PALÆO VERTEBRATA

The new Algerian locality of Bir el Ater 3: validity of *Libycosaurus algeriensis* (Mammalia, Hippopotamoidea) and the age of the Nementcha Formation

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Abstract: The description of original material of anthracothere and proboscidean in the new locality of Bir el Ater 3 from East Algeria, and a thorough review of early *Libycosaurus* remains of Bir el Ater 2 allows us validating *L. algeriensis* as the smallest and earliest species of *Libycosaurus* and probably the earliest migrant of the genus from Asia. The presence of a *Tetralophodon* in the Neogene Nementcha formation might represent the earliest occurrence of the genus in Africa. These original fossil remains allow us to discuss the age of the Neogene part of the Nementcha formation close to the Serravalian/Tortonian boundary.

Keywords: Dispersal event, Miocene, North Africa, *Tetralophodon*

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INTRODUCTION

The transition between middle and late Miocene in North Africa is scarcely recorded and faunal transitions are largely unknown in this part of the world and for this time interval (see review in Werdelin, 2010). In that context, the fossil collection established from Bled Douarah in the Beglia formation, central Tunisia (Robinson and Black, 1974) is key to understand African faunal evolution and dispersion prior to the setting of the arid Saharan barrier (Douady *et al*., 2003; Griffin, 2002; Lihoreau *et al*., 2006).

Discoveries of new localities from this time interval are critical. We describe here new Miocene fossils from the locality of Bir el Ater 3 in the Nementcha formation (East Algeria). Bir el Ater is renowned for its Late Eocene locality (e.g., Coiffait *et al*., 1984; Bonis de *et al*., 1988) but this area also yielded Miocene mammalian remains in Bir el Ater 2 (Ducrocq *et al*., 2001; Mahboubi *et al*., 2003). The Nementcha formation in Bir el Ater can be considered either as a probable western extension of the Beglia formation, or as an earlier sedimentary phase, when considered the general progradation of the fluvio-lacustrine series toward the East in this part of the Maghreb (Mannaï-Tayech & Otero, 2005). The anthracothere species from Bir el Ater 2, *Libycosaurus algeriensis* Ducrocq *et al*., 2001 was first described as a basal representative of the genus (Ducrocq *et al*., 2001; Lihoreau *et al*., 2014). However, the validity of this species has then been challenged due to the low number of associated remains and the lack of clear diagnostic characters observable (e.g. Pickford, 2006). We present here original material from a new Miocene locality near Bir el Ater 2 that completes the description of *L. algeriensis* and provides evidence of the presence of a tetralophodontine proboscidean. It allows us discussing the age of the basalmost part of the Nementcha formation and proposing an evolutionary history scenario for the *Libycosaurus* lineage, which involves a dispersal event of anthracothere from Asia toward Africa during the Middle Miocene (Lihoreau *et al*., 2006).

GEOLOGICAL CONTEXT AND MATERIAL

The original fossil materials have been unearthed in 1987 by one of us (MM) in a lenticular bed located on the right bank of the Oued Halail River, on the southern side of the Nementcha mounts, 60 km west from the city of Bir el Ater. The new locality is close to Bir el Ater 2, about one kilometer north on the same river bank, and about four kilometers west of the Eocene Bir el Ater locality (Fig. 1). Part of this new material was evoked in a previous work on the Neogene from Bir el Ater 2 (Ducrocq *et al*., 2001) and in a review of stratigraphical context of the area (Mahboubi *et al*., 2003). The undescribed remains belong to a Neogene sedimentary series that can reach 1000 m in thickness in this area (Mahboubi *et al*., 2003). These fossils were found about 250 m stratigraphically lower than Bir el Ater 2 and 150 m above Bir el Ater (Eocene continental, Fig. 1). Due to stratigraphical and geographical differences, we have decided to name the new locality Bir el Ater 3. It corresponds to the closest fossiliferous level to the Eocene/Miocene contact in this area. The Miocene is represented by fluvial to fluvio-deltaic weakly agglutinated sandstones with alternation of red silts and gritstones. This Miocene continental series can be compared to the well-described Beglia formation in Tunisia (see Mannaï-Tayech, 2009) but lithographical correlations are difficult due to the presence of heterogeneous facies in the latter (Mannaï-Tayech, 2006). Considering that the continental series of the Beglia formation is supposed to be progradant toward Northeast, the Algerian localities might represent the lowest known fossiliferous locality of this formation. Biochronological correlation with Bled Douarah (in the Beglia fm) was proposed on the ground of the presence of *Libycosaurus* and the Nementcha formation was hypothesized to be late Middle to early late Miocene (Ducrocq *et al*., 2001). However, the age of the Beglia formation is poorly constrained (Serravalian and early Tortonian; Werdelin, 2010), the Bled Douarah locality in particular, which is supposed to be close to middle-late Miocene boundary (near 11.63 Ma following

Hilgens *et al*., 2012). Difference in *Libycosaurus* species attribution (Ducrocq *et al*., 2001) would rather support heterochrony between the two localities.

SYSTEMATIC PALEONTOLOGY

CETARTIODACTYLA Montgelard, Catzeflis & Douzery, 1997

CETANCODONTA Arnason *et al*., 2000

HIPPOPOTAMOIDEA Gray, 1821 (*sensu* Gentry & Hooker, 1988)

ANTHRACOTHERIIDAE *sensu* Leidy, 1869

BOTHRIODONTINAE Scott, 1940

Libycosaurus Bonarelli, 1947

Type species. *Libycosaurus petrocchii* Bonarelli, 1947

Included species. *Libycosaurus petrocchii* from Libya (restricted to the type considered as lost; see Lihoreau *et al*., 2014), *L. anisae* (Black, 1972) from Tunisia and possibly Uganda, *L. bahri* Lihoreau *et al*. 2014 from Libya and Chad, *L. algeriensis* Ducrocq *et al.* 2001 from Algeria.

Range and distribution. Late middle Miocene (11 Ma) to late Miocene (7 Ma) in Africa.

Libycosaurus algeriensis Ducrocq *et al.* 2001 (Figs 2-4)

Holotype. Fragmentary maxilla with left M2/-M3/ (UONM1)

Paratypes. Twelve tooth fragments (see Ducrocq *et al*., 2001 for list)

New material. A left fragment of mandible with complete m/2-m/3 from the Algerian locality of Bir el Ater 3 (UONM-14). This material is housed at the University of Oran 2, Algeria.

Type Locality. Bir el Ater 2, Nementcha, Algeria

Type horizon. Nementcha formation, considered to be late Serravalian.

Emended diagnosis. Smallest known species of the genus; retention of a small endometacristid on lower molars that connects preprotocristid; ectocristylids that form cusplets in the transverse valleys near a developed labial cingulid; only one postentostylid on the posthypocristulid separated with hypoconulid apex by a lingual groove. Enamel microstructure of molars retains large and blurry Hunter Schreger Bands. Shallow mandible with a weak vascular impression. Retention of a lingual cingulum around protocone in upper molars even in worn specimen.

