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A new large mammal from the Ypresian of Morocco: Evidence of surprising diversity of early proboscideans

EMMANUEL GHEERBRANT, JEAN SUDRE, HENRI CAPPETTA, MOHAMED IAROCHÈNE, MBAREK AMAGHZAZ, and BAÂDI BOUYA



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We describe a new primitive proboscidean, *Daouitherium rebouli* gen. et sp. nov., from the early Ypresian of the Ouled Abdoun Basin, Morocco, which also yielded *Phosphatherium*. It is the earliest known large mammal from Africa and one of the oldest known proboscideans. It has true lophodont molars similar to those of *Barytherium* and *Numidotherium*. It is closer to these genera and more advanced than *Phosphatherium* (e.g., morphology of the mandible), but it is also primitive in striking features known also in *Phosphatherium* (absence of diastema, retention of two additional teeth in front of p2). A parsimony analysis of *Daouitherium* suggests its intermediate phylogenetic position between the basal, small *Phosphatherium* and the large, more derived *Numidotherium* and *Barytherium*. *Daouitherium* is a better candidate for the ancestry of *N. koholense* than *Phosphatherium*, but it is also specialized. *Daouitherium* and *Numidotherium* may belong to the same basal radiation of “Barytherioidea”. However, the family referral of *Daouitherium* is uncertain (Numidotheriidae?). The discovery of such a large and derived proboscidean with respect to *Phosphatherium* in the same African beds of such antiquity is evidence of an unexpected early diversity of proboscideans and of the old origin of the order. It also supports the African origin of Proboscidea s.s.

Key words: Mammalia, Proboscidea, early Eocene, Africa, Ouled Abdoun Basin, new taxa.

Emmanuel Gheerbrant [gheerbra@mnhn.fr], Laboratoire de Paléontologie (UMR 8569 du CNRS), Muséum National d’Histoire Naturelle, 8 rue Buffon, F-75005 Paris, France (corresponding author);

Jean Sudre and Henri Cappetta, Laboratoire de Paléontologie (UMR 5554 du CNRS), Université Montpellier II, case courrier 064, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France;

Mohamed Iarochène, Direction de la Géologie, Ministère de l’Energie et des Mines, BP6208 Rabat-Instituts, Morocco;

Mbarek Amaghazaz and Baâdi Bouya, Groupe Office Chérifien des Phosphates, Centre Minier de Khouribga, Service Géologique et Direction du Développement, Khouribga, Morocco.

Introduction

Early Paleogene mammal localities known in Africa are very few. These are mainly the Thanetian and Ypresian Moroccan sites from the Ouarzazate Basin (e.g., Adrar Mgorn 1 and N’Tagourt 2; see Gheerbrant et al. 1992), and the Ouled Abdoun Phosphate Basin recently reported with the discovery of the oldest known proboscidean, *Phosphatherium escuilliei* Gheerbrant, Sudre, and Cappetta, 1996 (Gheerbrant et al. 1996, 1998). Ouarzazate Basin sites have yielded mostly micromammals, aside from fragmentary dental remains possibly belonging to undetermined “condylarths” and ungulates.

Ouled Abdoun Basin mammals are extremely rare, documented by very marginal occurrences with respect to the famously rich marine vertebrate fauna known there. There is indeed no concentration of fossil remains of species of continental origin because of their peculiar taphonomy (floated bodies), which will be discussed elsewhere. Ouled Abdoun Basin sites are, however, of major importance for early Afri-

can placental mammalian history because of the good preservation of vertebrate remains. This is especially true for large mammals, which are otherwise unknown in the Early Eocene and Paleocene of Africa. Most Ouled Abdoun mammal remains consist of dental series, aside from some more complete fossils (e.g., skulls), rather than of isolated teeth as, for instance, in the Ouarzazate Basin sites.

