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The first *Tetralophodon* cranium (Mammalia, Proboscidea) from Africa

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RH: GERAADS ET AL.—*TETRALOPHODON* CRANIUM FROM MOROCCO

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ABSTRACT—We describe a virtually complete Proboscidean cranium and other remains from the late Miocene of Skoura near Ouarzazate, Morocco, assigning them to a derived species of *Tetralophodon*. African finds of this genus are scarce, and of additional interest due to their potential importance for elephantid phylogeny. The Skoura material adds significantly to the African record of non-anancine tetralophodonts, and to the Neogene proboscidean record of northwestern Africa.

INTRODUCTION

By comparison with other regions, especially Europe, Africa is relatively poor in rich late Miocene large mammals sites, and the dearth of fossils of this age hampers our understanding of the origin and evolution of many groups, as is well-known for hominins. In particular, the fossil record of proboscideans in North Africa is very imperfect, and strongly biased towards dental remains. The cranium described below contributes to filling a wide gap in the history of this group.

Discovery and Context

Zouhri et al. (2012) made the first report of a late Miocene mammal fauna from near the village of Skoura and the road pass of Tizi N'Tadderht, about 50 km ENE of Ouarzazate, Morocco. It was based upon fossils that were collected during a short visit to the sites by S. El Boughabi, D. Geraads and S. Zouhri in 2010, and are now stored in the Aïn Chock Faculty of Sciences, Casablanca, and upon those collected by local fossil hunters, and now housed in Brahim Tahiri's private museum in Erfoud, Morocco. A longer field season was organized by the same team in October 2013, leading to more discoveries of fossils in situ.

The Ouarzazate basin is an elongated tectonic depression, wedged between the central High Atlas to the north and the Anti-Atlas to the south; its outcrops range from the Upper Cretaceous to the Quaternary (Supplementary Information). The thickness of the Neogene deposits decreases from the North, where it can reach 700m, to the South, where the sediments are beveled on the Anti-Atlas Precambrian basement. Görler et al. (1988) attributed them to the Aït Kandoula Formation, consisting of three members, reduced to two by El Harfi et al. (2001). The fossils described by Zouhri et al. (2012) and the proboscidean material described here come from its upper member, which consists of alluvial deposits: sandstones and especially conglomerates. The detailed stratigraphy has not been established yet but, given the coarse nature of the sediments, it is likely that deposition was relatively rapid, and that the whole sequence does not cover a long time-span, although there is no evidence that all fossils can be regarded as strictly contemporaneous, even at the geological scale. The updated faunal list includes: cf. *Struthio* sp., cf. *Centrochelys* sp., *Crocodylus* cf. *niloticus*, Felidae indet., cf. *Hippotherium primigenium*, aff. *Cremohipparion periafricanum*, Hippotheriini gen. et sp. indet., cf. *Ceratotherium* sp., Elasmotheriinae gen. et sp. indet., Suidae gen. et sp., indet., Giraffidae gen. et sp. indet., cf. *Prostrepsiceros* sp., and the new caprine bovid *Skouraia helicoides* Geraads, El Boughabi and Zouhri, 2012. The biochronological significance of this relatively short faunal list is limited; this composite fauna was regarded as more probably of Turolian-equivalent age by Zouhri et al. (2012), but the resemblances of *Skouraia* with the middle Miocene *Benicerus* Heintz, 1973, and the presence of an elasmothere rhinoceros would be more in agreement with an earlier age in the Upper Miocene. Thus, the issue of the age of the Skoura assemblages is not fully settled.

On October 15, 2013, we spotted a proboscidean tusk at 31°11'30.2" N, 6°30'28.7" W; when trying to extract it, it was soon realized that it was attached to a virtually complete cranium embedded in a concrete-hard matrix, which was eventually extracted on October 18.

The cranium is now housed in the Aïn Chock Faculty of Science, Casablanca. Its 3D surface model (Figure 1) was prepared with Agisoft Photoscan. Dental nomenclature follows Tassy (1983); measurements are in millimeters; upper teeth are in uppercase, lower teeth in lowercase. Recent reviews of the taxonomy of late Miocene Old World proboscideans can be found in Markov (2008), Sanders et al. (2010), Tassy (2016), Konidaris and Koufos (2012), Konidaris et al. (2014).

