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

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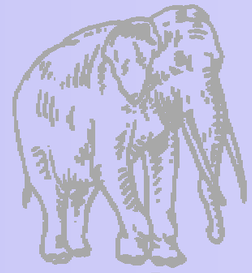
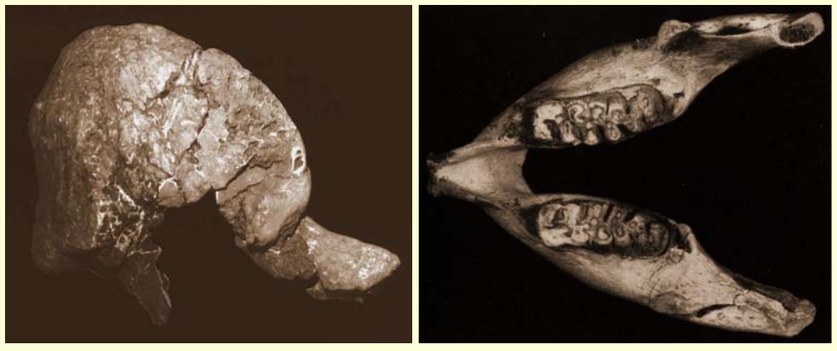


The Proboscidea have developed an incredible diversity of forms in the Eurasian Neogene and Quaternary faunas, adapted to a variety of palaeoenvironments. Proboscidean remains are known in the Greek fossil record from the Middle Miocene to the Holocene times, attributed to several continental and insular forms. This presentation deals with the proboscidean remains that are of known stratigraphical context and come from Pliocene–Early Pleistocene faunas of this geographic area. The biochronological and palaeoecological significance of proboscidean remains in the Greek Pliocene and Early Pleistocene fossil record is discussed.

Mammut borsoni (HAYS, 1834)

It is very rare in Greece, usually known from isolated fragmentary material. All findings come from Northern Greece (DOUKAS & ATHANASSIOU *in press*). The most complete and impressive find of this species is described by TSOUKALA (2000): a partial skeleton, including a complete mandible and two very long tusks, found in Miliá (Grevená). The locality could be of Ruscinian or (more possibly) Early Villafranchian age.



Anancus arvernensis from Sésklo

Mammuthus meridionalis (NESTI, 1825)

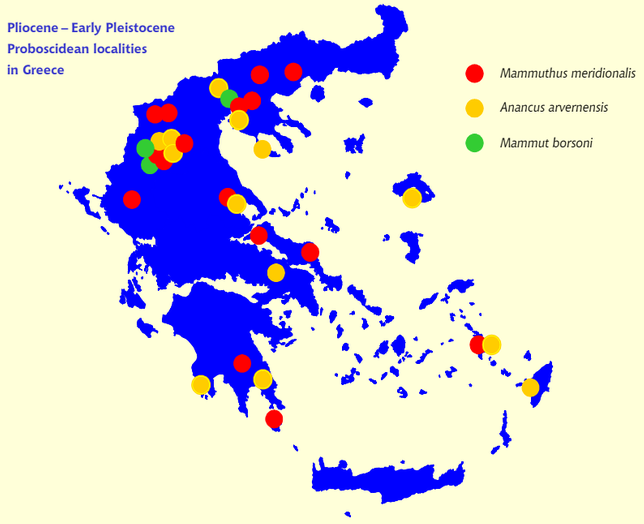
This species is typical of the "Villafranchian" faunas of Greece, and it is found in most fossil mammal localities of this stage (DOUKAS & ATHANASSIOU *in press*).

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 Sésklo has a maximal diameter of 130 mm and a retained length of 121 cm. The specimen shows a weak torsion, which is characteristic of the species.

Postcranial material is known from Sésklo and Gerakaroú and it comprises mainly carpal bones. A pyramidal and a lunate from Sésklo are of extremely large dimensions. The few postcranial remains from Gerakaroú (trapezium, scaphoid, unciform, magnum and phalanx I ant.$_{iii}$) indicate metrical and morphological similarities with *Mammuthus meridionalis*. Gerakaroú is dated at the very end of Pliocene (end of MNQ 18, KOUFOS & KOSTOPOULOS 1997).

A single elephant specimen is also known from the late Early Pleistocene locality of Apollonía (Mygdonía basin, N. Greece). It is a maxillary fragment with D^2–D^3, belonging to a young individual. According to its morphological and metrical characters, this specimen is placed in an intermediate position between *Mammuthus meridionalis* and later forms (*Mammuthus trogontherii*), but a specific determination is quite difficult for the moment.



Anancus arvernensis (CROIZET & JOBERT, 1828)

A rather frequent Gomphothere in the Greek fossil record. Some findings are of known stratigraphical context.

SYMEONIDIS & TATARIS (1983) describe a complete, very well preserved mandible from Sésklo (Thessaly) with both M_3 *in situ*. 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. It is high with short snout. Sésklo yielded a rich mammal fauna dated in the lower MN17 (Late Pliocene).

STEENSMA (1988) reports the presence of *Anancus arvernensis* at Klíma and possibly at Polýlakkon (North-western Macedonia). Klíma may correspond to Early Pliocene (based on a correlation to a marine fauna), while Polýlakkon is dated in the Late Pliocene.

THEODOROU *et al.* (2000) describe a juvenile cranial part from Apolakkiá (Rhodes Island) with both tusks, M^1, as well as the erupting M^2 of both sides. It is dated in the Late Pliocene.

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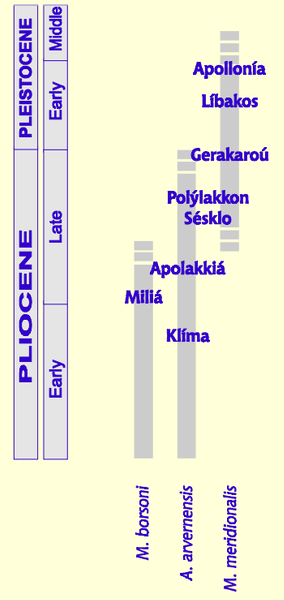
Mammuthus meridionalis tusk from Sésklo

Elephant molars from Apollonía



BIOCHRONOLOGY

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

The available Greek material of *Anancus arvernensis* generally represents the Late Pliocene populations 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. The latest well-documented occurrence of the species is in the Late Pliocene of Sésklo.

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 found at Sésklo, 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 Polýlakkon. At the very end of Pliocene and during the Early Pleistocene *Mammuthus meridionalis* appears to be the only representative of Proboscidea.

PALAEOECOLOGY

The successive changes in the proboscidean species plausibly reflect climatic and environmental shifts during the considered time span. The mastodonts, *Mammut* 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. This gradual environmental change caused a trend of the *Mammuthus* lineage during the Early 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.