50) of a medium-sized artiodactyl were found in association with the proboscidean. The fossils occurred in gray-yellowish fine sand (Fig. 1d, e), belonging to the upper Miocene Lagorachi Formation (Fm) of the Katerini Basin deposits (Sylvestrou, 2002). Overlying the middle Miocene Ryakia Fm, the lower part of the Lagorachi Fm consists of conglomerates, whereas in the middle and upper parts predominate sands (Sylvestrou, 2002). The presence in these sands of hipparionine horses (locality Palaio Keramidi) with similarities to those from the Turolian locality Vathylakkos from Axios Valley (Northern Greece), indicates a late Miocene age (Sylvestrou, 2002). Moreover, from the same locality and stratigraphic horizon with the previous specimens (personal communication Syrides, 2019), a proboscidean zygolophodont molar (discovered by local people during the ‘80s and brought to the LGPUT collections by Prof. Syrides in 1989) presents features consistent with an attribution to *Mammut* (GK observations), and supports additionally a post-Vallesian age. The pre-Pliocene age of the Lagorachi Fm is further corroborated by the fact that the overlying Sfendami and Makrygialos Fms include a characteristic “Paratethyan” mollusk faunas of “Pontian” age (late Turolian) the former, and a micro- and macrofauna of latest Miocene (latest Turolian, uppermost MN 13) the latter (localities Asprogiannos and Paliambela-A, B; Sylvestrou, 2000; 2002; Sylvestrou and Kostopoulos, 2007; Koufos and Vassileiadou, 2015). Therefore, a correlation to

the first part of the Turolian could be possible for NKP. The NKP material is stored at the building of the cultural association “Mastodontas” in the village of Neokaisareia.

1.3. Platania

The palaeontological research in the site of Platania (Drama, PLD; Fig. 1a, c; N 41°11'48.4" E 24°23'42.0", elevation 257 m a.s.l.) began in 2012, with the systematic excavations carried out from 2013 until 2016. Vertebrate fossils have been collected from fluvial yellow–brownish sands silts and clays. The collection includes 760 fossils and is stored at LGPUT. The fossils contain high levels of natural radionuclides and are dark-colored due to the high concentrations of manganese (Mn) during the fossilization processes (Zougrou et al., 2018). Most of the bones are found disarticulated and several are complete, whereas some of them present taphonomic modifications in the form of carnivore gnawing, possibly due to scavenging action of hyaenids. The preliminary faunal list includes *Testudo* cf. *graeca*, *Adcrocuta eximia*, *Konobelodon* cf. *atticus*, hipparionine horses, *Ceratotherium neumayri*, *Gazella* sp., *Gazella* cf. *ancyrensis*, *Prostrepsiceros* aff. *syridisi*, cf. *Palaeoreas*, *Palaeoryx minor*, *Tragoreas?* aff. *oryxoides*, *Miotragocerus* sp., giraffids, suids and cervids (Vlachos and Tsoukala, 2014; Tsoukala, 2018; Vasileiadis et al., in press; this study). As a whole, the PLD fossil assemblage clearly indicates a late Miocene age. The PLD bovids correspond to a transitional late Vallesian to early Turolian fauna and therefore an age close to the Vallesian/Turolian boundary is possible for the locality (Vasileiadis et al., in press).

Institutional abbreviations: **AMPG**, Athens Museum of Palaeontology and Geology (Greece); **FSL**, Faculté des Sciences de Lyon (France); **HLMD**, Hessisches Landesmuseum Darmstadt (Germany); **HNHM**, Hungarian National History Museum (Budapest); **LGPUT**, Laboratory of

Geology and Palaeontology, Artistotle University of Thessaloniki; **MNHN**, Muséum national d'Histoire naturelle (Paris, France); **NHMW**, Naturhistorisches Museum Wien (Austria); **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, München (Germany); **SU**, Palaeontology Museum of Sofia University (Bulgaria).

Dental abbreviations: **aprcc**, anterior pretrite central conule; **apocc**, anterior posttrite central conule; **DP**, upper deciduous premolar; **M**, upper molar; **ppocc**, posterior posttrite central conule.

2. Systematic palaeontology

Mammalia Linnaeus, 1758

Proboscidea Illiger, 1811

Deinotheriidae Bonaparte, 1845

Deinotherium Kaup, 1829

Deinotherium sp.

Locality: Thermopigi (Serres).

Age: Turolian (late Miocene).

Material: Left scapula fragment, SIT-607 (Fig. 2a–c; Table 1).

Description: On the lateral surface of the large scapula fragment SIT-607, the spine lacks acromion and metacromion, whereas small parts of the infra- and supra spinous fossae are preserved. The scapular neck is not notably constricted. The glenoid cavity is cranio-caudally elongated and sub-rectangular.

Remarks: According to Harris (1978), the scapula of *Deinotherium* is characterized by the absence of acromion and metacromion, whereas they are present in *Prodeinotherium* and

Elephantimorpha. This morphology can be observed in the scapulae of *D. levius* Jourdan, 1861 from Gusyatin (Ukraine; Svistun, 1974) and *D. proavum* (Eichwald, 1831) from Pikermi (Greece; MNHN-PIK-3609, Gaudry, 1862, 1867: pl. 25, fig. 1; Weithofer, 1888: pl. 19, fig. 2), Manzati (Romania; Ștefănescu, 1910: pl. 8) and Ezerovo (Bulgaria, SU; Kovachev and Nikolov, 2006). Therefore, SIT-607 can be assigned to *Deinotherium*. Allthough an attribution to *D. proavum* would be plausible taking into account the Turolian age of the locality, in the absence of dental deinotheriid material a specific attribution is not possible for the moment.

Figure 2.

Elephantimorpha Tassy and Shoshani 1997 in Shoshani et al., 1998

Elephantimorpha indet.

Locality: Thermopigi (Serres).

Age: Turolian (late Miocene).

Material: Right humerus, SIT-605; right ulna, SIT-609; left proximal ulna articulated with proximal radius, SIT-602; left femur, SIT-601; right tibia, SIT-608; left tibia, SIT-28; proximal epiphysis of left tibia, SIT-606 (Fig. 2d–p; Table 1).

Description: In the humerus SIT-605 the head is eroded and the distal epiphysis with the trochlea is missing (Fig. 2d). The diaphysis is proportionately long and slender above the supracondyloid crest. The deltoid tuberosity is rather weak. In the distal extremity, the lateral border of the lateral epicondyle is missing. The medial epicondyle is markedly pronounced. The ulna SIT-609 is almost complete, missing only the distal epiphysis (Fig. 2e–g). It belongs to an ontogenetically young individual, because the proximal epiphysis is incompletely fused. The olecranon is relatively short; the medial and lateral coronoid processes form a large obtuse angle, where the ulna articulates with the radius. The corpus is elongated and slender. In the ulna SIT-

602 the tuber olecrani is missing, but the process smoothly overhangs the shaft (Fig. 2h). The hook-like anconeal process is preserved and projects cranially above the well-preserved semilunar notch. The proximal extremity of the femur SIT-601 lacks most of the epiphysis with the head and the major trochanter, but part of the trochanteric fossa is preserved on the caudal aspect (Fig. 2i, j). On the medial border of the proximal extremity, the lesser trochanter is well developed. The shaft is long but relatively slender, flattened caudally, with slightly concave medial border and almost straight lateral one. At the distal extremity, the medial epicondyle is pronounced, whereas the lateral one is very weak. The medial condyle is about twice the size of the lateral one and projects distally (Fig. 2k, l). Of the three tibia specimens, SIT-28 and 608 are more complete and have approximately the same dimensions (Fig, 2m, Table 1). Both are relatively elongated and slender bones with weak cranial border. The cochlea of SIT-28 is ovoid and shallow (Fig. 2n). In SIT-606 the condyles are well preserved and subcircular in shape (Fig. 2o, p); this specimen matches with SIT-28 forming one single and complete tibia.

Remarks: About 20 specimens of the SIT faunal assemblage are attributed to proboscideans. Most of them are indeterminable bone fragments, whereas 10 could be attributed to a specific skeletal element. The SIT proboscidean sample includes exclusively postcranial elements. The lack of dental material, the limited number of securely identified comparative material, and the unknown inter- and intrageneric morphological variability, makes safe identifications difficult. Apart from the deinotheriid scapula described above, the most of the SIT postcranials are morphologically distinct from *Deinotherium* and are attributed to Elephantimorpha indet. In particular, based on the comparison with postcranial specimens of *Deinotherium proavum* from Pikermi (MNHN; Gaudry, 1862, 1867: pl. 25, figs. 4, 5), Manzati (Ștefănescu, 1910: pl. 5, 9, 11) and Ezerovo (SU; Kovachev and Nikolov, 2006), we can conclude the following for the SIT postcranials:

- The humerus of deinotheriids differs from that of elephantimorphs in the less protuberant epicondyles in the distal extremity (Harris, 1978). In SIT-605 the lateral epicondyle is

strongly protuberant and different from the less expressed one of *D. proavum* from Manzati and Ezerovo. Moreover, compared to the latter two specimens, whose general humerus form appears to be short and wide, the SIT humerus is long and slender (Fig. 2d).

