

Proboscidea of the Greek Pliocene-Early Pleistocene faunas: biochronological and palaeoecological implications

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SUMMARY: Proboscidea constitute a very important element of the Neogene and Quaternary continental faunas of Greece, being present in almost every fossil mammal locality. Isolated, fragmentary findings are numerous, all over area. Nevertheless, well-preserved elephant remains are rather sporadic. The most common Pliocene species is *Mammuthus meridionalis*, which coexisted with *Anancus arvernensis* during the Late Pliocene. Some *Mammuthus borsoni* findings come from Early Pliocene deposits. During the Early Pleistocene only *Mammuthus meridionalis* exists in the fossil record. The palaeoecological and biochronological implications of these species are discussed.

1. INTRODUCTION

The Proboscidea have developed an incredible diversity of forms in the Eurasian Neogene and Quaternary faunas, adapted to a variety of palaeoenvironments. Proboscidean remains are known in the Greek fossil record from the Middle Miocene to the Holocene times, attributed to several continental and insular forms. However, their biochronological and palaeoecological relationships have been barely studied. Recently, Doukas & Athanassiou (in press) gave an extensive review of the Pliocene and Pleistocene Proboscidea from Greece. The present article deals with the proboscidean remains that are of known stratigraphical context and come from Pliocene–Early Pleistocene faunas of this geographic area. Short systematic descriptions of less known or even unknown specimens are followed by biochronological and palaeoecological remarks, in order to investigate the significance of proboscidean remains in the Pliocene and Early Pleistocene fossil record.

2. PALAEONTOLOGY

2.1 *Mammuthus borsoni* (Hays 1834)

This mammutid mastodont is rare in Greece, usually known from isolated fragmentary material. All findings come from Northern Greece (Tsoukala 2000; Doukas & Athanassiou in press). Mitzopoulos (1967) reports the presence of the species in Vathýlakkos (valley of Axiós), but there is no biochronological information about this finding. Dermitzakis *et al.* 1982 also mention its presence at two localities in Neápolis district (Grevená basin, W. Macedonia). Although the exact age of the sites is unknown, Pliocene and Pleistocene deposits, overlying molassic sediments, cover the area.

Tsoukala (2000) describes a partial skeleton attributed to this species, including a complete mandible and two impressively long tusks, found in Miliá (Grevená). According to the author the locality could be of Ruscinian age (MN14–MN15). Nevertheless, the lithological character of the deposits in the context of the regional geology rather points to a somewhat

younger age (personal data). A dating in MN16 is also possible (as *Mammuth borsoni* is present in this zone too — Mein 1990), which seems to fit pretty well with the advanced features of the Miliá mastodont.

2.2 *Anancus arvernensis* Croizet & Jobert, 1828

This bunodont gomphotheriid with tetralophodont molars is rather frequent in the Greek fossil record (Doukas & Athanassiou in press). Nevertheless, among the numerous evidences of its presence only a few are of known stratigraphical context and therefore could offer accurate chronological data.

Symeonidis & Tataris (1983) describe a complete, very well preserved mandible from

Sésklo (Thessaly) with both M_3 *in situ*. It is a massive specimen of an aged individual. Its teeth have the typical anancoid cusp pattern. Later on, Athanassiou (1996) describes a partly preserved skull without teeth, from the same locality, that belongs to a large male (as deduced by the large tusk sheaths). The skull is high with short snout. The tusk sheath is almost horizontal. The nasal opening is placed above and behind the orbit, which is rather large and it is placed at the front of the skull. The occipital region is very large and almost flat, with strong occipital crest. The frontal region is markedly convex. The basal region and the dentition are not preserved. Measurements of this specimen are given in table 1.



Fig.1 - Geographical distribution of the Pliocene–Early Pleistocene Proboscidean findings in Greece. Open circles indicate *Mammuthus meridionalis*, slashed circles indicate *Anancus arvernensis* and crossed circles indicate *Mammuth borsoni*.

