Proboscideans (Mammalia) from the late Miocene of Akkaşdağ, Turkey

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KEY WORDS
Mammalia, Proboscidea, Elephantoidea, Miocene, Akkaşdağ, Central Anatolia, Turkey.

ABSTRACT
The proboscidean remains discovered at Akkaşdağ (late Miocene of Turkey) belong to two elephantoid species: Choerolophodon pentelici (Gaudry & Lartet, 1856) and “Tetralophodon” atticus (Wagner, 1857). This association was previously known in the Turolian locality of Pikermi.

MOTS CLÉS
Mammalia, Proboscidea, Elephantoidea, Miocene, Akkaşdağ, Anatolie Centrale, Turquie.

RÉSUMÉ
Les proboscidiens (Mammalia) du Miocène supérieur d’Akkaşdağ, Turquie.
Les restes de proboscidiens découverts dans le gisement d’Akkaşdağ (Miocène supérieur de Turquie) appartiennent à deux espèces d’éléphantoides : Choerolophodon pentelici (Gaudry & Lartet, 1856) et « Tetralophodon » atticus (Wagner, 1857). Cette association était déjà connue dans le gisement turolien de Pikermi.
INTRODUCTION

The proboscidean remains described in this paper were discovered between 1997 and 2001 by a team led by Sevket Sen (Muséum national d’Histoire naturelle, Paris). The bone pockets at Akkaşdağlı are labelled AK1, AK2... or AKA or AKB. The specimens labelled as AKK are surface collects or of unknown pockets. The studied material is housed in the collections of the Natural History Museum in Ankara. The geological setting is given by Seyitoğlu et al. (2005) and Kazancı et al. (2005). Although proboscideans are rare at Akkaşdağlı (and represented mostly by postcranial remains), deciduous teeth allow the identification of two elephantoid taxa. No specimen in the collection can be allocated to a deinother. The elephantoids are *Choerolophodon pentelici* (Gaudry & Lartet, 1856) and “Tetralophodon” atticus (Wagner, 1857). This association is typical of the Turolian faunas of the Eastern Mediterranean area. It accords with the middle Turolian age for Akkaşdağlı given by Karadenizli et al. (2005).

Most of the proboscidean finds are postcranial specimens (bones and partial bones). The majority of them is broken, eroded and/or gnawed by a predator (hyaena). Although large mature bones are more common than small juvenile ones, only deciduous teeth were recovered at Akkaşdağlı. These teeth allow undoubted identification of two species. This association renders the allocation of the postcranial remains tentative in many cases. No postcranial remains have so far been found in direct association with teeth of “Tetralophodon” atticus, an elusive species only known from craniomandibular and dental remains. Although the manus of *Choerolophodon pentelici* displays derived characters, these characters mainly involve the articulation between the trapezoid and magnum. Although no magnum was found at Akkaşdağlı (and the only trapezoid is poorly preserved), several postcranial remains can be allocated to *Choerolophodon pentelici*. What is left is allocated to unknown genus and species, although some of them may reasonably belong to “Tetralophodon” atticus.

SYSTEMATICS

**PROBOSCIDEA** Illiger, 1811  
**ELEPHANTOIDEA** Gray, 1821  
**Genus Choerolophodon** Schlesinger, 1917

*Choerolophodon pentelici*  
(Gaudry & Lartet, 1856)

**Material.** — Left Dp2 (AK2-300); right dp3 (AK10-2); right lunar (AK4-93); right lunar (AK6-89); left unciform (AKA29); left McIV and McV (AK2-93ab); right MdIII (AK11-68); left cuboid (AK14).
DESCRIPTION (FIGS 1-6)
The left upper second deciduous premolar (Dp2) AK2-300 (Fig. 1) is fresh, comprising four main cusps forming two bunodont lophs. It belongs to an elephantoid of trilophodont grade. It bears two roots, a narrow anterior root and a larger posterior one.