Here we describe a new large true proboscidean which comes from the same fossiliferous beds of the Ouled Abdoun phosphatic series that have yielded *Phosphatherium escuilliei*. This is both one of the oldest known proboscideans along with *Phosphatherium* and possibly *Khamsaconus* Sudre, Jaeger, Sigé, and Vianey-Liaud, 1993, and the oldest known large mammal from Africa. Other earliest African localities that have yielded large mammals are the early/middle Eocene site of El Kohol, with the proboscidean *Numidotherium koholense* Jaeger, 1986 (in Mahboubi et al. 1986), the early/middle Eocene site of Chambi, with the hyracoid *Titanohyrax tantulus* (Court and Hartenberger 1992), and the middle Eocene site of Glib Zegdou, with the hyracoid *Titanohyrax mongereaui* (Sudre 1979).

The new proboscidean reported here is one of several new mammals that have been discovered in the Ouled Abdoun Phosphate Basin, mostly by local people searching for fossils to sell. We have been fortunate in the recovery of the most important mammalian material discovered, both locally during our field work with the collaboration of the Office Chérifien des Phosphates (OCP), and in France with the help of the paleontological association Rhinopolis (Gannat). Recovered material also includes two new “condylarths” described by Gheerbrant et al. (2001) and several new taxa now in the course of study.

The material reported here comes from the quarries of Grand Daoui area, North-East of the Ouled Abdoun Basin. The exact locality within Grand Daoui quarries remains to be confirmed (possibly site “TS”). However, the fossiliferous level of origin in the phosphatic series has been identified (“intercalaire couches I/II”) with the help of information from local people who discovered the fossils, from our own field observations (lithological and fossiliferous facies in the local phosphatic series), and from the analysis of the micro-fauna of the matrix of the mammalian specimens (by H.C.). The Grand Daoui mammal localities will be described in a separate paper devoted to their geological and stratigraphical context (work in preparation).

The most important part of the studied material, including specimens MNHN PM3 and CPSGM MA4, was recovered from fossil dealers by an amateur, R. Reboul, and was passed along by Rhinopolis for study and for preservation in a public scientific collection.

Abbreviations.—CPSGM, Collections Paléontologiques du Service Géologique du Maroc, Direction de la Géologie, Ministère de l’Energie et des Mines, Rabat, Morocco; OCP, Office Chérifien des Phosphates, Morocco; MNHN, collections of the Muséum national d’Histoire naturelle de Paris; PM, Ouled Abdoun Basin (Morocco).

Systematic study

Order Proboscidea Illiger, 1811

Suborder Barytherioidea Andrews, 1906

Family Numidotheriidae? Shoshani and Tassy, 1992

Genus *Daouitherium* Gheerbrant and Sudre, gen. nov.

Etymology: From Sidi Daoui, the quarrying area where most of the Ouled Abdoun mammal remains have been discovered, and *therion*, wild animal in Greek.

Type species: *Daouitherium rebouli* gen. et sp. nov., the only known species.

Diagnosis and distribution.—The same as of the type species.

Daouitherium rebouli Gheerbrant and Sudre, gen. et sp. nov.

Figs. 1–8, 10A.

Etymology: Species dedicated to Roland Reboul who donated speci-

mens MNHN PM3 and CPSGM MA4 for study and preservation in a scientific public institution.

Holotype: CPSGM MA4, left dentary bearing p2–4, m1–3 (Figs. 1–5, 10A), Paleontological Collections of the Office Chérifien des Phosphates (OCP) and the Geological Survey of Morocco, Rabat.

Hypodigm (lower dentition).—Holotype CPSGM MA4, left dentary (corpus) bearing p2–4, m1–3 (Figs. 1–5, 10A); MNHN PM3, right dentary bearing p3, m1–3 and preserving most part of the ascending ramus (Figs. 6, 7); MNHN PM3 and CPSGM MA4 have both an erupting m3 and a similar wear degree, which suggests they belong to the same individual.