Differential diagnosis. *Libycosaurus algeriensis* differs from other species of *Libycosaurus* by its smaller dimensions with shallow mandible, the presence a small endometacristid on lower molars, the ectocristylids always developed in cusplets in the transverse valleys, which is rare in other species, the large lingual cingulum around protocone of upper molar even in worn specimens. It also differs from *L. anisae* by the presence of only one entostylid on the third lobe of the M/3. It differs from *L. bahri* by the presence of a posthypocristulid on M/3, a weak vascular impression on mandible and by large and blurry Hunter Schreger Bands on enamel.

Comparative description

Teeth. The teeth description follows the dental nomenclature established for Hippopotamoidea (Boisserie *et al*., 2010;

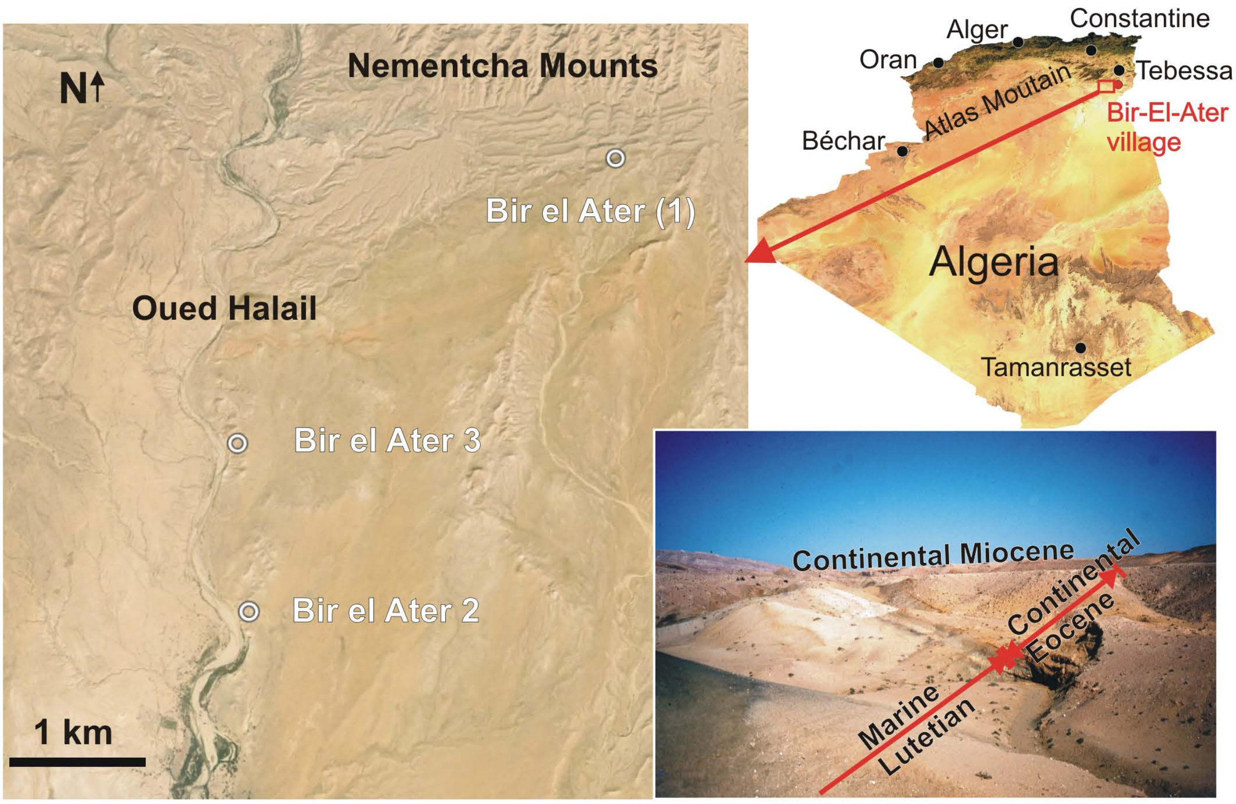


Figure 1. Geographic position of the fossiliferous localities of Bir el Ater (Eocene -(1), and Miocene -2) in Algeria, with the localisation of the new locality, Bir el Ater 3. On the right lower corner the photograph of the Eocene-Miocene unconformity near the locality of Bir el Ater (1).

Fig. 3). The lower molars present the characteristic features of bothriodontines (see Lihoreau & Ducrocq, 2007; Figs. 2-3) including the long development of prehypocristid that reaches the lingual margin of the tooth. The presence of a strong labial cingulid, considered as diagnostic for the species *L. algeriensis* (Ducrocq *et al*., 2001), is also observed in other *Libycosaurus* and *Merycopotamus* species. It is slightly developed in *Sivameryx* but never enlarged in front of labial cuspids in other bothriodontines.

The lower molars from Bir el Ater 3 (Fig. 2C) present characteristic features of the genus *Libycosaurus* such as the lack of premetacristid, the presence of a small postentocristid wedged between the base of the entoconid and the posthypocristid (also known in derived *Merycopotamus* species; Lihoreau *et al*., 2007), a labial loop-like hypoconulid with a notch (incomplete posthypocristulid displaying at least one accessory cuspid), and the presence of an ectoentocristid. This morphology differs from the genera described in the African Miocene *Brachyodus*, *Sivameryx* (Fig. 3) and *Afromeryx*.