- In the deinotheriid ulna, the olecranon is stout and large (Harris, 1978), whereas in SIT-609, the olecranon is rather short (Fig. 2e, g). Moreover, the angle formed between the medial and lateral coronoid processes for the articulation of the ulna with the radius is more obtuse in SIT-609 than the ulna of *D. proavum* from Pikermi (MNHN-PIK-3663). The anconeal process of the ulna SIT-602 is pointed (Fig. 2f), whereas in MNHN-PIK-3663, Manzati and Ezerovo, this projection is much reduced. The two SIT ulnae belong possibly to two different genera.
- According to Harris (1978), in the femur of deinotheriids the medial epicondyle is located lower compared to its higher position in elephantimorphs. In the femur SIT-601 the medial epicondyle is located in a higher position than in *D. proavum* from Manzati and Ezerovo (Fig. 2).
- The SIT tibiae (Fig. 2) differ from those of *D. proavum* from Pikermi (MNHN-PIK-3664), Ezerovo and Manzati, which have more robust proximal and distal ends compared to the shaft.

Table 1.

Mammutida Tassy and Shoshani 1997 in Shoshani et al., 1998

Mammutidae Hay, 1922

Mammut Blumenbach, 1799

***Mammut* sp. (*M. obliquelophus*?)**

Locality: Neokaisareia (Katerini, Pieria).

Age: Turolian, late Miocene.

Material: Right I2, NKP-1; axis, NKP-2; 2 thoracic spinal processes, NKP-5, 8; vertebra fragments, NKP-4, 9, 18; 31 rib fragments, NKP-3, 7, 10–12, 14, 15, 19–25, 31–48; bone fragments, NKP-17, 26–30; right humerus fragment (diaphysis and distal extremity), NKP-13 (Fig. 3; Tables 1, 2).

Description: The absence of an enamel cap in the upper tusk NKP-1 in combination with its preserved length (930 mm), maximum diameter (87.3 mm) and maximum circumference (275 mm) indicate that it represents a permanent tusk of an adult individual (Fig. 3b–e, Table 1). The tusk is almost straight with a slight dorsal (upward) curvature in lateral view, slender and torsioned (twisted). The tusk's circumference and dorso-ventral/medio-lateral diameters achieve their maximum values between 50 and 60 cm from the tip, and slightly decrease towards the base. Longitudinal furrows run along the tusk, clearly visible at its proximal part. The cross-sections are oval at the proximal end and become more circular towards the distal end (Fig. 3f). Enamel band is absent. The tip is rounded and a swallow groove exists close to it (Fig. 3b–d). Towards the distal end the dentine is thick, whereas towards the proximal end it becomes thinner and the pulp cavity is open; thus, although some fragments of the most basal were detached, the tusk preserves most of its length and is regarded as almost complete (Tassy, 2014). Therefore, the part which presents clearly the longitudinal furrows and is mory strongly torsioned was probably embedded in the sockets within the cranium.

The axis NKP-2 is poorly preserved and eroded (Fig. 3g). It is a large vertebra with a broad vertebral foramen, with well-defined odontoid process (dens) and antero-posterior notch along the crest of the spine. The ventral crest (the ventral ridge and the two central tubercles) is weak.

The humerus NKP-13 is missing the proximal extremity, but preserves the entire diaphysis with the deltoid tuberosity and the distal extremity (Fig. 3h–j; Table 1). In cranial view, the deltoid tuberosity is relatively weak and the medial border of the diaphysis concave. The

lateral condyloid crest extends laterally in an oblique angle relative to the long axis of the bone and then turns distally to form the lateral border of the musculospiral groove. The medial epicondyle is located slightly more distally than the lateral one. In the distal articular surface for the ulna, the trochlea is formed by the larger medial and the smaller lateral condyles, separated by a groove.

Figure 3.

Table 2.

Remarks: The proximate spatial accumulation of the NKP proboscidean bones and the consistency in size indicate that most possibly all belong to a single individual. The skeletal remains are disarticulated and there is no anatomical connection between the bones (Fig. 3a). Post-depositional cracking is evident on all bone surfaces.

Proboscidean genera known from the late Miocene of western Eurasia include the deinotheriid *Deinotherium*, the mammutids *Zygolophodon* and *Mammut*, the gomphotheriids *Gomphotherium*, *Tetralophodon* and *Anancus*, the choerolophodontid *Choerolophodon*, the amebelodontid *Konobelodon* and the elephantid *Stegotetrabelodon*. The morphology of the NKP tusk is markedly different from the strongly curved and robust lower tusks of *Deinotherium* (e.g., Tassy, 2016) and can be allocated to upper tusk of an elephantimorph [or elephantoid *sensu* Tassy (1988); clade (Mammutida, Elephantida)] proboscidean (Shoshani 1996a, 2002). The absence of an enamel band excludes an attribution to *Gomphotherium* and *Zygolophodon*, the latter additionally bearing upper tusks with ventral curvature (Pontier, 1926; Osborn, 1936: fig. 657; Tobien, 1996). The rest of the aforementioned genera lack enamel bands on their upper tusks (derived trait). The tusks of the European *Tetralophodon longirostris* (Kaup, 1832) are ventrally curved (Tassy, 1999). *Konobelodon* has more curved upper tusks than the NKP one and with no torsion (Pestszentlörinc, Hungary, HNHM-V.79.34; Schlesinger, 1922: pl. 2, figs. 1, 2,

pl. 3, fig. 1) and Oryahovo, Bulgaria, SU; Bakalov and Nikolov, 1962: pl. 67, figs. 2, 2a, pl. 68, fig. 3). *Choerolophodon*, the most well-documented proboscidean during the late Miocene of Southeastern Europe-Southwestern Asia, shows strongly curved, double twisted (outwards and upwards) and robust upper tusks, increasing significantly in circumference and diameter from the distal to the proximal end (e.g., Nikiti-2, Greece; Konidaris and Koufos, 2016; Jafarzadeh and Konidaris, accepted). The upper tusks of *Stegotetrabelodon* are straight but not twisted upwards (Tassy, 1999). The only candidate genera having straight/almost straight, and in some cases twisted tusks, are *Anancus* and *Mammut* (Tobien, 1996; Tsoukala, 2000; Athanassiou, 2016; Tsoukala and Mol, 2016). Yet, the upper tusks of the late Miocene *Anancus lehmanni* from Hohenwarth (Austria) they do not show torsion and although they are almost straight, they present a slight ventral (downward) curvature (Fig. 4; Zapfe, 1957; Konidaris and Roussiakis, 2019), that is the tusk retains the plesiomorphic condition within Proboscidea (Shoshani, 1996b; Tassy, 1996, 1999). In this trait, NKP-1 possesses and shares with *Mammut* the derived condition within the order: straight or dorsally (upward) curved upper tusks. The only known upper tusk of the late Miocene *Mammut* representative, *M. obliquelophus* (Mucha, 1980), is known from the Balta Sands in Podolia (Ukraine; originally as "*Mammut praetypicum*"; Kubiak, 1972; Markov, 2008). The Balta tusk is almost straight with a slight dorsal curvature in lateral view and therefore similar to the NKP one (Figs. 3b, 4b). From the provided figures in Kubiak (1972) and because the tusk is inside the maxillary alveolus, the presence or absence of a torsion (present towards the distal end of NKP tusk) cannot be evaluated. Similarly, almost straight and with very weak curvature are the upper tusks of the *Mammut* belonging to the "Nikolaef skeleton" found near the town of Voskresenske (Ukraine; Brandt, 1860; Pavlow, 1894). Comparable morphological features with the NKP tusk (although more curved) are present in the two pairs of upper tusks of *Mammut borsoni* (Hays 1834) from Milia in Grevena, Greece (relatively straight with a dorsal curvature, slender, torsioned, presence of longitudinal furrows on the proximal part), although in both pairs there is asymmetry between right and left ones in

terms of curvature, torsion and length (Tsoukala, 2000; Tsoukala and Mol, 2016). The dimensions of the Milia upper tusks are clearly larger than the NKP one, but they belong to very robust adult male individuals (bearing the M2–M3), whereas the NKP belongs to an ontogenetically younger (and/or female) individual, considering the smaller dimensions of the humerus, whose distal epiphysis is not fully fused (see below).

Figure 4.