The cranium (Figures 1 and 2) is virtually complete except for the occipital condyles, the superficial bone layer on the right half of the occipital and parietal, and the left tusk; the right tusk is incomplete. Some dorso-ventral compression certainly occurred, as shown by folding and antero-posterior fissures of the squamosal area in the posterior part of the temporal fossa, and horizontal cracks of the occipital surface. It is unlikely that this distortion significantly modified the general cranium pattern, but the numerous cracks of the bone surface that it induced hinders the reading of many details; in addition, the sediment preserved to hold the zygomatic arches hides parts of the temporal fossae. Still, this cranium is one of the best preserved Miocene African proboscidean crania, next to the *Anancus* skull from Toros-Menalla in Chad (Hautier et al., 2009)

Comparative Material

In North Africa, the only site having yielded a large sample of proboscidean material is Sahabi in Libya, now usually assigned to the late Miocene (El-Shawaihdi et al., 2016). Following Petrocchi (1941, 1954), Gaziry (1987) described *Stegotetrabelodon syrticus* Petrocchi, 1941 (which he erroneously regarded as a synonym of *S. lybicus*, but this latter name dates only from 1943 – see Tassy, 1999) and a new species, *Amebelodon cyrenaicus,* which seems to be either conspecific with, or very close to, a Eurasian form called '*Mastodon*' *grandincisivus* (see below). In Tunisia, Robinson and Black (1974) identified (but did not

figure) molar fragments from Testour as *Gomphotherium angustidens* (Cuvier, 1817), an identification that most probably is incorrect. No proboscideans have been identified from the relatively rich sites of Bled Douarah. From Jebel Krechem el Artsouma, Geraads (1989) described a single tooth fragment as *Choerolophodon* sp., and isolated teeth as *Tetralophodon* cf. *longirostris* (Kaup, 1832); he also reported as *Tetralophodon* sp. a complete molar from the 'corbeille' of Nefta, a small basin in southwestern Tunisia. Bergounioux and Crouzel (1956) also described as *T. longirostris* an incomplete tooth from the middle Miocene of Cherichira, and (as a premaxilla fragment – a mistake corrected by Tobien, 1978) a mandibular symphysis from the early late Miocene of Jebel Sémène. In Algeria, the site of Bou Hanifia (Arambourg, 1959) yielded only limb-bones of ?*Deinotherium*, but Lihoreau et al. (2015) described a few teeth of *Tetralophodon* from the late middle Miocene of Bir el Ater 3. Very few proboscidean remains have previously been reported from the late Miocene of Morocco. The locality of Zidania between Tadla and Beni Mellal yielded fragmentary remains attributed to *Tetralophodon longirostris* by Coppens et al. (1978) and to ?*Tetralophodon* sp. by Sanders et al. (2010). In the Upper Miocene deposits of the Aït Kandoula Basin, a small satellite basin north of the Ouarzazate basin, the Afoud 6 level of the well-calibrated Afoud section yielded undescribed postcranial elements and a molar fragment identified as Gomphotheriidae indet. thanks to its enamel microstructure (Remy and Benammi, 2006).

The eastern African record, especially in Kenya, is less scrappy but still very poor. From the Nawata Formation of Lothagam, dating from 7.5 to perhaps 5.5 Ma, Maglio (1973) described two Elephantidae, *Stegotetrabelodon orbus* Maglio, 1970 and *Primelephas gomphotheroides* Maglio, 1970 (now regarded as a synonym of *P. korotorensis* [Coppens, 1965]), to which Tassy (2003) added a new species of the same family, *Elephas nawataensis* (also regarded as a synonym of *P. korotorensis* by Sanders et al. [2010]), probably a fourth