The lower molars differ from *L. anisae* and *L. bahri* by the

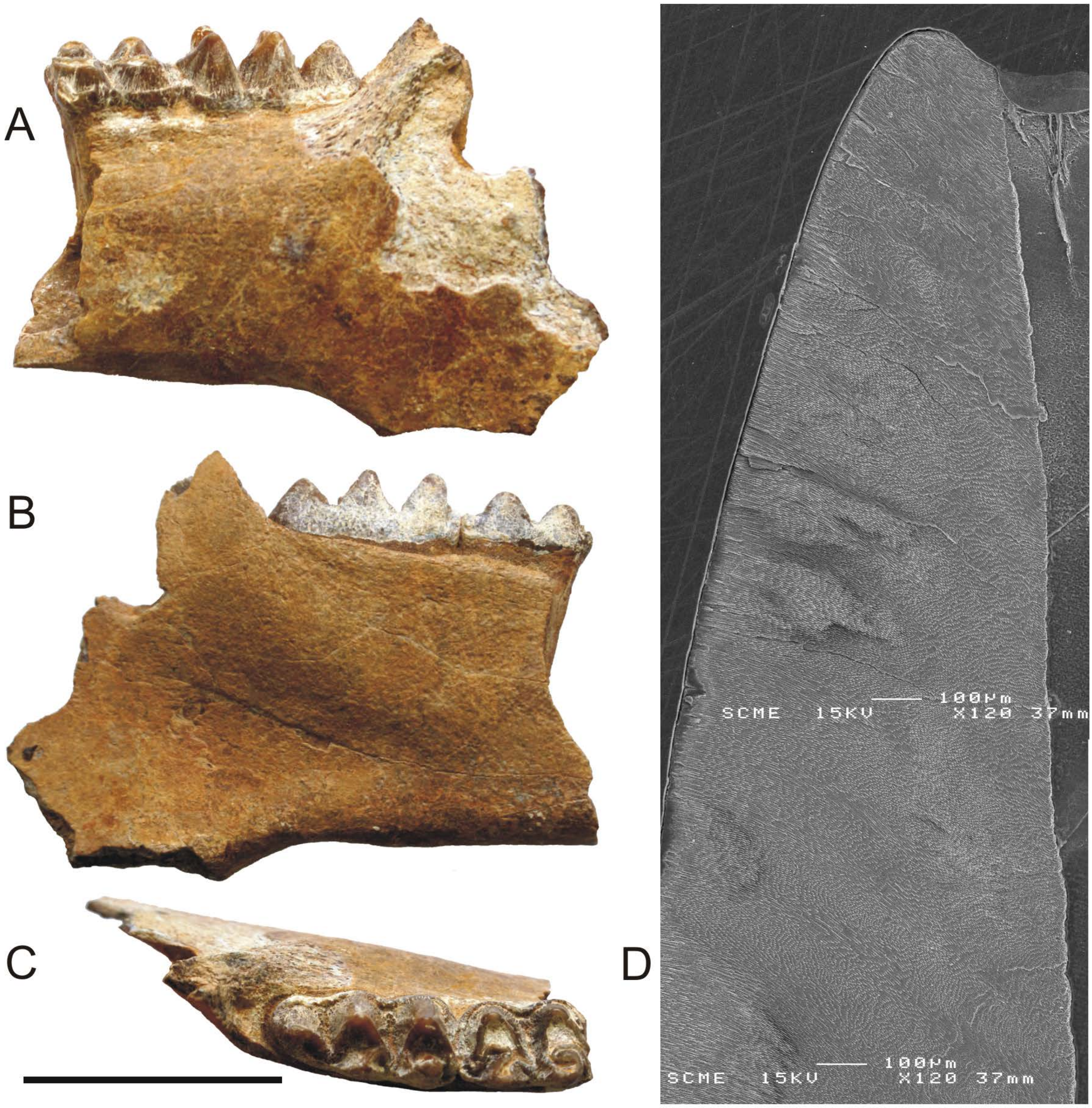


Figure 2. *Libycosaurus algeriensis* from Nementcha Formation, Algeria. A-C, (UONM-14) left hemi-mandibular fragment with m/2-m/3 of *L. algeriensis* from Bir el Ater 3. **A,** labial view. **B,** lingual view. **C,** occlusal view. **D,** SEM picture of a vertical section of enamel of a molar of *L. algeriensis* from Bir el Ater 2. Scale bar equals 5cm.

retention of a small endometacristid that connects preprotocristid (Figs. 2-3). The labial cingulid is adorned with ectostylids, which reinforces the idea of a large cingulid (see Ducrocq *et al*., 2001).

There are cusplets in the transverse valleys of lower molars considered as ectocristilids also present in the four known specimens of *L. algeriensis*. Ectocristilids in *L. anisae* and *L. bahri* do not form cusplets but a succession of small tubercles in line and when cusplets can be observed in these species the frequencies are of 0% in *L. anisae* (n=23) and 2.5% in *L. bahri* (n= 40).

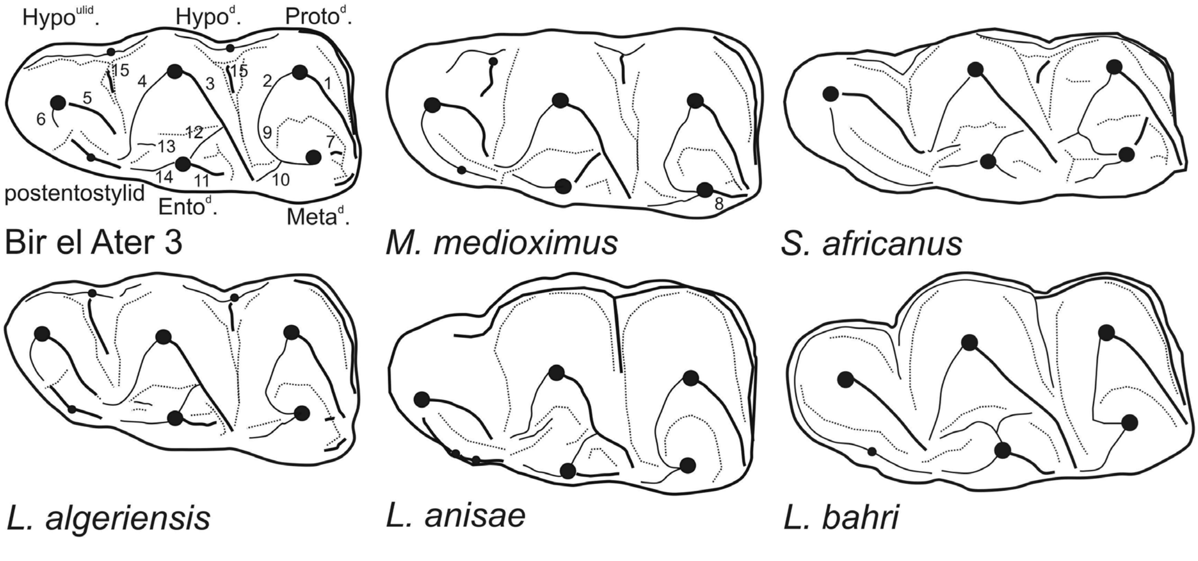
A postentostylid is present on the third lobe of the M/3 and is separated by a distal groove with the hypoconulid apex in all known specimens of *L. algeriensis* (n=4). In *L. anisae*, the condition differs by the presence of many stylids of equivalent size (in 13 specimens among 14) and the lack of clear groove that separates the entostylid from the rest of the posthypocristulid (Fig. 3). In *L. bahri*, the posthypocristulid lacks and thus the stylid remains only on the cingulid. Lingual cuspids of lower molar are more linguo-labially flattened whereas they present a rounded outline in occlusal view in other *Libycosaurus* species. This is probably due to more sharpened cristids in *L. algeriensis* than in the other species. This condition also exists in early *Merycopotamus* species.

The lower molars of the new specimen are always shorter mesio-distally (m/2 = 25.7 mm; m/3 = 35.9 mm) and linguo-labially (m/2 = 17.1 mm; m/3 = 16.8mm) than *L. anisae* specimens, but they are very similar in size to *L. algeriensis* (Fig. 4). When comparing the mean length and breadth of m/3, we found differences between the group including *L. algeriensis* and Bir el Ater 3 specimen (36.2 mm /17.6 mm) and the group including the specimens from loc17 of Bled Douarah (44.2 mm / 23.9 mm), the upper level of Bled Douarah (44.4 mm / 23.6 mm) , the Djebel Krechem el Artsouma (40.5 mm / 21 mm), Sahabi (58.8 mm / 25.7mm), and Toros-Menalla (59.1 mm /30.8 mm). Unfortunately, there are too few known specimens of *L. algeriensis* to apply a t-test on these measurements. In contrast, there is no mean difference between Bled Douarah localities, between Bled Douarah and Djebel Krechem, and between Sahabi and Toros-Menalla.