The shallow groove near to the upper tusk's tip raises the question of the cause of its formation (Fig. 3b–d). Based on observations of recent elephants, this morphology, referred to as "grass-notch", is related to the laterality of tusks (tuskedness), that is the side preference for the more frequent use of right or left upper tusk (Marais and Hadaway, 2008, Bielert et al., 2018). The tusk that it is used more than the other is called the master tusk, and in addition to its shorter length and the more rounded tip due to greater wear, it occasionally bears a groove near the tip. This is the result of the constant action of grass, which wears a transverse furrow in the tusk and to the beating grass, branches and roots over the tusk to clean the food of dirt (Capstick, 1977; Shoshani, 2002). Therefore, the combination of a rounded tip and the transverse groove near it indicate that right upper tusk NKP-1 represents possibly the master tusk of the individual.

If a similar epiphyseal sequence of the skeletal elements as the recent elephants is assumed for *Mammut*, then the incompletely fused NKP distal humerus epiphysis (Fig. 3g–i), which is the first long bone extremity to be fused in the African elephant *Loxodonta africana*, suggests a young adult individual (considering also the size of the upper tusk), regardless of whether it was male or female (Haynes, 2017). The NKP humerus is similar to the humerus MIL-100 of *M. borsoni* from Milia (Tsoukala, 2000), apart from the weaker deltoid tuberosity, the less pronounced medial and lateral epicondyles, and the overall smaller dimensions of the NKP specimen, but these features are related to the fact the MIL-100 belongs to a robust adult

male. Indeed, NKP-13 is metrically close and morphologically similar to the female humerus MIL-160 (Tsoukala and Mol, 2016), in which the deltoid tuberosity and the epicondyles are less developed.

The overall similarities of NKP-1 with *Mammut* permit the attribution to this genus. According to Markov (2008) the distinguishing features between the late Miocene *M. obliquelophus* and the Pliocene–Early Pleistocene *M. borsoni* are the length of the mandibular symphysis and the degree of development of the lower tusks. In particular, the symphysis is longer than the tooth row and equipped with well-developed tusks in *M. obliquelophus*, whereas in *M. borsoni* it is much reduced and bears small tusks. However, these features cannot be examined in the available NKP material. Although extracting taxonomical results based on chronological data (late Miocene age of the NKP find-bearing sediments) is not favoring, an allocation to *M. obliquelophus* could be plausible judjing from the similar morphology of the upper tusk NKP-1 with that from the Balta Sands, associated with a mandible having long symphysis and well-developed lower tusks (Kubiak, 1972). Nonetheless, we prefer to adopt a more cautious approach and pending more material from the Turolian *Mammut*, we allocate the NKP skeleton to *Mammut* sp. (*M. obliquelophus*?).

Elephantida Tassy and Shoshani 1997 in Shoshani et al., 1998

Amebelodontidae Barbour, 1927

Konobelodon Lambert, 1990

Konobelodon* cf. *atticus

Locality: Platania (Drama).

Age: late Miocene (close to the Vallesian/ Turolian boundary).

Material: lower tusk fragment, LGPUT-PLD-642; left maxilla fragment with DP2–DP3, LGPUT-PLD-92 (Figs. 5, 6; Table 3).

Description: The lower tusk fragment PLD-642 represents a permanent tusk of an adult individual (Fig. 5 a–c). The outer surface is not well preserved; it shows also several cracks and it is slightly deformed. The preserved length is 154 mm and its cross-section measures 119 × 77 mm. It has a slightly dorsoventrally flattened pyriform cross-section, rounded medial border and has a weak longitudinal dorsal concavity. The tusk consists of a core of tubular dentine and intervals that are filled with sediment (Fig. 5c). The dentinal tubules, where present, are closely spaced.

The maxilla fragment PLD-92 bears the well preserved DP2 and DP3 (Fig. 6a–c). The DP2 is oval in shape with two slightly worn lophs, the distal one broader than the mesial one. The enamel is wrinkled. A mesial cingulum is developed mesio-lingually; it is formed by low conelets in the mesial side, which progressively increase in height until they connect with the protocone. In the first loph, para- and protocone are appresed to each other. The paracone has a pyramidal shape, and it is the strongest and highest cusp of the tooth, whereas the protocone is much weaker and lower. A transverse valley, more open lingually, clearly separates the mesial and distal lophs. In the second loph, metacone and hypocone (its lingual side is damaged) are low, almost aligned and connected through worn mesoconelets; a median sulcus is visible. The distal cingulum extends towards the labial side.

The DP3 is trilophodont with anteroposteriorly compressed lophs, the third one being the broadest and with well-marked second ento- and ectoflexus (Fig. 6a–c). The tooth is slightly worn and the enamel is wrinkled as a character of the deciduous teeth. The lophs are divided by a median sulcus into half-lophs and the transverse valleys are open both lingually than labially. The mesial cingulum is low but strong and consists of a series of worn cusplets, connected to the first pretrite half-loph. The first and second pretrite half-lophs are located slightly mesially in relation to the posttrite ones, whereas the third pretrite and posttrite half-lophs are opposite each other. In the first and second interlophs, there is weak alternate connection between post- and

pretrite half-lophs, established between ppocc1 and aprcc2, and ppocc2 and aprcc3. The distal cingulum is narrower than the mesial one.

Figure 5.

Table 3.

Remarks: The adult lower tusk from Platania differs from those of the gomphotheriids *Gomphotherium* and *Tetralophodon*, the amebelodontids *Archaeobelodon* and *Protanancus*, and the elephantid *Stegotetrabelodon*, which are smaller in size and/or more dorsoventrally compressed (Fig. 5d), and have inner morphology formed exclusively from concentric lamellar dentine. The lower tusks of the Gebel Sémène (Tunisia) and Crevilente 2 (Spain) taxon/taxa with possible *Stegotetrabelodon* affinities are large, but consist also of concentric lamellar dentine (Bergounioux and Crouzel, 1956; Tassy, 1999, 2016; Mazo and Montoya, 2003; Mazo and van der Made, 2012). The inner morphology of the PLD tusk clearly indicates affinities with the amebelodontids bearing tubular dentine that is *Platybelodon* (trilophodont grade, DP3 with two lophs), *Torynobelodon* (*T. loomisi* Barbour, 1929; unknown grade) and *Konobelodon* (tetralophodont grade, DP3 with three lophs). The lower tusks of the Old World *Platybelodon* are plate-like and strongly dorsoventrally flattened (Fig. 5d; e.g., Maglio, 1969: figs. 1, 2; Gaziry, 1976: pl. 3 fig. 2). The lower tusk of the North American *Torynobelodon loomisi* is also more dorsoventrally flattened with a different cross-sectional shape than the PLD one, having wide and straight medial border, roughly the same width in the middle and lateral parts, and with very shallow dorsal and ventral concavities (Fig. 4d; Barbour, 1929: fig. 98). On the other side, the cross-sectional diameters of the PLD tusk are plotted well within the convex hull of the Holarctic *Konobelodon*. Although the PLD tusk is not well-preserved, its dimensions separate it from most of the *K. robustus* Wang et al., 2016 sample from China, as well as from *K. britti* Lambert, 1990 from the U.S.A., *K. cyrenaicus* (Gaziry, 1987) from Sahabi (Libya) and

Konobelodon sp. from Kertch (Ukraine), which show a smaller dorso-ventral diameter (Fig. 5d). The lower tusk from Yulafli (late Vallesian; Turkey) is slightly more compressed than the PLD one, has a more angular medial border and bears two longitudinal dorsal concavities (Geraads et al., 2005). The PLD tusk preserves a similar height with *K. atticus* (Wagner, 1857) and morphologically, its more pyriform cross-sectional shape with rounded medial border fits well with the *K. atticus* sample from the Turolian localities Maragheh (Iran; NHMW-1893/0012/0006), Pikermi (Greece; AMPG- PA1972/61) and Pestszentlörinc (Hungary; HNHM-V.79.34) (Fig. 5d; Konidaris et al., 2014: figs. 5, 6g–j).