unidentified species, and, among the Gomphotheriidae, *Anancus kenyensis* (MacInnes, 1942) and possibly another taxon. From the early late Miocene of Ngorora, Maglio (1974) and Tassy (1986) described *Choerolophodon ngorora* (Maglio, 1974) and a partial cranium of a juvenile tetralophodont gomphothere that could be *Tetralophodon*. From the Namurungule Fm of the Samburu Hills, Nakaya et al. (1987) reported a partial cranium as *Tetralophodon* sp., and Tsujikawa (2005) described teeth of *Choerolophodon* sp. The latter genus is also present at Nakali (Tassy, 1986; Sanders et al., 2010), along with a derived *Tetralophodon* (Saegusa et al., 2014). From Chorora in Ethiopia, Geraads et al. (2002) described as *Stegotetrabelodon* n.sp.? an m3 that Sanders et al. (2010) tentatively referred to the same species as in the Namurungule Fm. The early Pliocene species *Loxodonta adaurora* is relatively common but, although relatively complete skulls are known, they have been incompletely described and illustrated (Maglio, 1970, 1973; Maglio and Ricca, 1977; Sanders, 2018).

The late Miocene European record is definitely richer in terms of dental remains, but skulls are also quite rare. *Choerolophodon*, the most common genus of this time period, is reasonably well-known (review in Konidaris et al., 2016), but only a handful of incomplete specimens represent other taxa. Leaving aside the readily identifiable deinotheres and mammutids, the most significant specimens are: 1) a partial cranium from Pestszentlörincz, Hungary, that Schlesinger (1922) described as *Mastodon (Bunolophodon) grandincisivus* and of which he gave a largely conjectural reconstruction; 2) the anterior portion of a skull with mandible from Hohenwarth, Austria, described as *Tetralophodon longirostris* by Zapfe (1957); 3) a similar cranium fragment from Esselborn, Germany, described by Bergounioux and Crouzel (1960) as *T. curvirostris* and also illustrated by Tobien (1986, fig. 28); 4) a partial cranium from the Vallesian of Barcelona, preserving the cranial basis, identified as *T. longirostris* by Alberdi (1971) but as *Gomphotherium angustidens* by Tobien (1978), a re-

identification that Mazo and Montoya (2003) rejected; 5) an almost complete adult cranium from Kornberg, Austria, described as *T. longirostris* by Mottl (1969); 6) a partial cranium from Dolni Disan, North Macedonia, described by Garevski (1976) as *Bunolophodon longirostris*, but re-identified as *Tetralophodon atticus* by Spassov et al. (2018); 7) the dorsal part of a cranium from the suburbs of Valladolid, Spain, described by Mazo Pérez and Jordá Pardo (1997) as *T. longirostris*; 8) a cranium from Maritza-Iztok, Bulgaria, described as *Stegotetrabelodon grandincisivus* by Kovachev (2004) and which is, according to Markov (2008), the only known cranium of *'Mastodon' grandincisivus*.

The best-known cranium of a late Miocene gomphothere is that of *Paratetralophodon hasnotensis* (Osborn, 1929), from Pakistan, represented by two virtually complete specimens, AMNH 19686 (Osborn, 1936, fig. 324, as *Tetralophodon punjabiensis*) and GSP 15032 (Tassy, 1983, figs. 28–29). The skull of the middle Miocene *Gomphotherium angustidens* is well-known through the work of Tassy (2013).

SYSTEMATIC PALEONTOLOGY

Order PROBOSCIDEA Illiger, 1811

Superfamily ELEPHANTOIDEA Gray, 1821

Family GOMPHOTHERIIDAE Hay, 1922

Genus *TETRALOPHODON* Falconer, 1857

TETRALOPHODON sp.

(Figs. 1 and 2)

Material— Cranium FSC-Sk-180 stored in the Aïn Chock Faculty of Science, Casablanca, Morocco. We tentatively refer to the same taxon an unnumbered partial mandible

and an upper tusk housed in the Brahim Tahiri Museum, Erfoud, Morocco. All from Tizi N'Tadderht near Skoura, Ouarzazate, Morocco. Late Miocene (Zouhri et al., 2012).