Referred material.—Lower dentition: CPSGM MA5, strongly worn isolated right m1. Upper dentition: CPSGM MA6, left P3 or more probably P4 (Figs. 8, 11).

Locality and age.—Ouled Abdoun, area of Grand Daoui, exact site unknown, possibly site “TS”; level 1 of the local phosphatic series, “intercalaire couches I/II” of earliest Ypresian age, which is the same local fossiliferous level which has yielded *Phosphatherium escuilliei* (work in preparation).

Study by H. Cappetta of the selachian fauna preserved in the matrix of MNHN PM3 supports a probable earliest Ypresian age of the species. The taxa recovered and identified are as follows: *Striatolamia macrotia striata* (Winkler, 1874) (*sensu* Arambourg 1952); *Carcharias atlasi* (Arambourg, 1952); *Abdounia beaugei* (Arambourg, 1935); *Casiera* sp.; *Rhinobatos* sp.; *Myliobatis* sp.; and *Archaeomanta* sp.

The most significant taxon for an Ypresian age is *Abdounia beaugei*; this is in accordance with the rarity of the micro-selachians in the recovered fauna, in contrast with Thanetian phosphatic levels. A basal Ypresian age is indicated by the frequency of *Casiera* sp., which is rarer in higher Ypresian phosphatic levels. The Thanetian age previously referred to *Phosphatherium escuilliei* on the basis of associated selachians in the matrix of the holotype (Gheerbrant et al. 1996, 1998) was based on taxa which are now considered as being reworked from the underlying phosphatic level 2 (Thanetian). This will be discussed with more detail in a paper devoted to the geology and stratigraphy of the mammals sites from Ouled Abdoun Basin (work in preparation).

Diagnosis (lower jaw and lower dentition).—Primitive proboscidean with true lophodont and bilophodont molars similar to those of *Phosphatherium*, *Numidotherium*, and *Barytherium*. It is closer to *Numidotherium* and *Barytherium* and more advanced than *Phosphatherium* in the molarization of the premolars, the semi-bilophodont p4 with incipient entolophid, the articular condyle of the mandible very high above the dental row, the deep dentary, the entocristid slightly curved or labially oblique in the molars, and its large size close to that of *N. koholense* (80–90% smaller than *N. koholense*).

It differs from *Numidotherium* and *Barytherium* and is closer to *Phosphatherium* in the more primitive anterior dentition which lacks a lower diastema, indicating a distinctive brevirostrine large-sized proboscidean, and which preserves four dental alveoli in front of p2 (retention of one or two additional anterior teeth). It is also distinct from *Numido-*

therium koholense by the greater molarization of its lower premolars, the distinct trace of entolophid in p3, and the overall less bunodont jugal teeth. It is characterized by a very large, probably autapomorphic, hypoconid on p3 and p2, and by the original extension of the enamel on the labial side of its premolars anterior roots.

Description

Lower molars.—Molar size increases strongly from m1 to m3 (area ratio of m2/m1: 189.5%; area ratio of m3/m1: 268.4%). They are characterized by a typical true lophodont and bilophodont pattern close to that of *Phosphatherium*, *Numidothierium* and *Barytherium*. The protolophid and entolophid (= hypolophid) are long, parallel, sharp, anteriorly concave and continuous (no sulci or notch). Their strictly transverse orientation is due to the transversal alignment of labial and lingual cusps. The entolophid is longer than the protolophid.

The cusps are crestiform. The lingual cusps are slightly higher than the labial ones. The trigonid is higher than the talonid, whereas the talonid is slightly wider (m1–2) and much longer. The occlusal outline is extended longitudinally and concave on the labial flank at the level of the wide and deep hypoflexid. A well developed distal cingulid occurs on m1 and m2 and it is distally extended as a third small lobe on m3. It is most likely homologous with the postcrisid of tribosphenic molars. The basins (pre- and postfossid) are shallow.