The bunodont and trilophodont DP3 with clearly formed third loph and distal cingulum, indicates that the maxilla fragment PLD-92 belongs to an elephantimorph of tetralophodont grade (Fig. 6a–c). In the two DP2s of *T. longirostris* from Eppelsheim (Germany; HLMD-Din 1062 and cast MNHN-A.C. 1987; Kaup, 1835: pl. 16, fig. 1a, pl. 20, fig. 2) the protocone is large, whereas in the DP2 from Laaerberg (Austria; Schlesinger, 1917:pl. 12, fig. 1) it is weak and similar to the PLD one. However, in the Laarberg specimen the distal cingulum is formed by strong cusplets, in contrast to its weaker development in the PLD specimen. On the other side, all the described morphological features of the PLD DP2 fit well with the *Konobelodon atticus* material from Pikermi (Konidaris et al., 2014: fig. 2a–d). The DP3s of *Tetralophodon longirostris* from Eppelsheim (HLMD-Din 1062 and casts MNHN-268, A.C. 1987; Kaup, 1835: pl. 16, fig. 1a, pl. 17, fig. 12, pl. 20, fig. 2), Laaerberg (Schlesinger, 1917:pl. 12, fig. 1) and Azambujeira (Portugal; Antunes and Mazo, 1983:pl. 1 fig. 6), have slightly smaller dimensions (Fig. 6d), the third loph is not enlarged, the second ectoflexus is weaker (more marked in HLMD-Din 1062), and the second entoflexus is absent or not very marked. In comparison with *Anancus*, although PLD-92 shows alternate contact (posttrite-pretrite) between the successive lophs (a derived trait shared among advanced gomphotheres and elephants; Tassy, 2005), the dislocation of the half-lophs in the second loph is very weak, the main cusps are placed almost the one opposite to the other, and the interlophs (transverse valleys) are almost straight. In

contrast, the DP3s of *Anancus lehmanni* (Gaziry, 1997) and *A. arvernensis* (Croizet and Jobert, 1828) from Concud (Spain; Mazo, 1981), Middle Awash-Kuseralee Mb. (Ethiopia; Saegusa and Haile-Selassie, 2009), Montpellier and Perrier-les-Etouaires (France; FSL-40462, FSL-211225, MNHN-A.C. 1830, MNHN-no number), exhibit a significant dislocation in the second loph and the interlophs (especially the first one) have a rather sigmoid form (Konidaris and Roussiakis, 2019). Compared to *A. lehmanni* from Chomateri and Concud, the PLD DP3 is smaller (Fig. 6d). The latter differs also from the DP3 of the tetralophodont gen. and sp. indet. from Ngorora Fm, Member D, in which the second pretrite half-loph is anteriorly offset relative to the posttrite one, the small anterior pretrite central conule of the second loph is not connected with the first posttrite half-loph, the distal loph is reduced and there is no second entoflexus (Tassy, 1986); the Ngorora DP3 is shorter but wider (Fig. 6d). On the other side, the combination of the weak dislocation of the half-lophs in the second loph, the position of the main cusps almost opposite to each other, the almost straight interlophs, the alternate contact, the enlarged third loph, the well-expressed ectoflexus and the marked second entoflexus matches well with *Konobelodon atticus*, including the specimens from its type locality Pikermi (holotype SNSB-BSPG-AS II 182, MNHN PIK-1704a and AMPG-PA3933/91). The PLD DP3 has the same loph morphology with the DP3 from Akkaşdağı (Turkey; Tassy, 2005) of approximately similar dental wear stage. Yet, the dimensions of the DP2 and DP3 from Platania are slightly smaller than the known sample of the Turolian *K. atticus* and close (for DP3) or within (for DP2, damaged pretrite second loph) the lower values of the Vallesian *K. robustus*, which presents a considerably wide size range, encompassing in both DP2 and DP3 the convex hulls of *K. atticus* (Fig. 6d, Table 4). On the other side, the hypsodonty (HI) and robustness (RI) indices for the DP3 are close between Platania (Table 3) and Pikermi, being on average HI = 63.8 (n = 2) and RI = 78.1 (n = 4) for the latter locality (Konidaris et al., 2014).

Figure 6.

The lower tusk PLD-642 and the maxilla fragment PLD-92 belong to the same taxon, which is the tetralophodont amebelodontid *Konobelodon*. The PLD tusk is morphologically and metrically different from *K. robustus*, *K. britti* and *K. cyrenaicus*, as well as from the *Konobelodon* tusk from Yulafli. On the other side, both PLD specimens show similarities with *Konobelodon atticus*, including the material from its type locality Pikermi (middle Turolian). The smaller dimensions of the PLD deciduous dentition could be important at the species/subspecific level and may have biostratigraphic value. However, given the wide dimensional variability known for *K. robustus* encompassing the whole *K. atticus* metrical range for the case of DP3 (Fig. 6), and in particular within the same faunal community of the Dashenggou Fauna (Table 4), this is not warranted, and the small sample from PLD does not allow for safe conclusions. Moreover, although deciduous dentition of the Vallesian *Konobelodon* from western Eurasia is so far unknown prohibiting any comparisons for the moment, the PLD lower tusk is different from the Yulafli one, which is of Vallesian age. Pending the discovery of more material, we attribute the PLD shovel-tusker to *Konobelodon* cf. *atticus*.

Table 4.

3. Biostratigraphic remarks – Conclusions

The proboscidean material from the Turolian of Thermopigi, includes only postcranial elements. The presence of the deinotheriid *Deinotherium* sp. is recognized by a scapula, whereas the rest of the specimens are morphologically distinct from *Deinotherium* and can be referred to Elephantimorpha indet. The presence of *Deinotherium* sp. cannot provide important biostratigraphic data, because the genus was already present in Europe from the late Astraracian (middle Miocene) and until the end of the Turolian (late Miocene) (e.g., Konidaris et al., 2017).

The Neokaisareia proboscidean remains belong to a partial skeleton of a young adult individual. Based on the morphology of the upper tusk, the remains belong to the mammutid *Mammut* sp. (*M. obliquelophus*?), suggesting a post-Vallesian age for NKP. This is in agreement with the stratigraphic and faunal data from the Katerini basin, which indicate a late Miocene age and a correlation to the Turolian for the find-bearing sediments. In Greece, *Mammut* is known during the late Miocene from the early Turolian (MN 11) locality Ravin des Zouaves-5, and the middle Turolian localities Pikermi, Mytilinii-1A and Halmyropotamos (Konidaris, 2013; Konidaris and Koufos, 2013). Finally, the Platania proboscidean belongs to the tetralophodont amebelodontid *Konobelodon* cf. *atticus*. *Konobelodon atticus* is known from the Turolian of western Eurasia, and in Greece it is recorded in Pikermi, Samos and Kerassia; however, the genus is already known from the Vallesian in Turkey (Geraads et al., 2005; Konidaris et al., 2014; Konidaris and Koufos, 2019). Considering the correlation of the locality close to Vallesian/Turolian boundary (Vasileiadis et al., in press), the PLD record could potentially document one of the earliest occurrences of this species.

Disclosure of interest

The authors declare that they have no competing interest.

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CAPTIONS

Fig. 1. a, Geographic position of the studied fossiliferous localities (map taken from Google Earth); **b**, excavation site of Thermopigi (field season 2015) and proboscidean postcranial bones *in situ* (field season 2002); **c**, excavation site of Platania and the maxilla LGPUT-PLD-92 *in situ*; **d–e**, excavation site of Neokaisareia showing the find-bearing sediments and proboscidean ribs *in situ*.

Fig. 1. a, Position géographique des localités fossilifères étudiées (carte tirée de Google Earth); **b**, site d'excavation de Thermopigi (saison 2015) et os postcrâniens proboscidiens *in situ* (saison 2002); **c**, site d'excavation de Platania et du maxillaire LGPUT-PLD-92 *in situ*; **d–e**, site d'excavation de Neokaisareia montrant les sédiments porteurs et les côtes proboscidiennes *in situ*.

Fig. 2. Postcranial specimens of *Deinotherium* sp. (**a–c**) and Elephantimorpha indet. (**c–p**) from Thermopigi. **a–c**, left scapula fragment, SIT-607 in **a**, lateral; **b**, medial; and **c**, ventral view; **d**, right humerus, SIT-605, caudal view; **e–g**, right ulna, SIT-609 in **e**, medial; **f**, cranial; and **g**, proximal view; **h**, proximal fragments of left ulna and radius, SIT-602, medial view; **i–l**, left femur, SIT-601 in **i**, cranial view; **j**, proximal extremity in caudal view; **k**, distal epiphysis in distal view; **l**, distal extremity in caudal view; **m–n**, left tibia, SIT-28 in **m**, cranial view; and **n**,

distal epiphysis in distal view; **o–p**, proximal epiphysis of left tibia, SIT-606 in **o**, caudal view; and **p**, proximal view.

Fig. 2. Les spécimens postcrâniens de *Deinotherium* sp. (**a–c**) et Elephantimorpha indet. (**c–p**) de Thermopigi. **a–c**, fragment de l'omoplate gauche, SIT-607 en vue **a**, latérale; **b**, médiale; et **c**, ventrale; **d**, humérus droit, SIT-605, vue caudale; **e–g**, ulna droit, SIT-609 en vue **e**, mediale; **f**, craniale; et **g**, proximale; **h**, fragments proximale de l'ulna and du radius gauche, SIT-602, vue mediale; **i–l**, fémur gauche, SIT-601 **i**, en vue craniale; **j**, extrémité proximale en vue caudale; **k**, épiphyse distale en vue distale; **l**, extrémité distale en vue caudale; **m–n**, tibia gauche, SIT-28 **m**, en vue craniale; and **n**, épiphyse distale en vue distale; **o–p**, épiphyse proximale du tibia gauche, SIT-606 en vue **o**, caudale; et **p**, proximale.