Description

Ontogenic Age of the Skoura cranium— The cheek teeth consist of well-worn P4s, moderately worn M1s, and unworn M2s; M3s are not visible. Although elephant age classes cannot directly be transposed to mastodonts, this corresponds to age class IV(1–3) of Sikes (1967), or stages XI–XII of Laws (1966) (Beden, 1979, Tab. 8), and to dental age XIII of trilophodont elephantoids (Tassy, 2013). Thus, the cranium was clearly from a sub-adult individual, about 15 years old. To evaluate the dimensions that it might have reached when adult, we have computed the measurements for four samples of *Loxodonta africana*, using the measurements provided by Beden (1979): two samples of similar age as the Skoura mastodont, one from Kenya, one from Uganda, and two samples of almost fully-grown animals (cranial growth never ceases), from the same provenances. Although the Ugandan elephants are smaller than the Kenyan ones, the ontogenic increase in linear measurements is similar in both populations. Table 1 shows that growth is strongly differential: measurements associated with the tusks, trunk and cranial vault increase much more than those related to the cranial basis, which is almost stable. Using the average growth coefficients of both populations for each measurement, we have estimated the measurements of the Skoura specimen, had it reached a fully adult age (Table 1).

Cranium—In its overall proportions, the cranium is distinctly shorter than those of extant elephants. It is broader across the zygomatic arches than across the occipital (but the difference is less marked than in *Loxodonta africana*) and narrower across the orbits. The fronto-parietal region is very short, even compared to *L. africana*. This apparent shortness of

the cranial roof is increased by the relatively great distance between the tops of the temporal fossae.

By contrast, the naso-orbital area is quite long. The nasal fossa assumes the shape of an inverted W, but it is much higher (antero-posteriorly longer) than in *L. africana*. The tips of the nasals remain far more caudal than the caudal bottom of the intermaxillary fossa, which is at about the same level as the lateral rostral ends of the nasal fossa. There is a depression at the postero-medial corner of the nasal fossae, on either sides of the V-shaped nasal eminence, so that their posterior borders form a double concavity, instead of being regularly concave as in *L. africana*.

By comparison with the shortness of the cerebral part of the cranium, the rostrum is long and, if the growth of that part was positively allometric as it is in *L. africana* (Beden, 1979) it would have been relatively longer still in the adult individual, thus sharply differing from the short rostrum of *L africana*. The lateral borders of the premaxillae are only slightly divergent forwards, and the tusks were certainly poorly divergent. The partially preserved right incisor is small compared to the size of the animal, suggesting a female individual, although its young ontogenic age urges caution in this regard. Between the incisor sheaths, the V-shaped incisive fossa is long, broad anteriorly, and sharply delimited.

The interpretation of the lateral view depends on the estimation of the amount of dorso-ventral crushing. In its present state, the cranium is not very deep, but it is likely that it was in fact deeper in life. The cranial basis, now almost in line with the occlusal profile of M2, was certainly steeper, although not as upright as in *L. africana*. The orbit is relatively small, and located above M2, well behind the tooth that is in use (M1). It is thus much less anterior than in *L. africana*, and the difference is likely to have been greater in the adult, because Tassy (2013) showed that in *G. angustidens* the tooth-row shifts forwards relative to the orbit during ontogeny.

The slightly concave facial profile can hardly be regarded as faithfully reflecting the original condition because of likely distortion, but the degree of downward slope of the premaxillae is reliable, because the tusk sheaths, including the right one that lacks the tusk, are undistorted. This downward slope is certainly less marked than in *L. africana*. Together with the orientation of the cranial basis, it indicates a head posture less derived than in extant elephants, in which the cranium is dorso-ventrally much deeper.

The orbit is relatively small; the supra-orbital process is poorly defined, but the ventral post-orbital process is prominent; it seems to be formed by the zygomatic, as in *L. africana*. The zygomatic is a long bone with a straight ventral border. The well-preserved left temporal fossa is clearly delimited, as the sharp ridge that separates it from the cranial roof proceeds posteriorly along about half of the occipital height. The occipital is low and wide, in contrast to *L. africana*; as a whole it is roughly perpendicular to the occlusal plane of M1, and rather flat, but both halves are slightly concave. The fossae for the nuchal ligaments occupy a central position in the occipital; they are quite deep, and widen dorsally, so that they are triangular rather than oval as in *L. africana*.