Enamel microstructure. Alloing-Séguier *et al*. (2014) described in detail the enamel microstructure of *L. algeriensis*. We further compare here the previous analysis of enamel from Bir el Ater 2, *Libycosaurus bahri*, and *Merycopotamus* spp. On the vertical section, enamel is 856 µm thick on the metacone quite similar to *M. nanus* and *M. medioximus* but much smaller than in *L. bahri* (1330 µm). The Schmelzmuster presents three zones (Fig. 2D) with the presence of Hunter Schreger Bands (HSB; 47% of the whole thickness). In more recent *Libycosaurus* species, HSB are absent whereas they are slightly larger in *M. medioximus* and *M. nanus*. Indeed, the Inner Radial Enamel is more developed in Bir el Ater 2 specimen than in *Merycopotamus* species. Hunter Schreger Bands in *L. algeriensis* can be larger than 100µm and only *M. nanus* and *M. medioximus* show such large bands among anthracotheres (Alloing-Séguier *et al*., 2014). The low decussation angle of prisms between two HSB and the large transition zone between bands (several prisms correspond to intermediate decussating states between the two HSB) in Bir el Ater 2 specimen (Fig. 2) differ from *Merycopotamus*. However the Algerian enamel also displays blurry HSB which is a characteristic feature of *Merycopotamus*. Interrowsheet are present in the inner part of the enamel thickness as in *M. medioximus* and *L. bahri* and unlike *M. nanus* that only presents them in the middle part.

In regard of all the characteristics of enamel microstructure, we can notice that *L. algeriensis* (the specimen from Bir el Ater 2) differs from *L. bahri* and reminds *M. medioximus*. However, the large development of the inner radial enamel in *L. algeriensis* can be considered as transitional between *M. medioximus* and *L. bahri*. Unfortunately, no data exists for the enamel of *L. anisae* and *M. dissimilis*.

Mandible. The mandible is shallow (depth below m/3 = 54.5 mm; Figs. 2, 4). Lihoreau *et al*. (2014) demonstrated that the mandibular depth in *L. bahri* can vary markedly with the age



Bir el Ater 3 *M. medioximus* *S. africanus*

L. algeriensis *L. anisae* *L. bahri*

Figure 3. Comparisons of occlusal pattern of third left lower molar from Bir el Ater 3 (UONM-14) with five bothriodontine species. All specimens scaled at same length and oriented with mesial part of the tooth rightward and lingual part downward. Proto^{d}.: protoconid; Meta^{d}.: metaconid; Hypo^{d}.: hypoconid; Ento^{d}.: entoconid; Hypo^{ulid}.:hypoconulid; 1: preprotocristid; 2: postprotocristid; 3: prehypocristid; 4: posthypocristid; 5: prehypocristulid; 6: posthypocristulid; 7: endometacristid; 8: premetacristid; 9: postmetacristid; 10: postectometacristid; 11: ectoentocristid; 12: preentocristid; 13: postentocristid; 14: postectoentocristid; 15: ectocristylids.

and with the sex. Compared with adult specimens (age class of 5-8) of *L. anisae* (mean of 74.8 mm with values comprised between 64.8-82.9 mm) and adult specimens of *L. bahri* (mean of 117 mm with values comprised between 78.1-146.4 mm), the specimen from Bir el Ater 3 is always shallower than *L. anisae*, regardless of sex attribution. The mandibular height is more consistent with measurements taken on *Merycopotamus* specimens (mean of 45.7 mm for *M. nanus* and of 55.5 mm for *M. medioximus*; Lihoreau *et al*., 2004).

The ventral border of the mandible below M/3 is straight in specimens from Sahabi and TM, but a vascular impression is noticeable in some *L. anisae* specimens (e.g., T3528) as well as in *Merycopotamus* (Lihoreau *et al.,* 2007) and earlier bothriodontine species. In UONM-14, the slight mandibular vascular impression together with the small size are supposed to be a plesiomorphic condition for *Libycosaurus* (Lihoreau *et al*., 2014; Fig. 2).

PROBOSCIDEA Illiger, 1811
ELEPHANTIFORMES Tassy, 1988
ELEPHANTOIDEA Gray, 1821
GOMPHOTHERIIDAE Hay, 1922
TETRALOPHODONTINAE van der Maarel, 1932
Tetralophodon Falconer, 1857.

Type species. *Tetralophodon longirostris* (Kaup, 1832)

Included species. *Tetralophodon longirostris* (Kaup, 1832) from Austria, Germany, Georgia, Moldova, Spain, Turkey, Ukraine and possibly in Tunisia (Bergounioux & Crouzel, 1956); *T. punjabiensis* (Lydekker, 1886) from Pakistan; *T. xiaohensis* Qi *et al.* 2006 from China; *T. xiaolongtanensis* (Chow & Chang, 1974) from China.

Other possible included species. *T. falconeri* (Lydekker, 1877) from India (see Shoshani & Tassy, 1996: 363); *T. buzdarensis* Sarwar, 1977 from Pakistan; *T. exoletus* Hopwood, 1935 from China (possible synonymy with *T. xiaolongtanensis*, see Tobien *et al*., 1988); *T. hasnotensis* (Osborn, 1929) from Pakistan and China (considered as a *Paratetralophodon* by Tassy (1983) but attributed to *Tetralophodon* following Tobien *et al*. (1988))

Range and distribution. Late Miocene and early Pliocene of Europe, Asia, Africa.

Diagnosis. Based in part on Coppens *et al.* (1978), Sanders *et al.* (2010), and Tobien *et al.* (1988). Large gomphotheriid genus with tetralophodont intermediate molars (i.e. with four completely developed loph(id)s together with an individualised strong talon(id)) and third molars with five-six loph(id)s. Symphysis deflected, under reduction but not as short as that in the Anancinae. Lower incisors small relatively to molar sizes, likewise reduced, mostly separated without contact at their tips. Upper incisors without enamel band, slightly curved downward and/or outward. Second-fourth permanent premolars are retained; upper and lower tooth formulae 1-0-3-3, 1-0-2-3, respectively. Occasional development of secondary trefoils on posttrite half-loph(id)s. Differs from anancine gomphotheres in straighter transverse alignment of the half-loph(id)s. Enamel massively thick.

***Tetralophodon* sp.**

Material. left D/4 UONM-15, a right P4/ UONM-16 and a right M/2 UONM-17 (Figs 5-6). This material is housed at the University of Oran 2, Algeria.