Tab.1 - Cranial and dental measurements of *Anancus arvernensis* from several Greek localities. Measurements in parentheses are approximate.

<i>Anancus arvernensis</i>			
Skull			cm
Cranial DAP			93
Distance between the inion and the upper margin of the nasal opening			(30)
Total height			50
Length of the premaxillar bones			53
Height of the orbit			(12)
Diameter of the tusk sheath			(17)
<i>A. arvernensis</i>	M ¹	M ²	M ³
Teeth	mm	mm	mm
DAP	105	—	242
DT	65	66	87–98
	M ₁	M ₂	M ₃
	mm	mm	mm
DAP	—	135–144	204–242
DT	—	77	80–98

Sésklo yielded a rich mammal fauna that has been dated by Athanassiou (1996) in the lower MN17 (Late Pliocene).

Steensma (1988) reports the presence of *Anancus arvernensis* at Klíma and possibly at Polýlakkon (North-western Macedonia). The poor faunal content of both localities does not allow any accurate biochronological inference. According to the author, the first locality may correspond to Early Pliocene (based on a correlation to a marine fauna), while the second one to the Late Pliocene (the presence of a relatively small and slender *Equus*, very similar to that from Gerakaroú, support this dating).

Theodorou *et al.* (2000) describe a juvenile cranial part from Apolakkíá (Rhodes Island) with tusks, M¹, as well as the erupting M² of both sides. The straight tusks and alternating cusps of the cheek teeth characterise this specimen. The authors give a Pliocene age to the specimen, but they note that it comes from a higher horizon, which overlies already known fossiliferous levels of Apolakkíá Formation of probably MN15 age. This suggests that the age of the *Anancus* from Apolakkíá could be confined to the Late Pliocene.

2.3 *Mammuthus meridionalis* (Nesti 1825)

This species is typical of the “Villafranchian” faunas of Greece, and it is found in most fossil mammal localities of this stage (Doukas & Athanassiou in press). Also in this case, most of the available findings are scanty, mainly representing isolated molars. The available molars are mostly M₃ that are 172–320 mm long, 84–118 mm wide and 80–155 mm high. They consist of 11½–14 plates, and they have 4–5 plates per 10 cm of tooth length. These measurements are inside the variation of the species, given by Maglio (1973).

Steensma (1988) describes some fragmentary dental and osteological remains attributed to *M. meridionalis* from the localities of Líbakos, Kapetánios, Polýlakkon and Aliákmon Q-Profil (West Macedonia). The first locality is dated in the Early Pleistocene (possibly MNQ20), while a similar age is also probable for Kapetánios and Aliákmon Q-Profil. Polýlakkon is dated in the Late Pliocene.

Athanassiou (1996) describes *M. meridionalis* remains from the Late Pliocene (lower MN17) locality of Sésklo (Thessaly). A partial

tusk from Sésκλο has a maximal diameter of 130 mm and a retained length of 121 cm; the total length must have been much more than 200 cm. The specimen shows a weak torsion, which is characteristic of the species (Maglio 1973). Postcranial material is known from Sésκλο and Gerakaroú and it comprises mainly carpal bones. The carpals from Sésκλο are very large (Tab. 2).

The few postcranial remains from Gerakaroú (trapezium, GER-341, scaphoid, unciform, magnum, GER-353a, b, c, and phalanx I ant.-III, GER-342) indicate metrical and morphological similarities with *Mammuthus meridionalis* (Tab. 2). According to the rest of the fauna the locality of Gerakaroú is dated at the very end of Pliocene (upper MNQ18 — Koufos & Kostopoulos 1997).

A single elephant specimen is also known from the late Early Pleistocene locality of Apollonía (Mygdonía basin, N. Greece) (Koufos & Kostopoulos 1997). It is a maxillary fragment with dp²-dp³, belonging to a young individual. dp² is 21.5 mm long, 16.7 mm wide and oval-shaped, consisting of four plates. dp³ is relatively elongated and narrow ($L_{\max} = 80.5$ mm, $W_{\max} \approx 40$ mm), it consists of eight plates (lamellar frequency = 10) and it has rather thin enamel (2.0–2.5 mm). These morphological and metrical characters place this specimen in an intermediate position between *Mammuthus meridionalis* and later forms (*Mammuthus trogontherii*), but a specific determination is quite difficult for the moment.