A slight mesial precingulid occurs. It is upwardly concave in m1, but more horizontal in m2 and m3. The trigonid is compressed mesio-distally. The paraconid is absent and the paracristid is distinct only as a vestigial oblique ridge on the mesial flank of protoconid. There is also trace of a premetacristid on the mesial flank of the metaconid which is convergent downward with the paracristid. The metaconid is larger than the protoconid. The hypoconid is the most voluminous cusp of the tooth. The cristid obliqua is well developed and the entocristid is weaker and slightly curved labially. The cristid obliqua ends mesially on the trigonid slightly labially with respect to its mid-width, and it does not rise onto it significantly. The postfossid is noticeably extended mesio-distally. The distal cingulid is enlarged and inflated labially, especially in m2, as a small hypoconulid located behind the hypoconid; however there is no trace of postentoconulid. The hypoconulid is not linked by any crest to the hypoconid and entoconid. There is a weak trace of mesoconid on m3. On m3 the distal lobe bears an extended but shallow basin. It is surrounded by a low distal ridge, without inflated cusps. There are two labio-lingually expanded roots. The enamel is slightly wrinkled, especially at the apex of crests.

m1 differs from m2 by its smaller size (see area ratio above) and its talonid which is wider with respect to the trigonid. With wear a crescentiform facet is formed along the distal apex of the transverse lophs.

Lower premolars.—A notably increasing molariform morphology typifies the premolar series from p2 to p4: p4 is



Fig. 1. *Daouitherium rebouli* gen. et sp. nov. Holotype, CPSGM MA4, left dentary with m1–3, p2–4, and anterior alveoli in occlusal stereo-view.

molariform and semi-bilophodont, p3 and p2 are sub- or premolariform. p4 and p3 have a well developed and basined talonid, a paraconid and a metaconid. p2 is more simple (cusps reduced, crests mesio-distally aligned) and is triangular in occlusal outline, but it is nearly as large as p3–4 and it retains molariform features such as a large talonid, a large hypoconid linked to the protoconid by a strong crest, the distinct cingulids, and a paracristid linked to a small paraconid. p4 has a rectangular occlusal outline similar to the molar ones, whereas p2–3 are more triangular with a trigonid compressed transversally (much narrower than the talonid) and extended mesio-distally. In p4, the two transverse lophs are differentiated (though the entolophid is incipient: morphology semi-bilophodont) and parallel, whereas in p3 only the small entolophid is differentiated (metaconid reduced and more distal with respect to protoconid), and p2 lacks transverse crests. p4 differs from the molars by the more reduced entolophid (incipient), the higher and mesio-distally less compressed trigonid, and the narrower talonid.

With respect to molars, the enamel extends at a lower level on the labial side of the anterior root of p2–4, a striking feature.