Comparative description

Deciduous lower premolar. The left D/4 is brachyodont and tetralophodont (Fig. 5A-B). All the lophids are functional but the fourth posttrite half-lophid is not worn. The first lophid is largely broken. The decidual tooth was more than 76 mm long and the maximum widths of the second and third lophids are 42 and 43.5 mm respectively. The enamel is rugose, folded, and crenulated; it is 3 mm thick. Each half-lophid is composed of two main cuspids with the mesoconelets and principal tubercles being of similar size (Fig. 5A). There is no alternation of the half-lophids. The crown structure is very simplified with no accessory conule on the posttrite side, instead small anterior and posterior swelling crests prefigure a trefoil pattern. A central pretrite conule (acprc) is clearly individualized on

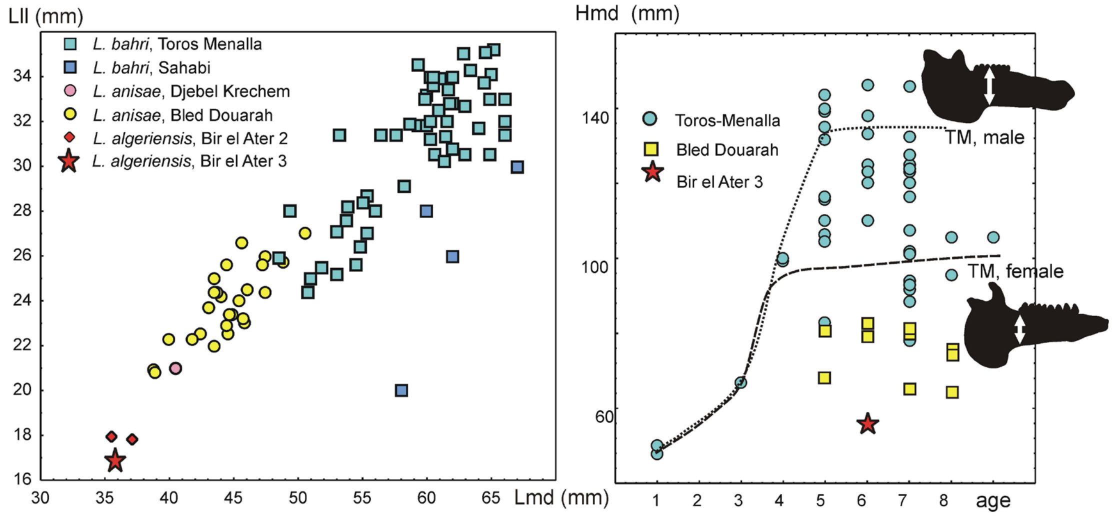


Figure 4. Biometric comparisons of anthracothere specimen UONM-14 from Bir el Ater 3. Left, distribution on bivariate graph of the m/3 measurements compared with species of *Libycosaurus* (measurements from Lihoreau *et al*. 2014). Right, comparison of mandibular depth below posteriormost erupted tooth for each age class of *Libycosaurus* species (measurements from Lihoreau *et al*. 2014).

the first lophid; it is more bulge-like on the lophid 2 and 3 and barely detectable on the fourth one. Posterior central pretrite conules (pcprc) are present on the first three lophids; they correspond to swellings that are not completely distinct from the mesoconelet. No clear contact is established between the pcprc and the acprc of the following lophid. A marked median sulcus is visible between each half lophids. In a worn state, the pretrite half-lophids form incomplete trefoil patterns, which only partially block the interlophid valleys. The last lophid is really simple. The last posttrite half-lophid is monocuspid, and so is the posterior cingulum.

Decidual teeth have been recovered for African nonanancine tetralophodont groups in Libya (Sahabi; Gaziry, 1987) and in Kenya (Nakali, Saegusa *et al.*, 2014; Samburu Hills, Nakaya *et al.*, 1984; Tugen Hills, Tassy, 1986). The specimen can be clearly differentiated from a D/4 of *Stegotetrabelodon* (Gaziry, 1987) in that the latter has more plate-like anterior lophids with wide interlophid valleys noticeably filled with cementum, as well as a fully developed fourth lophid where the two halves are angling backwards. All Libyan D/4 are also significantly larger with a crown measuring between 95 mm and 100 mm in length. The morphology of the Algerian D/4 is overall quite similar to the D4/ described in Ngorora (fig. 11, plate 9: Tassy, 1986) both in size and morphology. It is always delicate to compare lower teeth with upper ones but similar trends are observable between the D4/ from Ngorora and the Algerian D/4 regarding the complexity of the crown, the weak expression of the pretrite and posttrite accessory conules and the narrowness of the fourth loph(id).

***Lower premolar*.** The right P/4 is brachyodont and bilophodont (Fig. 5C-D). It is barely worn. The premolar is slightly longer (L=53.4 mm) than wide (l1=35.67 mm; l2=29.82 mm) and roughly rectangular in shape. The enamel thickness is 3 mm at the cervix on the second lophid. Each lophid is composed of two main cusps and incipient pretrite mesoconelets (Fig. 5C). A pcprc is present on each lophid whereas an acprc is present only on the first one. There is no clear contact between the pcprc1 and the acprc2, which are set apart by a marked transverse fold. The crown is longitudinally divided by a median sulcus separating pretrite and posttrite sides. The anterior cingulid is tetracuspid with two reduced lateral cuspids. No surface contact is visible anterior to it, so the presence of a P/3 (a characteristic of Miocene gomphotheres; Tassy, 1986) can be questioned. The posterior cingulid is bicuspid; a contact surface is present. No cementum is visible on the crown.

The most complete lower premolars of African nonanancine tetralophodont gomphotheres are known from Nakali (Kenya; Saegusa *et al.*, 2014), Samburu Hills (Kenya; Nakaya *et al.*, 1984), Tugen Hills (Kenya; Tassy, 1986), and Djebel Krechem (Tunisia; Geraads, 1989). The Algerian P/4 resembles the one of *Tetralophodon longirostris* in showing a cprp1 (Saegusa *et al.*, 2014). Fourth premolars of *Stegotetrabelodon* clearly differ from the latter in displaying cementum and no accessory conule in the first interlophid, they also display broadened second half-lophids with 3 pretrite and posttrite tubercles (fig. 8, plate 9 in Tassy, 1986). No P/4 is known from the Samburu Hills (Nakaya *et al.*, 1984, 1987) and the Tugen Hills (Kenya; Tassy, 1986). The overall morphology of a worn left P/3 of a tetralophodont form from Ngorora (fig. 10, plate 9 in Tassy, 1986) is similar to the Algerian P/4 but it is smaller (L=42.5 mm). Both teeth are characterized by the presence of marked median sulcus and incipient pcprc1 and acprc2 in the interlophid. However, no posterior cingulum is distinguishable on the Kenyan third premolar. The right P/4 from the Nakali formation (Saegusa *et al.*, 2014) is wholly worn; it is similar in shape to the Algerian P/4 but differs from the latter in size (the Kenyan premolar