Fig. 3. *Mammut* sp. (*M. obliquelophus*?) from Neokaisareia. **a**, Composite plan of the excavations 2014–2016 showing the distribution of the proboscidean remains belonging to a single individual (made by G. Lazaridis and the AUTH team); the white characters indicate the inventory number and the black ones the depth; **b–f**, right upper tusk, NKP-1 in **b**, lateral; **c**, medial; **d**, dorsal; **e**, ventral view; **f**, cross-sections; **g**, axis fragment, NKP-2, cranial view; **h–j**, right humerus (distal and diaphysis), NKP-13 in **h**, cranial; **i**, caudal; and **j**, lateral view.

Fig. 3. *Mammut* sp. (*M. obliquelophus*?) de Neokaisareia. **a**, Plan composite des fouilles 2014–2016 montrant la distribution des restes proboscidiens appartenant à un seul individu (réalisé par G. Lazaridis et l'équipe AUTH); les caractères blancs indiquent le numéro d'inventaire et les noirs la profondeur; **b–f**, défense droite supérieure, NKP-1 en vue **b**, laterale; **c**, mediale; **d**, dorsale; **e**, ventrale; **f**, sections transverse; **g**, fragment d'axis, NKP-2, vue craniale; **h–j**, humérus droit (distal et diaphyse), NKP-13 en vue **h**, craniale; **i**, caudale; et **j**, laterale.

Fig. 4. Comparison of the upper tusk morphology between **a**, *Anancus lehmanni* (Hohenwarth, Austria; modified from Zapfe, 1957) and **b**, *Mammut obliquelophus* (Balta Sands, Ukraine; modified from Kubiak, 1972).

Fig. 4. Comparaison de la morphologie des défenses supérieures entre **a**, *Anancus lehmanni* (Hohenwarth, Autriche; modifié de Zapfe, 1957) et **b**, *Mammut obliquelophus* (Balta Sands, Ukraine; modifié de Kubiak, 1972).

Fig. 5. Morphology and metrical comparison of the lower tusk of *Konobelodon* cf. *atticus* from Platania. **a–c**, lower tusk fragment, LGPUT-PLD-642; **a**, natural cross-section; **b**, ventral view; **c**, artificial cross-section; **d**, scatter plot comparing the lower tusks (width vs. height) of various Miocene proboscideans; note that the lower tusks belong to individuals of different ontogenetic ages and the location of the measurements differs among them (e.g., maximal preserved diameters if isolated or infront of the mandibular symphysis if embedded). The symbol '?' indicates incomplete or inadequately preserved specimens. Data from Barbour (1927, 1929), Borissiak (1929), Klähn (1931), Petrocchi (1954), Bergounioux and Crouzel (1956, 1960), Maglio (1969), Mottl (1969), Tobien (1973), Gaziry (1976, 1987), Maglio and Ricca (1977), Tassy (1983b, 1986, 2014), Wang and Qiu (2002), Ferretti et al. (2003), Mazo and Montoya (2003), Gasparik (2005), Konidaris et al. (2014), Wang et al. (2015, 2016, for *Konobelodon robustus* only lower tusks belonging to adult mandibles with at least the first molar were used), and GK measurements at HNHM, MNHN, NHMW and SU.

Fig. 5. Morphologie et comparaison métrique de la défense inférieure de *Konobelodon* cf. *atticus* de Platania. **a–c**, fragment de défense inférieur, LGPUT-PLD-642; une section transverse naturelle; **b**, vue ventrale; **c**, section transverse artificielle; **d**, diagramme comparant les défenses inférieures (largeur/hauteur) de divers proboscidiens du Miocène.

Fig. 6. Morphology and metrical comparison of the DP2 and DP3 of *Konobelodon* cf. *atticus* from Platania. **a–c**, left maxilla fragment with DP2–DP3, LGPUT-PLD-92 in **a**, occlusal; **b**, labial; and **c**, lingual view; **d**, scatter plots comparing the DP2 and DP3 (length vs. width) of various late Miocene proboscideans. The symbol '?' indicates incomplete or inadequately preserved specimens. Data from Khomenko (1914), Schlesinger (1917), Riabinin (1929), Burchak-Abramovich (1940), Lehmann (1950), Burchak-Abramovich and Korotkevich (1966),

Mazo (1981), Antunes and Mazo (1983), Tassy (1983a, 1986, 2005), Geraads et al. (2011), Konidaris et al. (2014), Wang et al. (2016), Konidaris and Roussiakis (2019), and author's (GK) measurements at HLMD and MNHN.

Fig. 6. Comparaison morphologique et métrique des DP2 et DP3 de *Konobelodon* cf. *atticus* de Platania. **a–c**, fragment maxillaire gauche avec DP2–DP3, LGPUT-PLD-92 en vue **a**, occlusale; **b**, labiale; et **c**, linguale; **d**, diagramme comparant les DP2 et DP3 (longueur/largeur) de divers proboscidiens du Miocène supérieur.

Table 1. Postcranial measurements (in mm) of *Deinotherium* sp. and Elephantimorpha indet. from Thermopigi, and *Mammut* sp. (*M. obliquelophus*?) from Neokaisareia. **art.**, articular surface; **cond.**, condyle; **DAP**, antero-posterior diameter; **dia.**, diaphysis; **dist.**, distal; **DT**, transversal diameter; **H**, height; **inc. sem.**, incisura semilunaris; **L**, length; **prox.**, proximal. Measurements in parentheses follow Göhlich (1998). Asterisks denote the greatest measurable value of the parameter.

Table 1. Mesures postcrâniennes (en mm) de *Deinotherium* sp. et Elephantimorpha indet. de Thermopigi et *Mammut* sp. (*M. obliquelophus*?) de Neokaisareia.

Table. 2. Upper tusk (NKP-1) measurements (in mm) of *Mammut* sp. (*M. obliquelophus*?) from Neokaisareia.

Table. 2. Mesures en défenses supérieures (NKP-1) (en mm) de *Mammut* sp. (*M. obliquelophus*?) de Neokaisareia.

Table 3. Dental measurements (in mm) of *Konobelodon* cf. *atticus* from Platania. **H**, height; **HI**, hypsodonty index (H × 100/W); **L**, Length; **me**, metacone; **RI**, robustness index (W × 100/L); **pa**, paracone; **W**, width. Measurement in parentheses indicates the greatest measurable value.

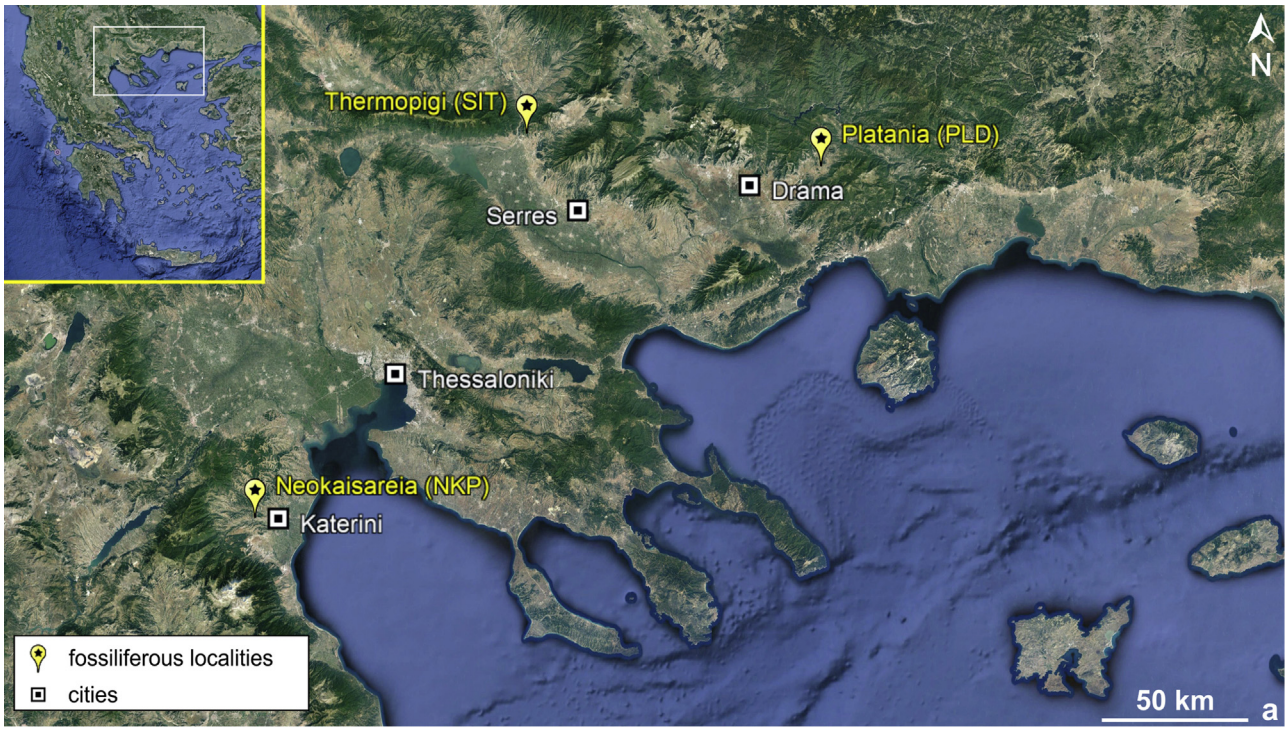
Table 3. Mesures dentaires (en mm) de *Konobelodon* cf. *atticus* de Platania.