In ventral view, the cranium is long and narrow. It reaches its maximum width over the posterior part of the zygomatic arches, which gently converge forwards. No details can be observed in the cranial basis, which is short. The pterygoid wings come close to each other; there is no longitudinal crest on the basioccipital.

Teeth—On both sides, P4–M2 are preserved (Table 2). The premolars, consisting of two lophs and a posterior cingulum, are heavily worn, especially the left one. Nevertheless, the generally suboval shape of the right P4 is still discernable. On the first lophs, pretrite and posttrite halves are fused by wear (confluent wear pattern); on the second lophs, pretrite and posttrite sides are still separate with the pretrites slightly more worn. The first molars are tetralophodont, with a very weak posterior cingulum. On both teeth, all lophs bear traces of

wear, with dentine exposed on the first three lophs. The first loph of the left M1 is deeply worn, with pretrite and posttrite halves fused. On the second loph, an anterior pretrite central conule (ccpra) is still visible, as well as an anterior posttrite central conule (ccpoa) of similar dimensions. Mesoconelets and main cusps are of similar size. There are no posterior conules, giving the loph a plate-like look. On the third loph, a ccpra contacts the mesoconelet of the preceding pretrite semiloph. The third posttrite semiloph has the main cusp in a more distal position than the mesoconelet, the two are uniformly worn. Posterior conules are absent. The fourth loph is only slightly worn and has a plate-like appearance: pretrite and posttrite halves are fused, with main cusps and mesoconelets of equal height, and reduced ccpra. Anteroposterior compression visible in all lophs is especially pronounced here. There are traces of cement in the interlophs. The morphology of the right M1 is similar, except that its ccpra2 seems better developed, and the displacement of the third posttrite semiloph slightly weaker.

The second molars, consisting of four lophs and a posterior cingulum, are unworn. The left M2 is slightly damaged on the first posttrite. On the first and second pretrite, the main cusp is higher than the mesoconelet, ccpra and ccprp are present, with ccprp1 contacting ccpra2, thus blocking the interloph. No ornamentation is seen on the posttrite semilophs. The third pretrite has a ccpra contacting ccprp2 but no posterior conule. A contact between pretrite semilophs is seen even better on the right M2, the third pretrite of which has a visible posterior central conule contacting ccpra4. On the left M2, the fourth loph is strongly antero-posteriorly compressed and has the pretrite and posttrite parts of equal height fused, with no central conules, leaving the third interloph open. The posterior cingulum consists of four conelets; at least four conelets are seen on the posterior cingulum of the right M2 as well.

Other Remains—The few other Proboscidean remains from Skoura do not provide evidence for another species, and we tentatively refer them to the same taxon as the cranium.

Besides a molar fragment with 1½ loph and a distal radius, there is a straight tusk fragment in Erfoud, about 750 mm long, with a cross-section measuring 110 x 83 mm, thus larger than that of the cranium, but with similar proportions, ovoid shape of cross-section, and concentric dentine; we assume that it is also an upper tusk, because lower tusks usually show at least a hint of longitudinal groove (e.g., Mazo and Montoya, 2003, fig. 3).

The best additional specimen is a mandible in Erfoud bearing only a heavily damaged cheek tooth. Relatively large incisors were certainly present, but the reconstruction of their alveoli is highly speculative. However, as preserved, the symphysis, about 20 cm in front of the cheek-teeth, is much broader ventrally than dorsally, and this looks hardly reconcilable with transversely broadened incisors, whose longest diameter would be ventro-medial to dorso-lateral; thus, it seems to be more in agreement with moderately-sized tusks, although the evidence is slight. The symphysis is only slightly sloping downwards, in agreement with the moderate inclination of the cranium premaxillae. What remains of the single broken tooth does not allow many observations; with estimated length x width measurements of 200 x 80 mm, it is probably an m3 rather than an m2 but, because it was at most slightly worn, the absence of evidence of another tooth behind it is not decisive in this regard. All that can be said about its morphology is that the tubercles were arranged in a few transverse rows, probably without distinct anancoid pattern. Overall length of the mandible is c. 600mm.