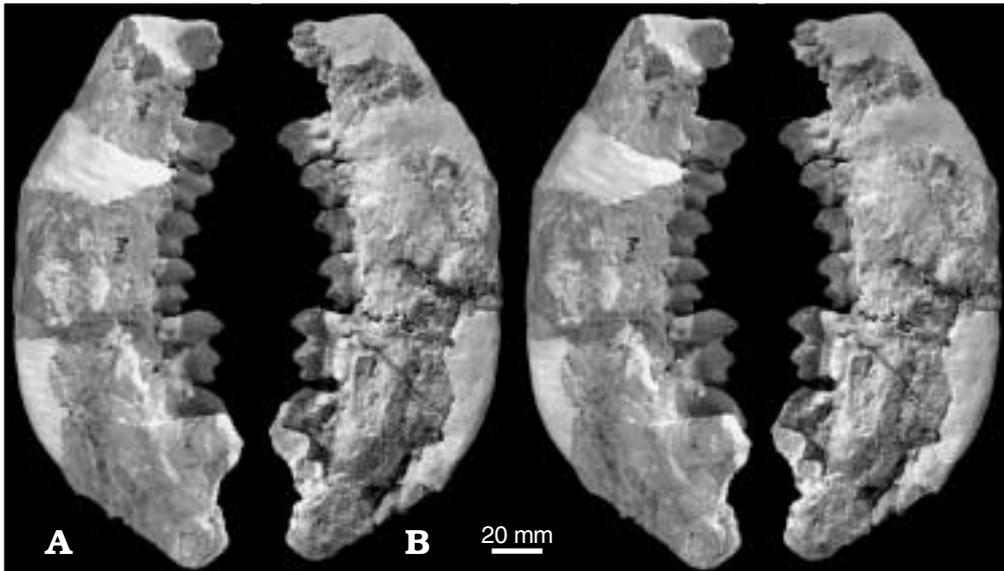


Fig. 2. *Daouitherium rebouli* gen. et sp. nov. Holotype, CPSGM MA4, left dentary with m1–3, p2–4, and anterior alveoli in labial stereo-view (A) and lingual stereo-view (B).

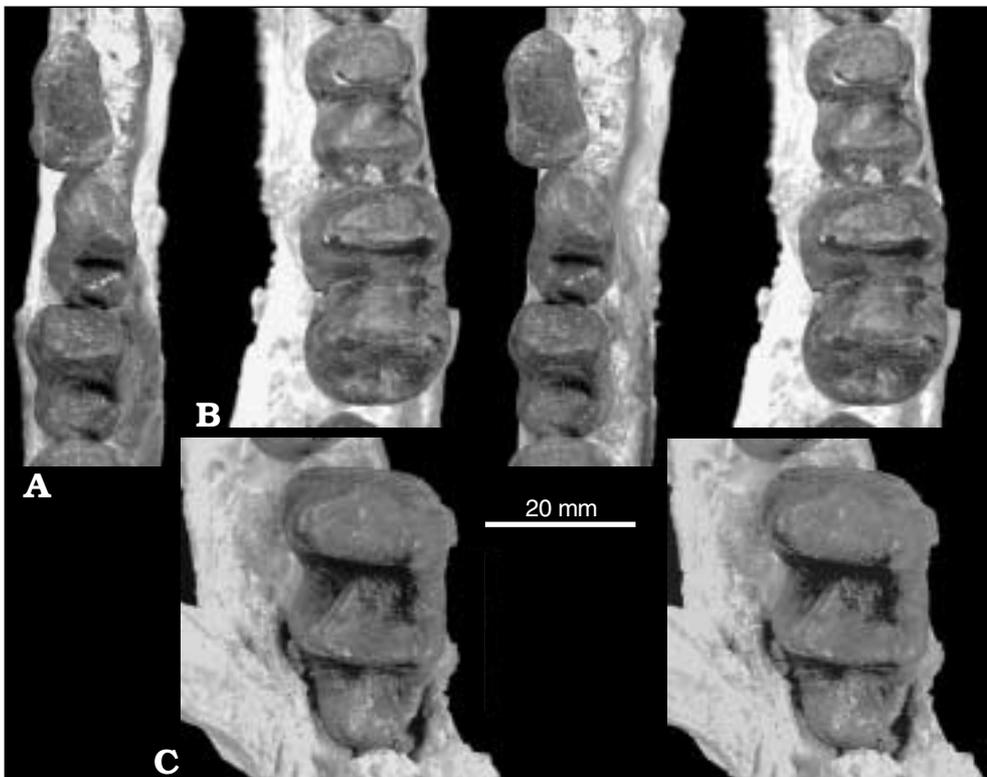


Fig. 3. *Daouitherium rebouli* gen. et sp. nov. Holotype, CPSGM MA4. Detailed occlusal stereo-view of p2–4 (A), m1–2 (B), and m3 (C).

p2–4 are biradicular. The tooth anterior to p2 (canine or p1?) was small and monoradicular, judging from its alveolus.