Table 4. Summary statistics of the length and width of the DP3 of *Konobelodon robustus* from the Bahean Dashenggou Fauna of the Linxia Basin in China (NMU 9, equivalent to MN 10; localities LX200007, LX200008, LX200009 and LX200027) and *K. atticus* from several

Turolian localities of western Eurasia (Pikermi, Samos, Maragheh, Taraklia, Grebeniki, Novaya Emetovka, Strumyani) compared to *K.* cf. *atticus* from Platania (Greece). **L**, length; **W**, width; **NS**, number of specimens; **V**, variation (minimum–maximum value); **M**, mean value; **SD**, standard deviation. For data sources, see references and institutions cited in Fig. 5.

Table 4. Statistiques sommaires sur la longueur et la largeur du DP3 de *Konobelodon robustus* de Dashenggou Fauna (Bahean) du bassin de Linxia en Chine (NMU 9, équivalent à MN 10; localities LX200007, LX200008, LX200009 et LX200027) et *K. atticus* de plusieurs localités de Turolien de l'Eurasie occidentale (Pikermi, Samos, Maragheh, Taraklia, Grebeniki, Novaya Emetovka, Strumyani) par rapport à *K.* cf. *atticus* de Platania (Grèce).

Fig.1


N
Thermopigi (SIT)
Platania (PLD)
Drama
Serres
Thessaloniki
Neokaisareia (NKP)
Katerini
fossiliferous localities
cities
50 km
a

b

c

d

e

Fig. 2

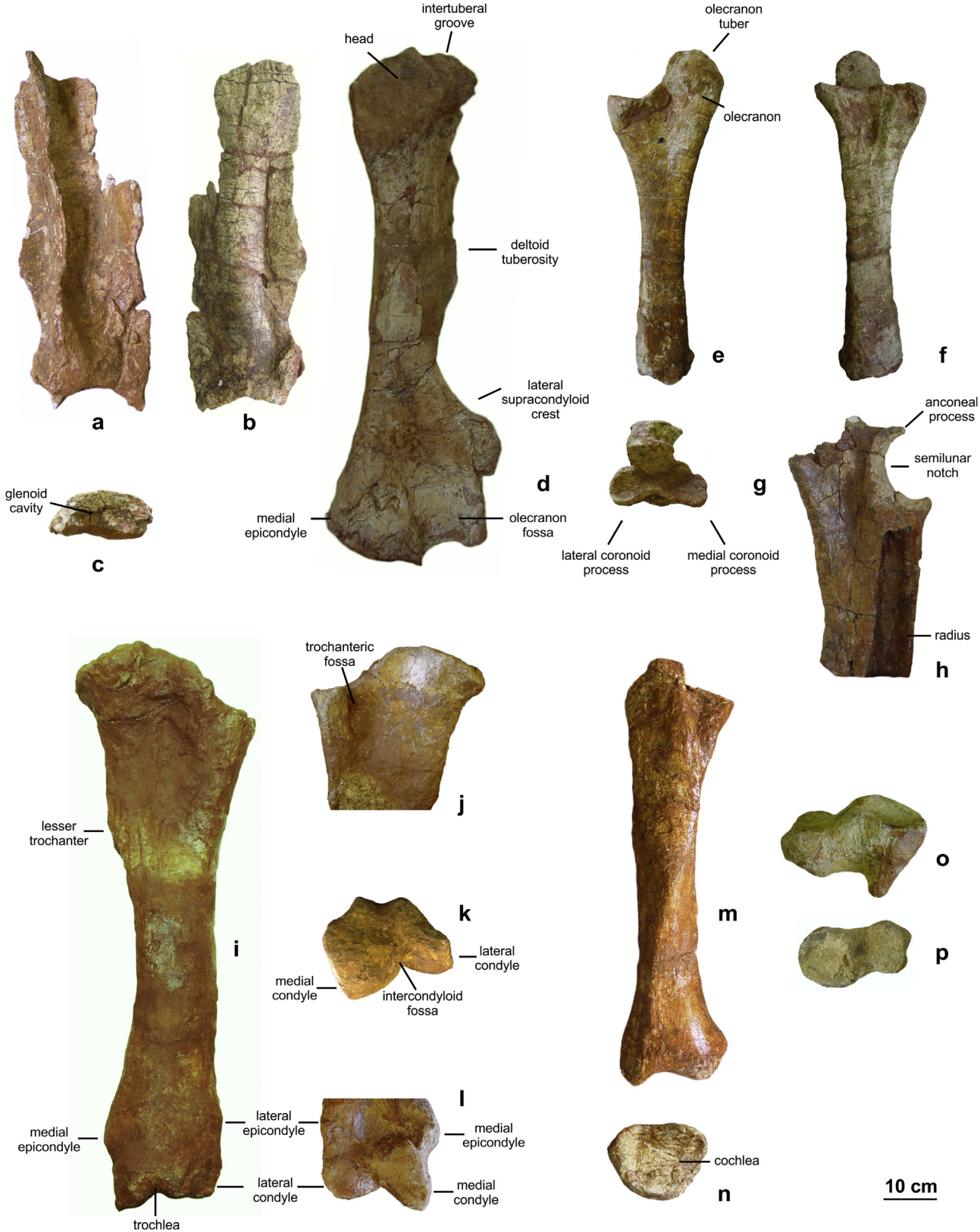

a
b
c
glenoid cavity
head
intertuberal groove
deltoid tuberosity
lateral supracondyloid crest
medial epicondyle
olecranon fossa
d
olecranon tuber
olecranon
e
f
g
lateral coronoid process
medial coronoid process
anconeal process
semilunar notch
radius
h
trochanteric fossa
j
lesser trochanter
i
trochlea
k
lateral condyle
medial condyle
intercondyloid fossa
l
lateral epicondyle
medial epicondyle
lateral condyle
medial condyle
m
cochlea
n
o
p
10 cm

Fig. 3

NKP25
-127
NKP1
-160
-156.5
-155
NKP13
-156.5
NKP12
NKP8
-149.5
NKP10
NKP3
-154.5
-161.5
-157.5
NKP5
-142.5
-139
NKP14
NKP15
NKP4
-147.5
-155.5
-172.5
NKP9
NKP7
-147
-161
NKP11
-154
[-163]
NKP2
N
1 m
a
spinous process
vertebral foramen
odontoid process (dens)
g
V
ventral crest
10 cm
deltoid tuberosity
lateral condyloid crest
musculospiral groove
h
coronoid fossa
lateral epicondyle
medial epicondyle
lateral condyle
trochlea
medial condyle
"grass-notch"
b
c
10 cm
b–e
10 cm
h–j
d
1
2
3
e
olecranon fossa
lateral epicondyle
5 cm
1
2
3
f
i
j