The two anterior cusps are connected. The labial cusp ("paracone") is the largest. The anterior cingulum is connected to the small lingual cusp ("protocone"). The two posterior cusps (the labial cusp – "metacone" – is the highest) are widely separated and the postcingulum does not form a loph. Small central conules are aligned to form a crest which connects the anterolabial cusp to the posterolingual one, that is, a contact between the posttrite anterior cusp and pretrite posterior cusp. This trait is present in Choerolophodon pentelici, including the Dp2 of the holotype cranium from Pikermi.

Measurements (mm): L = 34.3, W = 27.8 (second loph), H = 17.9 ("paracone").

The right lower third deciduous premolar (dp3) AK10-2 (Fig. 2) is slightly worn. It belongs to an elephantoid of trilophodont grade, with two lophs and an enlarged postcingulum. The enamel is heavily wrinkled, a character of milk teeth in general and especially marked on choerolophodont molars. The first loph is narrow, comprising two cusps, the labial one is anteroposteriorly enlarged, the lingual cusp is slightly displaced posteriorly compared to the labial, a choerolophodont character. In the interlophid a large posterior posttrite central conule connects the pretrite anterior central conule of the second lophid; a contact typical of choerolophodont dp3s.

The second lophid is transversely enlarged and separated from the inflated postcingulum by an entoflexus. No ectoflexus is marked.

All the characters described in this tooth match those of dp3s of Choerolophodon pentelici. The allocation of the Dp2 and the dp3 to C. pentelici is certain.

Measurements (mm): L = 47.0, W = 32.2 (second loph).

Two elephantoids are associated at Akkaşdağ, so that the allocation of the postcranial bones remains tentative. On the basis of associated teeth and carpals and metacarpals in localities were only Choerolophodon pentelici is present, and thus belong without doubt to this species (Samos: Schlesinger 1917; Kayadibi, Garkin: Gaziry 1976), seven handbones and footbones from Akkaşdağ are allocated to this taxon (comparisons with unpublished material on display in the Natural History Museum in Ankara were also helpful).

The two right lunars AK4-93 (Fig. 3) and AK6-89 show the same proportions as known lunars of C. pentelici with a strongly concave facet for the ulna. However, this bone is not especially modified in C. pentelici. The lunar AK6-89 is slightly narrower than AK4-93 but this does not change
the overall shape. The two lunars have a wide strongly concave lateral facet for the ulna. Both lunars show an enlargement of the medial border for the trapezoid and lateral border for the unciform. The protruding anteromedial corner of AK6-89 is gnawed (probably by a hyaena).

The unciform AKA29 (Fig. 4) has a rather vertical articular facet for the McV.

The metapodials (associated proximal parts of left McIV-McV AK2-93ab (Fig. 5) and the right MtIII AK11-68 (Fig. 6) bear heavily marked rugosities where ligaments insert on the cranial face, just beneath the proximal articular facets. The contact between the McIV and the McV is anteriorly narrowed, because of the articulation with an enlarged unciform. The facet of the McV for the unciform is not much heightened but anteriorly deepened.

In connection with the shape of the unciform (AKA29) it can be concluded that the McV is rather laterally oriented in *C. pentelici*.

The left cuboid AK14 shows two asymmetrical proximal articular facets. The calcaneal facet is much larger than the navicular facet. These two facets meet only in the center of the proximal face.

The MtIII AK11-68 has an oblique articular facet for the third cuneiform, heightened cranio-laterally. This implies a third cuneiform with an asymmetrical distal surface.

Measurements (mm):
Lunar AK4-93: width = 146.0, depth = 125.3, height = 82.5.
Lunar AK6-89: width = 138.5, depth = 122.6, height = 72.3.
Unciform AKA29: width = 107.8, depth = 115.0, height = 93.0.
McIV AK2-93b: depth = 119.8, width = 87.6.
McV AK2-93a: depth = 97.0, width = 86.8.