Anterior lower teeth (Figs. 4, 10A).—The holotype CPSGM MA4 preserves the anterior part of the dentary, although it is damaged. It exhibits four more or less distinct dental alveoli mesial to p2, and it is characterized by the complete absence of diastema, a striking feature of the species. The poor preservation of this anterior area makes only tentative the identifi-

cation of the tooth rank of these alveoli. The two most anterior alveoli are well distinct, rather proclive, and can be interpreted as incisors, either i1 and i2 or i2 and i3; the anteriormost one (i1 or i2) is rather enlarged and compressed labiolingually; the posterior one (i2 or i3) is smaller and more circular. More posteriorly, two small alveoli seem to occur: the posteriormost one is close to p2 and may account for a small and monoradicular c1, or possibly p1 or i3; the more anterior one is very small and may be that of i3 or of c1. The identifi-

cation of the central incisor as an *i2*, as possibly in *Numido-therium* (Mahboubi et al. 1986), would lead to the anterior dental formula *i2*, *i3*, *c1?*, *p1?*. However, our preferred interpretation of the anterior dental formula is *i1*, *i2*, *i3?*, *c1?*, mirroring the upper dentition of *Numido-therium* Jaeger, 1986 and agreement with the identified lower incisors of *Bary-therium* Andrews, 1901a and *Moeritherium* Andrews, 1901b (*i1*, *i2*). In other word we favour the loss of *p1*.

Dimensions.—Measurements of teeth: see Table 1; length of *p2*–*m3* (CPSGM MA4): 138 mm; length of *m1*–*m3* (CPSGM MA4): 88 mm.

Table 1. Dental measurements of *Daouitherium rebouli* gen. et sp. nov. L, length; W, width; H, height. In millimeters.

Specimen	Locus	L	W	H
MNHN PM3	m3	35.0	21.0	16.0
CPSGM MA4	m3	34.0	21.0	15.5
MNHN PM3	m2	28.0	18.0	16.0
CPSGM MA4	m2	28.0	18.0	15.0
MNHN PM3	m1	21.0	15.0	12.5
CPSGM MA4	m1	19.0	14.0	12.5
CPSGM MA4	p4	18.0	13.0	16.0
CPSGM MA5	m1	16.5	12.0	?
MNHN PM3	p3	18.0	12.0	16.0
CPSGM MA4	p3	17.5	11.0	17.0
CPSGM MA4	p2	17.0	9.0	17.0
CPSGM MA6	P4?	10.0	11.5	8.0

An estimation of the body mass based on size/mass regression equation of *m1* and *m2* (e.g., Damuth 1990), of the material described here, and especially based on their length, gives surprisingly very variable results, from about 170 Kg (MNHN PM3) to about 80 Kg (CPSGM MA5).

Fig. 9 illustrates the relative size of the jugal dentition of *Daouitherium* with respect to *Numido-therium*.

Dental formula.—*i3?*–*1?*, *c1?*, *p2*–*4*, *m1*–*3*; however, the retention of *p1* and loss of one incisor cannot be excluded on this basis of this material.

Dentary.—The horizontal ramus (= mandibular corpus) is dorso-ventrally deep. It shows one anterior mental foramina in front of the first alveolus anterior to *p2* (= canine or *p1?*). MNHN PM3 preserves the ascending ramus (Fig. 7). The apex of its anterior part (coronoid process) lies 65 mm above the *m3*. It is vertical or slightly inclined mesially and labially shifted, resulting in the labial position of its mesial flank with respect to *m3*. Its anterior margin is located at the level of *m3* talonid. The articular condyle is much higher than the dental row. The masseteric fossa is rather deep above the dental row. The symphysis is not preserved.

Height of the horizontal ramus below *m1* (CPSGM MA4): 58 mm; estimated height of the vertical ramus, from the coronoid apex: ≥ 120 mm (MNHN PM3); estimated height of the articular condyle 105 mm (MNHN PM3).