Fig. 4

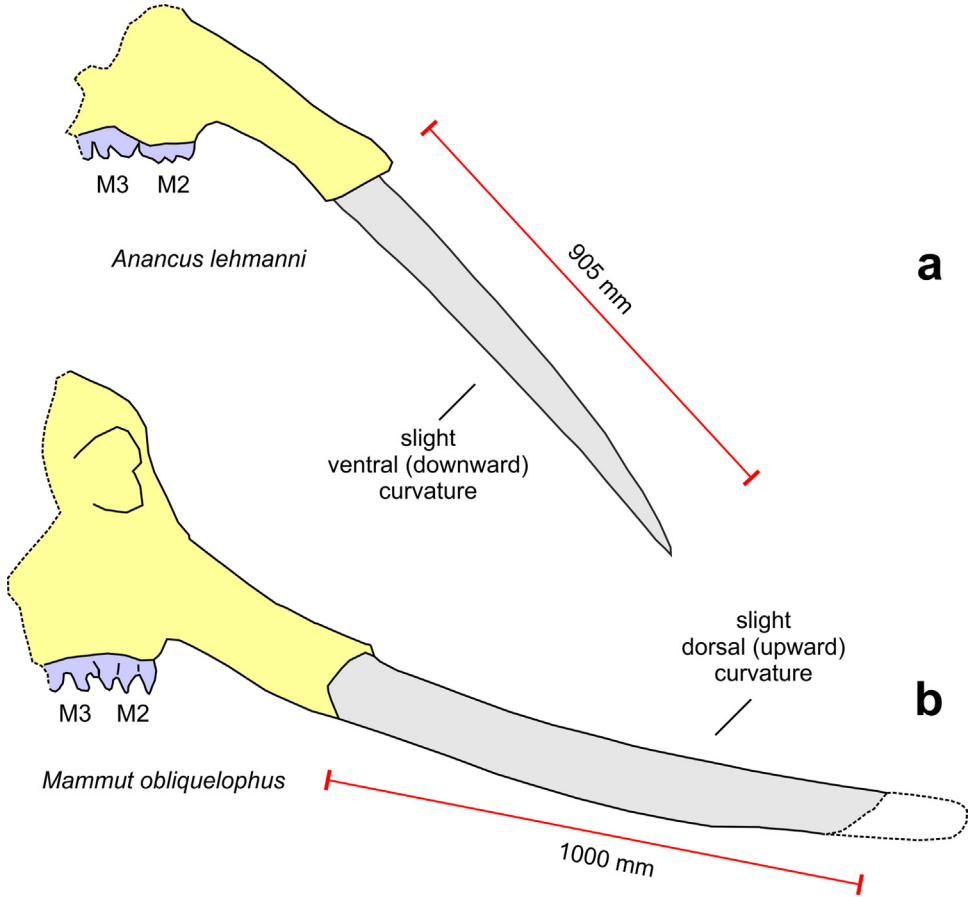
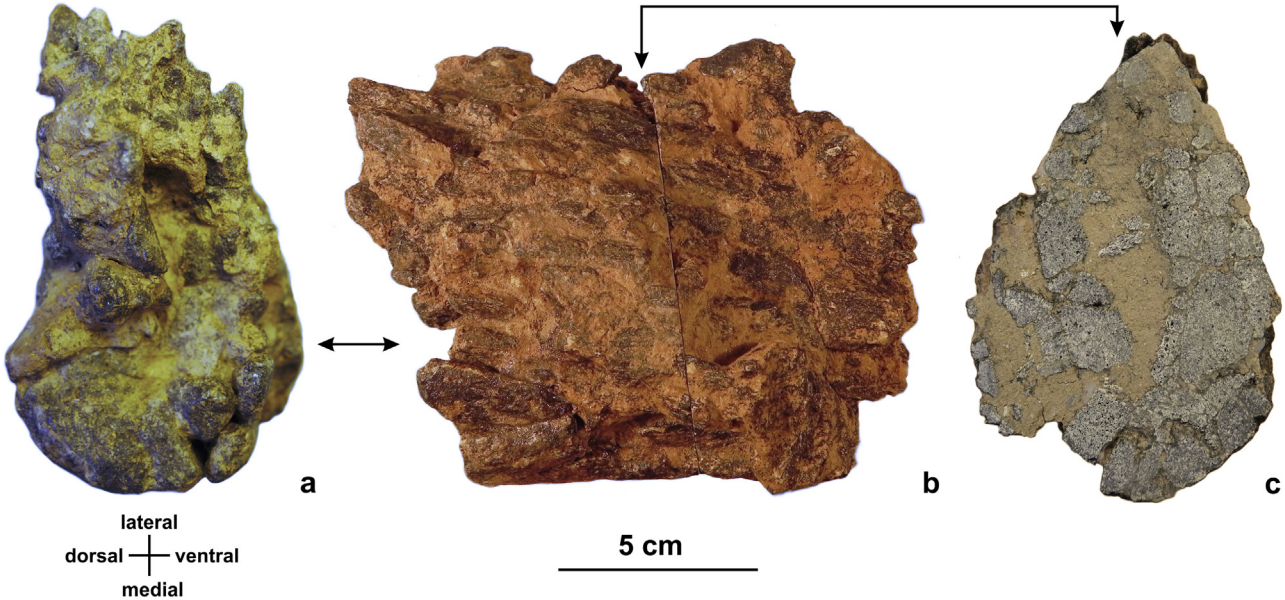
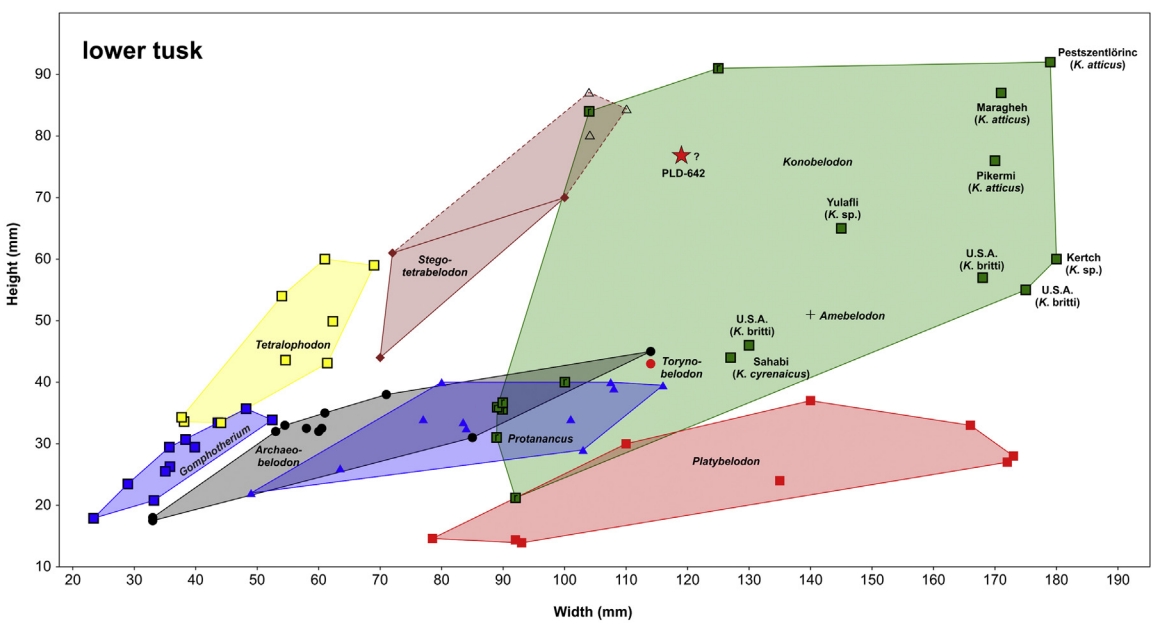

M3
M2
Anancus lehmanni
905 mm
a
slight
ventral (downward)
curvature
slight
dorsal (upward)
curvature
M3
M2
b
Mammut obliquelophus
1000 mm