Systematic Context

While the occurrence, in the early late Miocene of the western Old World, of *Tetralophodon longirostris*, is generally accepted and well-documented, Turolian or Turolian-equivalent faunas yield tetralophodont taxa of more debatable affinities, as observed and discussed by Markov (2008), Konidaris et al. (2014), and Tassy (2016). Especially relevant to the discussion on the affinities of the Skoura proboscidean is the presence of tetralophodont

amebelodontids in a number of late Miocene localities throughout the Old World, including north Africa (e.g. Sahabi). The Sahabi form, described by Gaziry (1987) as '*Amebelodon cyrenaicus*' is, as noted by Tassy (1999) close to, or conspecific with, a Eurasian species usually referred to as '*Mastodon*' *grandincisivus* Schlesinger, 1917. Recently, Konidaris et al. (2014) synonymized '*M.*' *grandincisivus* with *Mastodon atticus* Wagner, 1857, previously regarded as a derived *Tetralophodon* (or primitive *Stegotetrabelodon*: Tassy, 2005; but see comment in Markov, 2008) and referred the species to *Konobelodon*, raised by Lambert (1990) for North American material. This concept is not universally accepted (Tassy, 2016; Spassov et al., 2018). Here, we adopt a more conservative approach, assuming the co-occurrence of an amebelodontid and a tetralophodont gomphothere in the Turolian of central and eastern Europe and southwest Asia (Markov, 2008), using the name '*M.*' *grandincisivus* for the former and *Tetralophodon atticus* for the latter.

Comparisons

Cranium—the proportions of the cranium are intermediate between the long ones of *G. angustidens* (in Tassy, 2013) and the broad crania of *Loxodonta africana* (Beden, 1979) and *P. hasnotensis* (in Tassy, 1983). According to Mottl (1969) the Kornberg cranium is wider across the post-orbital processes than across the occipital, but this is perhaps due to the incomplete preservation of the latter, because this difference is not reflected in her figures. In its present state, the Skoura cranium is not much deeper than that of *G. angustidens*, but it is likely that it was in fact deeper in life, comparable in this regard to *P. hasnotensis*, although certainly less deep than that of *L. adaurora* (Maglio, 1970, fig. 2A). The cranial basis, now almost in line with the occlusal profile of M2, was certainly steeper in life, as in the Kornberg cranium of *T. longirostris*, although not as upright as in *L. africana* or *L. adaurora*.

The main differences between the Skoura cranium and the very few other late Miocene specimens lie in the proportions of the face and cranium roof. The fronto-parietal region of the Skoura cranium (from the top of the occipital to the tip of the nasals) is very short, especially by comparison with *G. angustidens*, but even compared to *L. africana* and *P. hasnotensis*, and probably also to *L. adaurora* (Maglio, 1970, fig. 2A; Maglio 1973, pl.5, fig.1; Maglio and Ricca [1977: 37] state that this species has a 'longer forehead' than the living one). This apparent shortness of the cranial roof is increased by the great distance between the tops of the temporal fossae; the Skoura cranium is the only one (except perhaps that of *L. adaurora*, but measurements have not been published) in which the width of the cranial roof (Table 1, measurement 11) is greater than its length (measurement 2). By contrast, the nasal fossa is much higher (antero-posteriorly longer); it is much less wide than in the cranium GSP 15032 of *P. hasnotensis*, both in comparison to its anteroposterior length and to the width over the orbits, but it is also narrow in AMNH 19686, assumed by Tassy (1983) to be of the same species; it is also quite wide in the Kornberg cranium of *T. longirostris*, but not in the one from Villavieja.

The orbit is distinctly less anterior than in the ontogenically older crania of *P. hasnotensis* and, as mentioned above for *L. africana*, the difference is likely to have been greater in the adult.