Fig. 4. — *Choeolophodon pentelici* (Gaudry & Lartet, 1856), left unciform AKA29, Akkaşdağ, Turonian; A, cranial view; B, distal view. Scale bar: 1 cm. Photo D. Serrette (MNHN).

Fig. 5. — *Choeolophodon pentelici* (Gaudry & Lartet, 1856), left 4th and 5th Metacarpals (McIV and McV) AK2-93ab, Akkaşdağ, Turonian; A, cranial view; B, proximal view. Scale bar: 1 cm. Photo D. Serrette (MNHN).
Cuboid AK14: width = 144.1, depth = 129.0, height = 53.0.
MtIII AK11-68: width = 95.9, depth = 111.0.

?Tetralophodon Falconer, 1857

"Tetralophodon" atticus (Wagner, 1857)

**MATERIAL.** — Left Dp3 (AK5-454).

**DESCRIPTION (FIG. 7).**
The left upper third deciduous premolar (Dp3) AK5-454 (Fig. 7) belongs to an elephantoid of tetralophodont grade: it shows three lophs and a postcingulum, with a posterolinguinal enlargement, characterizing Dp3s. Although the lophs are slightly compressed anteroposteriorly, the median sulcus is still present separating large pretrite hallophs and smaller postrite hallophs. The first loph is narrow and the tooth is enlarged on the lingual side at the level of the second interloph, two traits which are also known on Dp3s of tetralophodont elephantoid. The enamel is wrinkled (a character of a milk tooth). As in "Tetralophodon" atticus and gomphotheres in general, the trefoil pattern is preserved, in contrast to *Choerolophodon pentelicus*. The pretrite trefoil of the second loph comprised a distinct anterior pretrite central conule on the anterior side of the "hypocone" (aprcc2) and a posterior postrite central conule on the posterior side of the "metacone" (ppocc2). In the first interloph the aprcc2 connects to the labial anterior cusp ("paracone"). In the second interloph the ppocc2 connects to the anterior pretrite central conule of the third loph. This alternating contact between half sides of successive lophs is a derived trait, characteristic of advanced gomphotheres and elephants. Distinct buds on the posttrite part of the second and third lophs can be interpreted as posttrite conules.

Every character described on this Dp3 matches with the known Dp3s of "Tetralophodon" atticus (holotype from Pikermi described by Wagner [1857], and referred juvenile palate described by Gaudry & Lartet [1856] and Gaudry [1862] who confused it with *Choerolophodon pentelicus*).
Although the allocation of the binomen *Mastodon atticus* Wagner, 1857 to the genus *Tetralophodon* Falconer, 1857 is tentative (see Discussion below [and also Tassy 1985]), there is no doubt that this rare tetralophodont species is distinct from the rather common *C. pentelici*. Measurements (mm): length = 58.7, width = 42.4 (third loph), height = 25.4 (second loph, pretrite side).

Genus and species indet.

**Material.** — Two pieces of a rib (AK2-110); partial mesocuneiform (AK2-449); partial petrosal (AK4-94); partial caput humeri (AK5-3); right triquetrum (AK6-305); partial pelvis (acetabulum) (AK6-306); 1st phalanx of 4th anterior digit (AK6-90); left triquetrum (AK7-157); right unciform (AKB41); partial right trapezoid (AKK190).

**Description**

The material listed under “Elephantoid gen. and sp. indet.” consists of specimens that cannot be safely allocated to one or other of the two species identified at Akkaşdağ. The two portions of rib (AK2-110) and the partial mesocuneiform (AK2-449) were found in the same outcrop as the milk teeth of *C. pentelici* (AK2); the partial caput humeri (AK5-3) was found in the same outcrop as the Dp2 of “T.” *atticus*. However the material is too scarce for clear identification.