Upper dentition.—A single isolated left P3 or probably P4,

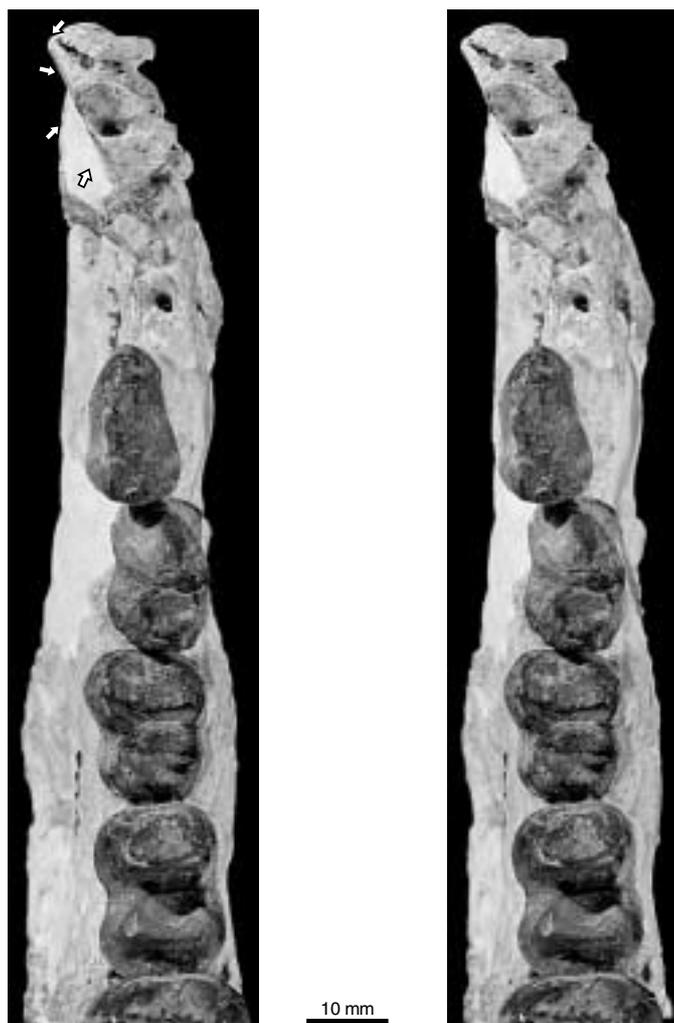


Fig. 4. *Daouitherium rebouli* gen. et sp. nov. Holotype, CPSGM MA4. Detail of the anterior part showing the *p2* and anterior alveoli (arrows) in sub-occlusal view.

specimen CPSGM MA6, is referable to the upper dentition of this species. It is bicuspid and bears one loph, the paraloph, which is extended between the paracone and the protocone. The distal cingulum is strong but the mesial cingulum is weak or absent. A small parastyle occurs; it is not linked by a crest to the paracone. The metacone is absent or very reduced. The paracone has a well developed distal crest. The postprotocrista is absent. An extensive wear facet is developed along the mesial flank of the paracone and the paralophid. The tooth bears three roots and two additional small mesial and distal root processes.

Comparisons and polarity of the main features of *Daouitherium rebouli* gen. et sp. nov.

The most important features of *Daouitherium rebouli* gen. et sp. nov. and their polarity with respect to primitive lophodont proboscideans such as *Phosphatherium escuilliei* Gheerbrant, Sudre, and Cappetta, 1996, *Numido-therium koholense*