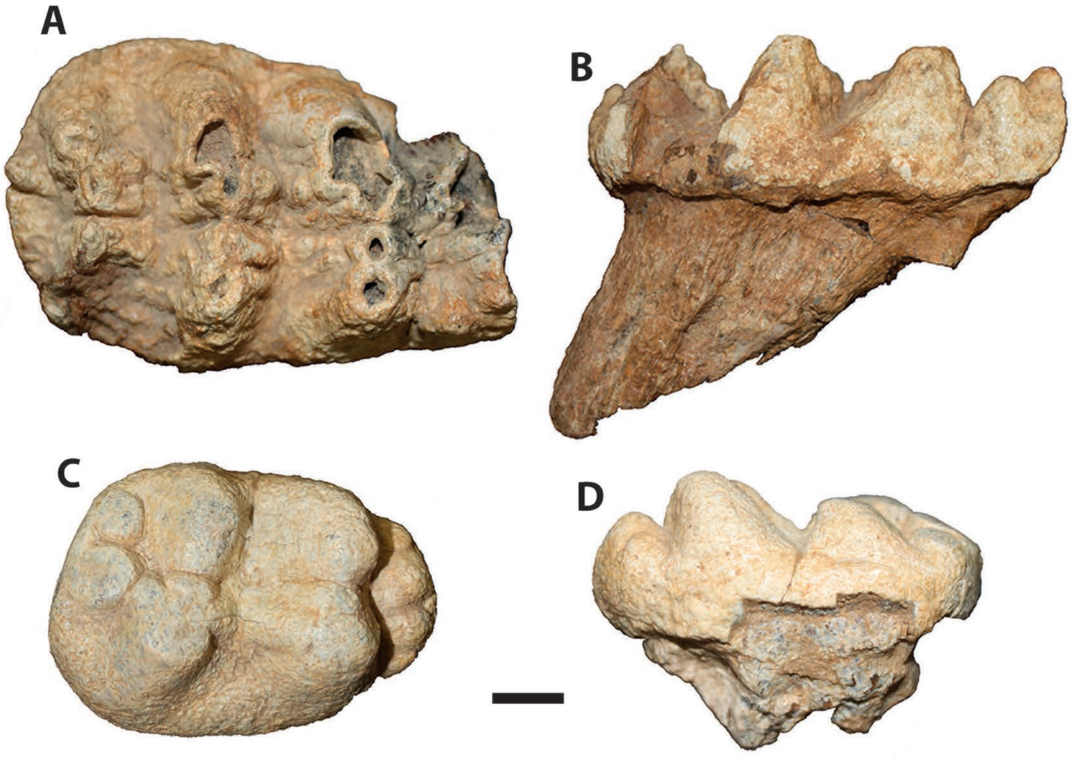


Figure 5. *Tetralophodon* remains from Bir el Ater 3. A-B UONM-15 left D/4. **A,** Occlusal view. **B,** lingual view. C-D UONM-16 right P/4. **C,** Occlusal view. **D,** lingual view. Scale bar equals 1cm.

being smaller) as well as in the complete absence of accessory conule, the lesser development of the anterior cingulum, and a putative presence of cementum (not specified but see fig. 1B in Saegusa *et al.*, 2014). Geraads (1989) described a P/4 from Djebel Krechem similar in size to the P/4 of Bir el Ater 3. However, the morphology of the Algerian premolar contrasts with the Tunisian one, which shows a strong central conule in the interlophid as well as a second lophid much wider than the first one (Geraads, 1989).

Lower molar. The right worn M/2 is brachyodont and tetralophodont (Fig. 6). The enamel is massively thick (between 6 and 10 mm). Even partially broken, the molar appears large at its fourth lophid (l4 = 68 mm) compared to its length (L = 147 mm). Lamellar frequency is low (between 2.5 and 3). The dislocation of the half-lophids is slight to absent. The crown structure is complex on the proximal side and simple on the distal side, with mesoconelets competing in size with the main conelets (Fig. 6A). The three first pretrite half-lophids are largely broken mesially. The mesoconelets of the first three lophids are accompanied with extended bulge-like anterior and posterior central pretrite conule (acprc and pcprc) that gives a trefoil shape to the half-lophids. A contact is established between the pcprc and the acprc of the following lophid, which blocks the valleys (Fig. 6A). The fourth half-lophid is simplified with the lack of pcprc and a mesoconelet largely jointed to the principal tubercle. On the posttrite side, the crown structure is slightly different. The anterior half-lophids are simpler with no anterior and posterior central posttrite conule (acpoc and pcpoc). The mesoconelets, weakly separated from principal tubercles by folds, are rounded. The last posttrite mesoconelet is slightly compressed buccolingually. The tubercles do not converge to the sagittal plane. The distal cingulum is simple and formed of three rounded tubercles; it does not prefigure a fifth lophid. The tooth probably had two roots, but only the rear one is preserved (Fig. 6B).

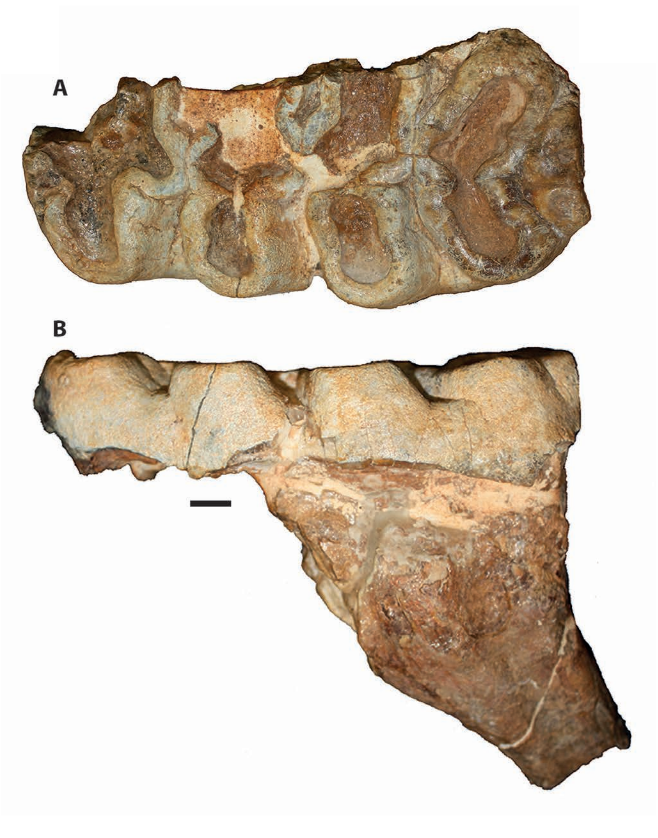


Figure 6. *Tetralophodon* remains from Bir el Ater 3. A-B UONM-17 right M/2 **A,** Occlusal view. **B,** lingual view. Scale bar equals 1cm.

Molars of nonanancine tetralophodonts are more commonly found than premolars or decidual teeth. An attribution to *T. falconeri*, *T. buzdarensis*, and *T hastonenis* can be ruled out since all these species show molars with a thick cement cover (Tobien *et al.*, 1988). Only one left M3/ is known for *T. punjabiensis* (Tobien *et al.*, 1988), which precludes any comparison with the Algerian specimen. The Bir el Ater 3 specimen is close morphologically to the molars of *T. longirostris* and *T. xiaolongtanensis*, which are characterized by a lack of cement and an absence of posttrite accessory conules. It differs from the type specimen of *T. longirostris* (Vallesian of Eppelsheim, Tobien, 1978: Plate 10) that is characterized by a fully developed and individualized posterior cingulid. However, this feature is likely to vary intraspecifically since the posterior cingulid remains reduced on a M/2 of *T. longirostris* from the Vallesian of Esselborn (Tobien, 1978: Plate 14). Both the Bir el Ater 3 M/2 and the intermediate molars of *T. longirostris* differ from *T. xiaolongtanensis* that shows a M/2 with reduced posterior cingulid and fourth posttrite lophid (Dong, 1987).