The long rostrum is shared with the Villavieja cranium, *P. hasnotensis* and *L. adaurora*. Between the incisor sheaths, the V-shaped incisive fossa is long but broad anteriorly, and sharply delimited, contrasting with the smooth lateral borders observed in most other specimens except GSP 15032 (*P. hasnotensis*) and the Kornberg cranium (*T. longirostris*). Its downward slope is similar to that of *G. angustidens* and of the Kornberg cranium, and certainly less marked than in *P. hasnotensis* or *Loxodonta*. Together with the orientation of the cranial basis, it indicates a head posture less derived than in these latter taxa,

in accordance with their much deeper cranium, as clearly observed in occipital view. Although dorso-ventral distortion prevents a reliable estimate of the basicranial angle, it was certainly low (around 30°), closer to that of *T. longirostris* than to those of *P. hasnotensis* (50° according to Tassy, 1983) or of the Samburu *Tetralophodon* (60° according to Nakaya et al. [1994]); the *Stegotetrabelodon* skull from Sahabi (Petrocchi, 1954) is heavily reconstructed, but the partial *Stegotetrabelodon* cranium from Abu Dhabi (Sanders, in press) shows a strong cranial flexure. Thus, the Skoura cranium was clearly less derived than these latter forms in this regard. The large, deep fossae for the nuchal ligaments look distinctly larger, especially dorsally, than in other Miocene taxa, but they are also large and deep in *L. adaurora* (Maglio and Ricca, 1977).

In ventral view, the zygomatic arches converge less sharply anteriorly than those of the Kornberg cranium, but this might be an effect of the younger ontogenic age of the Skoura cranium, like the absence of a central longitudinal crest; likewise, the still shorter cranial basis of the Kornberg cranium could be explained by the negative growth allometry of this part of the cranium.

Obviously, the very small number of preserved crania prevents the most basic estimates of intra- vs. interspecific variation but, on the whole, the Skoura cranium resembles the most complete known specimen of *T. longirostris*, from Kornberg (Mottl, 1969).

Mandible—The symphysis of *G. angustidens* is still less inclined; it is more downwardly sloping in the *Tetralophodon longirostris* from Esselborn (Tobien, 1980, fig. 8) but other specimens of this species also have a symphysis that is only slightly downturned (e.g., Schlesinger, 1917, pl. 13, fig. 4; Tobien, 1978, pl. 15; Tobien, 1980, fig. 7). This seems to be more in agreement with moderately-sized tusks, such as those of *T. longirostris* (e.g., Tobien, 1976, fig. 29, 30), but this is far from certain, as differences in symphyseal angulation could be related to ontogenic age (W. Sanders, pers. com.).

Teeth—Absence of anancoidy (no alternation of the semilophs, or cross-contacts between them) sets the teeth apart from members of the genus *Anancus*, and the sub-parallel upper tusks and large lower tusks confirm that the Skoura proboscidean is unconnected to this genus, so that comparisons can be limited to other tetralophodonts. Amebelodontids close to, or identical with the Eurasian species '*Mastodon*' *grandincisivus* are known from the late Miocene of Africa (Gaziry, 1987; discussion in Tassy, 1999, 2003; Markov, 2008; Konidaris et al., 2014). The Küçükçekmece second molars (Tassy, 2016), probably belonging to the latter species, are larger than Skoura and display a different morphology, including a more pronounced pretrite trefoil pattern, posttrite ornamentation, pseudoanancoidy, less pronounced antero-posterior compression, and these features on the Skoura teeth are a better match for the morphology in *Tetralophodon*. At Maragha, a locality that has yielded '*M.' grandincisivus*, the M1 in the cranium described by Schlesinger (1917) is smaller, has better developed cingulum and an almost V-shaped 4th loph, compared to the plate-like 4th loph on Skoura, but these differences might be regarded as individual variation. Compared to *T. longirostris*, type species of the genus, the Skoura proboscidean displays the following derived characters: strong antero-posterior compression of the lophs (plate-like appearance; this was also noted for the Nakali material by Saegusa et al., 2014), enlarged mesoconelets (see Sanders et al., 2010 for that condition in the *Tetralophodon* from Namurungule; Wang et al., 2017 on a M1 from Wuzhong, Ningxia, referred by those authors to *T.* cf. *euryrostris*), reduced accessory conules and, according to W. Sanders (pers. com.), less of a pre- to posttrite wear gradient of the molars (perhaps due to less lateral movement of phase II chewing and more anteroposterior grinding). It is more similar to Turolian Eurasian material referred to *T. atticus* by Markov (2008) and Spassov et al. (2018), although the M2 in the Dolni Disan cranium described by these latter authors has posttrite ornamentation. The combination of weak accessory conules and enlarged mesoconelets is shared by *Tetralophodon* teeth from Dorn-