The Middle–Late Pleistocene locality of Megalópolis (Peloponnesus) is rich in proboscidean material, described by Melentis (1961, 1963). The author refers some specimens to *M. meridionalis*, but there are many doubts about the presence of the species there,

as the studied molars are relatively narrow and hypsodont (hypsodonty index > 260 for a M³). Sondaar & Boekschoten (1967) interpret the material from Megalópolis as representing only the species *Elephas antiquus* and *Mammuthus primigenius*.

3. BIOCHRONOLOGY - PALAEOECOLOGY

The Early Pliocene (Ruscinian) faunas are not common in Greece, and only a couple of them include Proboscidean remains. *Mammuth borsoni*, a relatively rare species, marks the Early Pliocene faunas of Europe. Its presence in the Pliocene deposits of N. Greece is well documented. Despite the absence of well-dated findings, the species seems to survive until about the middle of the Pliocene (MN16) and it disappears thereafter.

Anancus arvernensis is the last mastodont that lived in Europe. It coexisted with *Mammuth borsoni* during the Early Pliocene and *Mammuthus meridionalis* during the Late Pliocene. The available Greek material generally represents the Late Pliocene representatives of the species (though there is no dating evidence for many isolated finds). This fact could be attributed to the scarcity of Ruscinian localities in Greece. The occurrence at Klíma could be one of the oldest in Greece, if the correlation of the site with marine Lower Pliocene deposits (Steensma 1988) is accurate. The latest well-documented occurrence of the species in Greece is in the Late Pliocene locality of Sésκλο.

Mammuthus meridionalis is the first representative of the family Elephantidae in Greece. It appeared during the Late Pliocene (MN17) and it coexisted for a short time period with *A. arvernensis*. This co-occurrence is

Tab.2 - Measurements (in mm) of *M. meridionalis* from Gerakaroú (GER) and Sésκλο (Σ).

	GER-353a Scaphoid	GER-353b Unciform	GER-353c Magnum	GER-341 Trapezium	GER-342 Phalanx I ant.-III	Σ-2 Lunate	Σ-1 Triquetral
L	137	107	120	67	71	179	166
I	77	105	92	44	DTprox 61.4	174	DAPprox 127
H	150	102	98	70	DTdist 56	102	DTprox 177

found at Sésκλο, though it is not absolutely sure that the findings of the two species come from exactly the same stratigraphic level. *Anancus arvernensis* and *Mammuthus meridionalis* may also co-occur at Polyákkon, as the former is possibly present in this locality (Steensma 1988).

At the very end of Pliocene and during the Early Pleistocene *Mammuthus meridionalis* appears to be the only representative of Proboscidea. At the beginning of Middle Pleistocene the species is transitionally replaced by new, more advanced forms of the same lineage, while more or less at the same time *Elephas antiquus* appears in Europe.

The successive changes in the proboscidean species plausibly reflect climatic and environmental shifts during the considered time span. The mastodonts, *Mammuthus* and *Anancus*, were browsers, as inferred by the bunodont morphology of their molars, and inhabited forest or woodland environments. The appearance of *Mammuthus meridionalis* may mark a transition from a rather wooded environment to a more open one, as this animal was less specialised and more broadly adapted feeder (Kurtén 1968). This gradual environmental change caused a trend of the *Mammuthus* lineage during the Lower Pleistocene towards more hypsodont molars with more densely packed plates. The associated mammal faunas of Late Pliocene – Early Pleistocene age also indicate open and rather dry habitats, as the dominant families are the Equidae and Bovidae, while forest elements, as Cervidae or Suidae, are rare.

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