Molars were described in a number of African Miocene deposits: Nakali formation (Kenya; Saegusa *et al.*, 2014), Samburu Hills (Kenya; Nakaya *et al.*, 1984, 1987), Tugen Hills (Kenya; Tassy, 1986), Lukeino formation (Kenya; Pickford, 1978), Lothagam (Kenya; Tassy, 2003), Wembere-Manonga (Tanzania; Sanders, 1997), Chorora formation (Ethiopia; Geraads *et al.*, 2002; Tiercelin *et al.*, 1979), Sahabi (Libya; Gaziry, 1987), Kakara formation (Uganda; Tassy, 1994), Lake Mobutu Sese Seko (Congo; Madden, 1977), Djebel Krechem (Tunisia; Geraads, 1989), Chérichera (Tunisia; Bergounioux & Crouzel, 1956). However, second lower molars were rarely found and were only described in the Samburu Hills (Nakaya *et al.*, 1984). The overall morphology of the Algerian M/2 recalls *Tetralophodon* molars regarding the low crown, the number of lophids, the low lamellar frequency, the small number of cones forming the lophids, the enlargement of the mesoconelets, the presence of anterior and posterior pretrite accessory conules, the trefoil pattern of the anterior lophids, the persistence of marked median sulcus, and the absence of cementum (Sanders *et al.*, 2010; Tassy, 1994; Tobien, 1978). However, the material is too fragmentary to warrant a specific distinction. The combination of morphological features allows us to reject an assignment to *Stegotetrabelodon* due to the small number of lophids (M2 plate formula is x5-x5x in *Stegotetrabelodon*), the absence of strong and individualized median posterior columns (pcprc) between each plate, the absence of deep V-shaped valleys between pyramidal plates in lateral view, the uneven wear of the pretrite and posttrite half lophids, and the absence of cementum (Gaziry, 1987; Sanders, 1997; Sanders *et al.*, 2010; Tassy, 1994). An allocation of the Algerian M/2 to *Choerolophodon* can also be discarded since the lophids are not arranged in chevrons (Sanders, 2010; Tassy, 1986; Tsujikawa, 2005). The M3/ (KI 64’92) from the Kakara formation, referred to as primitive Elephantidae (Tassy, 1994), differs from the present M/2 in showing more derived traits of Elephantidae such as cones slightly compressed antero-posteriorly, a reduction of the median sulcus, a lesser development of accessory conules (especially the absence acprc), an even wear of the half lophs, and the presence of cementum. Tassy (1994) considered this molar as very similar to the tetralophodont molars from the Samburu Hills, described as *Tetralophodon* sp. (Nakaya *et* *al*., 1984), but he refrained from giving a generic assignment. Sanders *et al.* (2010) recently argued in favour of the inclusion of this material inside the genus *Tetralophodon*. If the Kenyan molars do show some morphological similarities with the M3/ (KI 64'92), they differ from it by the complete lack of cementum and the development of secondary trefoils (Nakaya *et al.*, 1984). Unlike the Algerian molar, the Samburu teeth display more plate-like loph(id) and secondary trefoil patterns; they are also significantly bigger (i.e. >175mm). Tassy (1986) viewed the evolutionary level of these Ugandan (Kakara) and Kenyan (Samburu Hills) molars as more derived than the M/1 recovered in the Mobutu Sese Seko region (Madden, 1977) and more derived than the tetralophodont gomphotheres from the Ngorora formation. Unfortunately, no molar is known in the Ngorora material, which precludes any comparison with the Algerian molar. The Congolese M/1 from Mobutu Sese Seko is largely broken and worn but it does not show elephantid features such as plate-like tendency of the lophids (Madden, 1977; Tassy, 1994). It also wholly lacks cementum, and though resembles the Algerian M/2 in that way, but it can be differentiated from the latter by the presence of V-shaped valleys and triangular plates in sagittal section. This specimen was first recognized as *Tetralophodon* sp. (Madden, 1977), but Madden (1982) changed his first identification to refer the molar to as *Stegotetrabelodon grandincisivum*. More material will be needed to warrant this generic attribution. The same holds true for the material from the Nakali formation (Saegusa *et al.*, 2014), which has so far yielded only fragments of molars. A M/3 (AL1000-1) from the Chorora formation has been referred to as putative *Stegotetrabelodon* tooth and was considered as a good intermediate between the tetralophodont forms from the Samburu Hills (i.e. *Tetralophodon* sp.; Nakaya *et al.*, 1984) and the ones from the Kakara formation (i.e. primitive Elephantidae indet.; Tassy, 1994). This molar indisputably shows derived features compared to the Algerian M/2 including a lesser development of accessory conules (with the absence of all acprc but the first one), and more plate-like lophids coated with cementum. The morphology of the Algerian M/2 is overall very similar to the M2/ of *Tetralophodon* cf. *longirostris* described in Djebel Krechem (Geraads, 1989), both in size and morphology. Both molars are characterized by a low crown, four loph(id)s with a fully developed fourth loph(id) where the two halves are angling backwards and a distinct cingulum formed of three rounded tubercles, a low lamellar frequency, a trefoil pattern of the anterior pretrite half loph(id)s associated with more simple posterior loph(id)s, enlarged mesoconelets, a persistence of marked median sulcus, and an absence of cementum. However the Tunisian M2/ distinctly shows a pcpoc on its third loph. From North Africa again, Bergounioux & Crouzel (1956) also reported the presence of *T. longirostris* in the Miocene deposits of the Beglia Formation. Compared to the Bir el Ater 3 specimen, the crown structure of the pretrite portion of M/3 from Chérichera appears simpler with a lesser development of the accessory conules but this material is really fragmentary.

DISCUSSION

Validity of the species *L. algeriensis* and origin of the genus. Considering the hypodigm of *L. algeriensis* (Ducrocq *et al.*, 2001), Pickford (2006) proposed that "the case for a separate species is weak" even if he discussed the small size of its m/3 compared to *L. anisae*. The problem of validity of *L. algeriensis* is linked to the scarcity of the material, the few discriminant morphological characters on teeth, and our lack of knowledge on the size variability in *Libycosaurus* species. Indeed, on the original material from Bir el Ater 2, Ducrocq *et al.* (2001) mainly identified continuous character state for the species diagnosis such as the global size, the development of cingulum/id on molars, and the compression of lower molar cuspids, likely to show interspecific overlap. Indeed, in order to confirm the discriminant quality of these characters, we need to investigate their variation on a large sample of *Libycosaurus* species. Pickford (2006) first considered that the creation of this species was premature, but accepted it later based on the recognition of the size variation in *L. anisae* (Pickford 2009). He considers that the small size of the Algerian remains can fill a gap in an anthracothere lineage displaying a trend to size increase (Pickford, 2009). A rather equivalent conclusion was proposed by Lihoreau *et al*. (2014) based on teeth size, slender lower molar occlusal shape, and cristid sharpness, which follow the study on size and morphological variability of a large sample of *L. bahri*.