Dürkheim (referred to '*Stegolophodon caementifer*' by Gaziry, 1997) and indeed gives the teeth a superficial resemblance to *Stegolophodon*. However, unlike in the latter genus, ccpra and mesoconelets are not entirely fused (Wang et al., 2017; Saegusa et al., 2005:fig. 2). *Paratetralophodon hasnotensis* has stronger accessory conules (and posttrite ornamentation lacking in Skoura), and a thicker cement layer (Tassy, 1983). Compared to named species of *Stegotetrabelodon*, the Skoura proboscidean is more primitive in the loph number (M2 with 5 plates in both *S. syrticus* and *S. orbus*: Sanders et al., 2010), and morphology: accessory conules blocking the anterior interlophs (but they are still present in the *Stegotetrabelodon* from the Baynunah Fm: Sanders [in press]), small amounts of cement.

Metrically (Fig. 3), the Skoura teeth fall within the wide variation range of related taxa. The most notable point is perhaps the relatively large size of P4, especially by comparison with *Stegotetrabelodon*.

CONCLUSION

Given its geographic provenance and age, the Skoura cranium could belong either to an amebelodontid close to *'M.' grandincisivus*, or to a member of the clade comprising tetralophodont gomphotheres and elephants. The absence of lower incisors prevents a final conclusion, but the dental morphology (no posttrite ornamentation, reduced pretrite conules resulting in a confluent wear figure not unlike elephantid plates) supports affinities with the latter group, in agreement with a cranial morphology close to that of *T. longirostris*. In that case, the material from Skoura belongs to a derived *Tetralophodon* species but the young ontogenic age of the cranium, and the absence of associated lower incisors make it an unsuitable type In any case, it confirms the extension of this group over Africa. In addition, the derived dental characters compared to *T. longirostris*, and the similarities with early

elephants such as *L. adaurora* fully confirm the view of Sanders et al. (2010) who wrote: 'Morphologically and chronostratigraphically, African *Tetralophodon* is appropriately situated to be ancestral to elephants'.

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FIGURE CAPTIONS

FIGURE 1. Interactive 3D reconstruction of the Skoura cranium. [flat image prepared for column width: Geraads&al_Tetralophodon_Fig1_R1.tif; 3D files: Geraads&al_Tetralophodon3D.zip]

FIGURE 2. *Tetralophodon* sp. from Skoura. **A–E**, cranium FSC-Sk-180. **A**, occlusal view of P4–M1 (stereo); **B**, ventral view; **C**, left dorso-lateral view. **D**, antero-dorsal view; **E**, occipital view; **F**, antero-lateral view of unnumbered mandible in Brahim Tahiri's museum. Scale bar equals 15 cm for Fig. A, 50 cm for Figs. B−F (approx. for Figs. C–D; which are oblique views). [prepared for page width]

FIGURE 3. Measurements of upper cheek-teeth. Data from Göhlich, 1998, Sanders, in press, Tassy, 1983, Wang et al., 2017, and our own. [prepared for page width]

Supplementary information: geological map of the Ouarzazate Basin, with the location of the *Tetralophodon* cranium; legend refers to Cenozoic deposits only [file Geraads&al_Tetralophodon_Supinfo.kmz]