Fig. 5

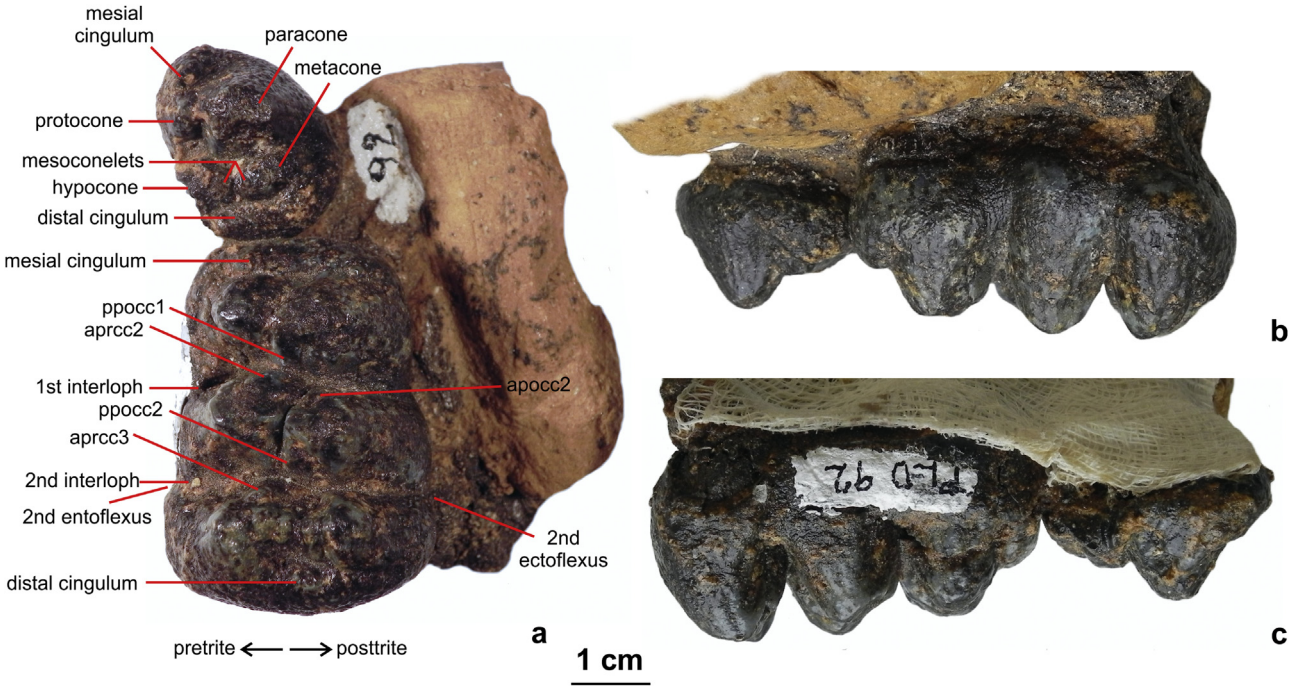




- *Gomphotherium* (En Péjuan, France)
- *Tetralophodon* (Esselborn, Germany; Bermersheim, Germany; Breitenfeld, Austria; Rudabánya, Hungary)
- *Stegotetrabelodon* (Cessaniti, Italy; Sahabi, Libya; Lothagam 1, Kenya)
- ?*Stegotetrabelodon* (Gebel Sémène, Tunisia; Crevillente 2, Spain)
- *Archaeobelodon* (Sansan, France)
- *Protanancus* (Yürükali, Turkey; Maboko, Kenya; Alengerr, Kenya; Chinji, Pakistan; China)
- *Platybelodon* (Belomechetskaya, Russia; Arapli, Turkey; Loperot, Kenya; Danghe area, China; Tungur, China)
- *Torynobelodon* (Sand Canyon-Nebraska, U.S.A.)
- *Amebelodon* (Freedom-Nebraska, U.S.A.)
- *Konobelodon* (Pikermi, Greece; Maragheh, Iran; Pestszentlörinc, Hungary; Yulafli, Turkey; Kertch, Ukraine; Sahabi, Libya; Florida, U.S.A.; Texas, U.S.A.; Kansas, U.S.A.; *K. robustus*, Linxia basin, China)
- *Konobelodon* cf. *atticus* (Platania, Greece)

d

Fig. 6


mesial cingulum
paracone
metacone
protocone
mesoconelets
hypocone
distal cingulum
mesial cingulum
ppocc1
aprcc2
1st interloph
apocc2
ppocc2
aprcc3
2nd interloph
2nd entoflexus
2nd ectoflexus
distal cingulum
pretrite ⟷ posttrite
a
1 cm
b
c

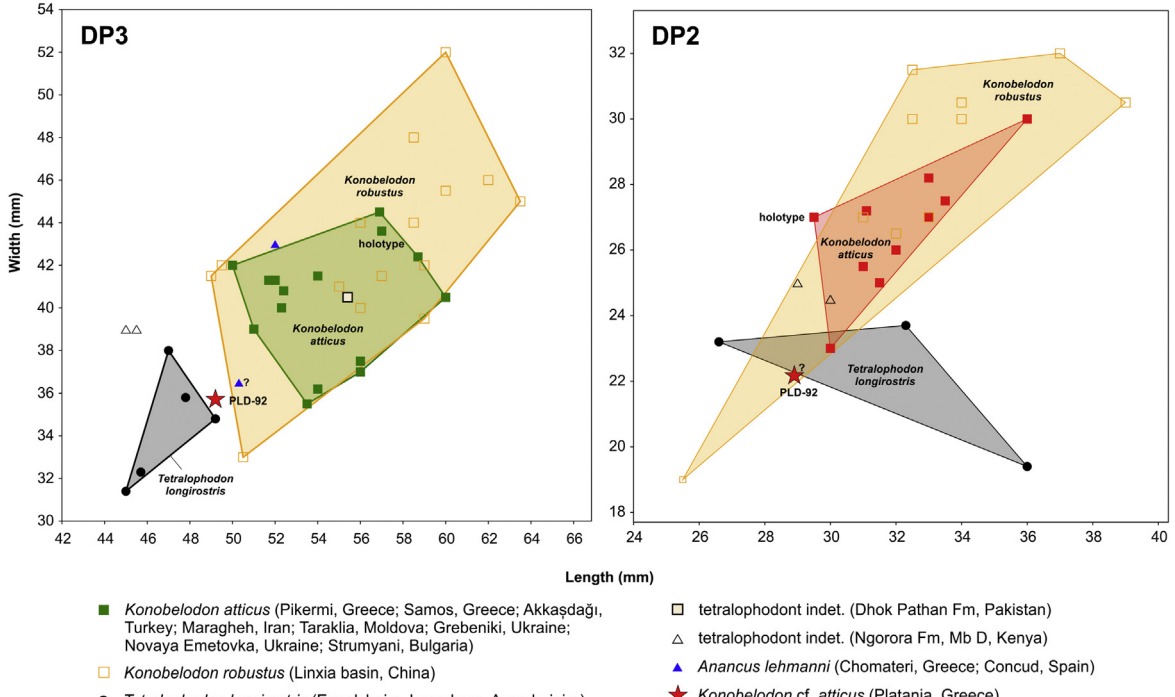

DP3
DP2
Width (mm)
Length (mm)
Konobelodon robustus
holotype
Konobelodon atticus
PLD-92
Tetralophodon longirostris
d
Konobelodon atticus (Pikermi, Greece; Samos, Greece; Akkaşdağı, Turkey; Maragheh, Iran; Taraklia, Moldova; Grebeniki, Ukraine; Novaya Emetovka, Ukraine; Strumyani, Bulgaria)
Konobelodon robustus (Linxia basin, China)
Tetralophodon longirostris (Eppelsheim, Laaerberg, Azambujeira)
tetralophodont indet. (Dhok Pathan Fm, Pakistan)
tetralophodont indet. (Ngorora Fm, Mb D, Kenya)
Anancus lehmanni (Chomateri, Greece; Concud, Spain)
Konobelodon cf. atticus (Platania, Greece)

Table 1.

Scapula		Humerus			Radius	
Deinotherium sp.		*Mammut* sp. (*M. obliquelophus* ?)		Elephantimorpha indet.		Elephantimorpha indet.
SIT-607		NKP-13		SIT-605		SIT-602
H	635*	L		965*	DT prox. (Bp)	115
DT dist.	113	DT prox. (Bp)		234	DT prox. art. (BFv)	103
DAP dist.	223	DAP prox. (Tp)		227	DAP prox. art. (Tp)	60
DT glenoid	74	DT dia. min (BD)	136	125	DT dia. min (BD)	39
DAP glenoid	151	DAP dia. min	149	157	DAP dia. min (TD)	56
DAP collum	190	Circumference min (UD)	500	465		
		DT dist. (Bd)	310	320		
		DAP dist. (Td)	ca. 180	144		
		DT trochlea (BTr)	208			

Ulna		Femur		Tibia			
Elephantimorpha indet.		Elephantimorpha indet.					Elephantimorpha indet.
SIT-609		SIT-601			SIT-606	SIT-28	SIT-608
L	570*	L	1070*	L		750*	685*
DT prox. art. (BP)	180	L lat. at trochanter major (GLTt)	985	DT prox. (Bp)	243		205*
DT olecranon (BTb)	93	DT prox. (Bp)	335	DAP prox. (Tp)	125		
H inc. sem. max	114	DT caput femoris (BC)	138	DT cond. med. (BmFp)	110		
H inc. sem. min	98	DAP caput femoris (TC)	145	DAP cond. med. (TmFp)	103		
DT dia. (BD)	73	DT dia. (BD)	160	DT cond. lat. (BLFp)	106		
DAP dia. (TD)	76	DAP dia. (TD)	92	DAP cond. lat. (TLFp)	95		
DT dist. (Bd)	115*	Circumference min (UD)	425	DT dia. (BD)		100	108
DAP dist. (Td)	93*	DT dist. (Bd)	249	DAP dia. (TD)		88	81
		DAP dist. (Td)	191	Circumference min (UD)		310	320
		DT trochlea (BTr)	85	DT dist. (Bd)		192	168*
		DT condylii (Bcd)	185	DAP dist. (Td)		144	122*

Table 2.

Upper tusk	NKP-1	
Length	930	
Distance from tip	Maximal diameters	Circumference
100	66.6 × 54.4	195
200	77.3 × 67.6	230
300	79.1 × 76.9	250
400	85.0 × 79.1	265
500	84.3 × 82.1	275
600	83.2 × 86.0	275
700	76.4 × 87.3	260
800	72.2 × 85.6	255
900	72.8 × 84.6	250

Table 3.

Tooth	Measurement	PLD-92
DP2–DP3	L	76.6
DP2	L	28.9
	W max	(22.2)
	H at pa	17.7
DP3	L	49.2
	W max	36.1
	W 1st	31.4
	W 2nd	34.9
	W 3rd	35.6
	H at me	24.0
	HI	66.5
	RI	73.4

Table 4.

DP3	PLD-92		*Konobelodon robustus*		*Konobelodon atticus*	
L	49.2		L	W	L	W
W max	36.1	NS	12	12	15	15
W 3rd	35.6	V	49.0–63.5	33.0–52.0	50.0–60.0	35.5–44.5
		M	56.79	42.67	54.37	40.21
		SD	4.97	4.84	2.95	2.67