**Discussion**

The evolutionary level of *Cherolophodon pentelici* with a tetralophodont species is known in the Turolian, although *C. pentelici* is always the dominant species. Two different Turolian tetralophodont species are recognized, associated with *C. pentelici* but there is no definitive evidence that they are synonymous – or not.

*“Tetralophodon” atticus* was firstly described at Pikermi. The other tetralophodont species is *“Mastodon” grandicisivus* Schlesinger, 1917, firstly described at Maragha (Iran) and Mannersdorf (Austria). The taxonomy of these two species is conjectural. Although “*Tetralophodon* atticus” is likely to be a gomphothere, it has no shared derived character known to support sister group relationships with the type species of the genus *Tetralophodon*, that is *T. longirostris* from the Vallesian of Western Europe. The species “*T.* atticus” is mainly known from juvenile specimens with deciduous teeth. Yet, from Pikermi, an upper M3 has been described by Vacek (1877). It shares with known deciduous premolars the shape of the lophs, which are relatively compressed antero-posteriorly, with reduced central conules, on which basis the allocation of the M3 and the deciduous premolars at Pikermi to the same species was supported by Tassy (1985).

The species “*Mastodon* grandicisivus” is likely to be an amebelodontid, perhaps close to *Platybelodon*, a hypothesis based on the shape of lower tusks and the tubular structure of the dentine. Hence this species would have reached the tetralophodont grade in parallel to tetralophodont gomphotheres (see Tassy 1999 for further discussions and refutation of Tobien’s [1978] hypothesis, in which he allocated “*M.* grandicisivus” to the elephantid genus *Stegotetrabelodon*).

The rarity of tetralophodont specimens associated with *Cherolophodon pentelici*, and the lack of articulated postcranial remains are responsible for these difficulties.

Schlesinger (1917, 1922) firstly described “*grandicisivus*” as *Mastodon (Bunophodon) grandicisivus*, because of the tetralophodont grade (*Bunophodon* is a junior synonym of *Tetralophodon*). The tusks are very large, the upper ones are devoid
of an enamel band and are slightly curved, the lowers are the widest known among elephantoids. The molars of this species are very large and show lophs comprised of round cusps, with complete trefoils and sometimes an anancoid-like pattern, not the rather regular lophs such as those of the M3 from Pikermi allocated to “T.” atticus. In Turkey, Gaziry (1976) described at Amasya (late Tuolian) a large upper tusk of “T.” grandiscisivus and at Sultaniç-Enos a large upper M3 with an anancoid-like pattern.

The new material described at Akkaşdağ is not enough to definitely assess or refute the possible synonymy between “Tetrapododon” atticus and “Mastodon” grandiscisivus – although synonymy is unlikely –, nor a safe allocation of these two species to clearly identified genera. It is the taxon named here “Tetrapododon” atticus that is listed at Pikermi by Bernor et al. (1996) as “Stegotettrabelodon grandiscisivus”. Yet, the association of Choerolophodon pentelicus and “Tetrapododon” atticus makes Akkaşdağ directly comparable to Pikermi, so that the Turkish locality can be considered to be of typical of the Tuolian fauna of the Eastern Mediterranean area.

Acknowledgements

Geological studies and excavations at Akkaşdağ have been authorized by the General Directorate of Mineral Research and Exploration (MTA) and Ankara University, Faculty of Sciences. The work was done thanks to grants from the CNRS (ECLIPSE Program and DRI), the Museum national d’Histoire naturelle, Paris, MTA and TUBITAK. They have financially supported fieldwork and reciprocal visits to the concerned institutions. I thank Sevket Sen for having invited me to study the Akkaşdağ material. My stay at the MTA of Ankara was especially fruitful thanks to the friendly and effective help of Gerçek Sarao. Photographs were made by Denis Serrette (MNHN). The illustration was prepared by Didier Geffard (MNHN). Suggestions and remarks by Denis Geraads and one anonymous referee were especially fruitful.

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Submitted on 13 February 2004; accepted on 20 January 2005.