The new material described in this study confirms the existence of a small *Libycosaurus* species in Bir el Ater 2 and 3, which retains a plesiomorphic occlusal pattern (endometacristid, ectocristylids in cusplets, developed labial cingulid on lower molars and lingual cingulum on upper molars, a single entostylid, a posthypocristulid only separated with hypoconulid apex by a lingual groove), a plesiomorphic schmelzmuster on molar enamel, and a shallow mandible with a weak vascular impression.

Lihoreau *et al*. (2006) proposed an Asian origin for the genus *Libycosaurus* with potential precursors to be found within the Asian stock of advanced Bothriodontinae (such as *Hemimeryx*, *Sivameryx*, and *Merycopotamus*). It is notably due to the retention of an endometacristid in *Libycosaurus*, which is also known in *Sivameryx* and *Hemimeryx* but lost in *Merycopotamus*. Another scenario (Lihoreau *et al*, 2015), still proposing an Asian origin, would be that *Libycosaurus* derived from a *Merycopotamus* stock, which implies the paraphyly of the latter genus. Indeed, the latter hypothesis seems supported by numerous morphological resemblances between *L. algeriensis* and *M. medioximus,* notably the slightly divided mesostyle and the ectocrystilid developed in cusplets. However, more material is needed to propose a well-supported phylogeny of this clade and precise the centre of origin of *Libycosaurus*.

Age of Bir el Ater 3 and dispersal events. The new proboscidean remains are of primary importance as Sanders *et al*. (2010) considered that "morphologically and stratigraphically, african tetralophodon is appropriately situated to be ancestral to elephants" and as nonanancine tetralophodonts are poorly represented in the African fossil record. Coppens *et al.* (1978) mentioned that several North African localities have yielded remains of *Tetralophodon longirostris* including Zidania and Melka el Ouidane (Morocco); Tozeur, Djebel M'Dilla, Djebel Semene, Sbeitla, Bled Douarah, Chérichera, and Foum el Kranga (Tunisia); and Smandou (Algeria). If this identification has been confirmed in Chérichera and Djebel Semene (Bergounioux & Crouzel, 1956), Coppens *et al*. (1978) acknowledged that, in most other cases, the material was too fragmentary to be clearly identifiable and that this identification mostly relied on stratigraphic position rather than morphological features. In fact, the fossil remains from Smendou and Djebel M'Dilla have never been described. The Miocene locality of Tizi N'Tadderht in the Central High Atlas (Morocco, Zouhri *et al*., 2013) has recently yielded a few fragmentary

Tetralophodon remains (one mandible with a small part of a badly preserved M/3 and one half of lophid without accessory conules), which appear to match with the material described from Chérichera.

The combination of morphological characters of the *Tetralophodon* teeth from Bir el Ater 3 is clearly more primitive than the dental remains of the tetralophodont forms found in Kakara formation (9 Ma; Tassy, 1994), Samburu Hills (9.3 to 9.6 Ma; Nakaya *et al*., 1984, 1987), and Chorora formation (10.1 to 10.7 Ma; Suwa *et al*., 2007); the dental traits are in return compatible with what is known from Djebel Krechem (10.5-10 Ma; Geraads, 1989) and Ngorora formation (11 Ma; Tassy, 1986). Nevertheless comparisons with the upper molar from Djebel Krechem must be taken with caution as important variation can exists between upper and lower molars of pre-elephantids (Hautier *et al*., 2009). Assuming that all these tetralophodont forms are closely related and that the intraspecific variation is low, which is rarely the case in gomphotheres, the evolutionary level of the Algerian proboscidean is compatible with an age of Bir el Ater 3 being more or less contemporaneous with the Member D of Ngorora Formation. Considering the early occurrence of the genus in Tunisia, Bergounioux & Crouzel (1956) suggested an African origin for the group directly from a *Gomphotherium* stock as proposed by Schlessinger (1917, 1922) and Osborn (1936). However, Coppens *et al.* (1978) and Tobien *et al.* (1988) considered that *Tetralophodon* more likely dispersed to Africa from Eurasia where the genus is well represented by several late middle-late Miocene species. The material from Bir el Ater 3 is, for now, too fragmentary to ascertain its specific attribution and more specimens will be needed to bridge the gap between Eurasian and African representatives of the genus.

The presence of a small species of *Libycosaurus* that does not display the advance character states of *L. anisae* and *L. bahri* supposed an older age than Bled Douarah (and even than the lower level of Bled Douarah, loc. 17). It could not be contemporaneous with Djebel Krechem that belongs to the Segui Formation stratigraphically above the Beglia formation (Mannaï-Tayech, 2009), which includes Bled Douarah. The age of Bled Douarah is not well constrained but generally considered to be late Serravalian-Early Tortonian (12-11 Ma, Geraads,1989; Pickford, 2000). The limit between the two fossiliferous levels in Bled Douarah is supposed to be early late Miocene and marked by the appearance of hipparions (Robinson and Black, 1969) in correlation with the earliest record of equids in Africa in Bou Hanifia (10.5 Ma, Bernor *et al*., 2010). The presence of *Kenyapotamus coryndoni* in the upper level allows comparison with levels in the Ngorora, Nakali and Namurungule formations in Kenya dated between 11 and 8.8 Ma (see Boisserie *et al*., 2010 for review). The localities of the lower level of Bled Douarah must therefore be older than 10.5 Ma.

Due to the presence of *L. algeriensis* at Bir el Ater 3 this locality must be older than the earliest localities of Bled Douarah where *L. anisae* (more advanced species of the genus) occurs. Unfortunately, we do not have a lowermost constrained age for the Algerian locality due to the unconformity between the Miocene Nementcha formation and the Eocene continental sequence and the temporal distribution of the found genera, which are not known in Africa prior to 11 Ma. Pickford (2009) proposed a Langhian age for Bir el Ater 2 (ca. 14 Ma), which is almost contemporaneous with Bir el Ater 3. The Asian origin of the genus *Libycosaurus* would constrain the age of the dispersal from Asia to Bir el Ater 3. For the moment, two hypotheses have been proposed: 1) *Libycosaurus* is the sister clade of *Merycopotamus* (Lihoreau *et al*., 2006) and thus its origin can be constrained with the earliest occurrence of its sister group, *Merycopotamus* (13.9 Ma, earliest occurrence of *Merycopotamus nanus*, Lihoreau *et al*., 2007), 2) *Libycosaurus* is included within *Merycopotamus* clade (Lihoreau *et al*., 2015) and its earliest occurrence might be younger. This point has to be resolved by new phylogenetic analysis of this clade including *L. algeriensis* which hypodigm clearly needs to be completed by new dental material (premolar and anterior teeth morphology). Depending on which scenario will be retained the new remains of *Tetralophodon* from Bir el Ater 3 might represent the earliest occurrence of this genus in Africa. This point is therefore critical to date dispersal events of large terrestrial mammals toward Africa during middle Miocene or early Late Miocene.

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