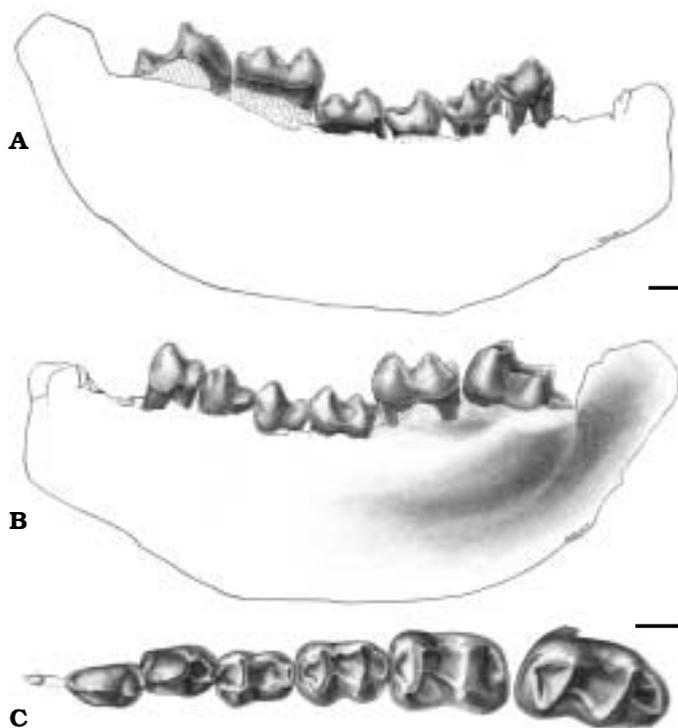


Fig. 5. *Daouitherium rebouli* gen. et sp. nov. Drawing of m1–3, p2–4 preserved in the holotype, CPSGM MA4 in lingual (A), labial (B), and occlusal (C) views. Scale bars 10 mm.

Jaeger, 1986 (in Mahboubi et al. 1986), *Numidothierium savagei* Court, 1995, and *Barytherium grave* Andrews, 1901b, are listed below. (0), (1), (2), (3) are successive, additive states of the examined features.

Feature 1. Anterior dentition: number of alveoli anterior to p2.

(0) 4 alveoli (2 or 3 i, c1 and/or p1): *Daouitherium rebouli*.

(1) 3 alveoli (2 i, c1): *Phosphatherium escuilliei*.

(2) 2 alveoli (2 i; loss of p1 and c1): *Numidothierium koholense*, *N. savagei*? (probably 2 alveoli, but feature unknown in available material), *Barytherium grave*.

Comments: 1(0) and the primitive eutherian anterior dental formula (i1–3, c1, p1) characterize outgroups such as phenacodontid “condylarths”, and also anthracobunids (*Pilgrimella* Dehm and Oettingen-Spielberg, 1958). *Moeritherium* is 1(2).

Feature 2. Diastema between lower incisors and p2.

(0) absent (brevirostrine morphology): *Phosphatherium escuilliei*, *Daouitherium rebouli*.

(1) present and large (longirostrine morphology): *Numidothierium koholense*, *Barytherium grave*; probably also *Numidothierium savagei*, though the feature is unknown in the species.

Comments: The outgroup condition known in many “condylarths” (e.g., phenacodontids) is 2(0), as for anthracobunids and phenacodontids (*Minchenella* Zhang, 1980). *Moeritherium* is 2(1).

Feature 3. Central lower incisor (i1?).

(0) small: primitive generalized eutherian condition.

(1) moderately enlarged: *Phosphatherium escuilliei*, *Daouitherium rebouli*? (feature poorly preserved).

(2) very enlarged (tusk-like): *Numidothierium koholense*, *Numidothierium savagei*, *Barytherium grave*.

Comments: The primitive outgroup condition is 3(0). *Moeritherium* has a very enlarged lower incisor (as in state 3(2)), but it may not be homologous (lateral incisor).

Feature 4. Premolars.

(0) all unmolarized (premolariform): *Phosphatherium escuilliei*.

(1) only p4 molariform: *Numidothierium koholense*.

(2) p3–4 molariform: *Daouitherium rebouli*.

(3) p2–4 molariform: *Numidothierium savagei*, *Barytherium grave*.

Comments: Unmolarized premolars characterize the primitive eutherian condition and especially many “condylarths”. However, an early trend for p4 molarization is known in phenacodontids and pantomesaxonians. Anthracobunids and *Moeritherium* are 4(2).

Feature 5. p4 morphology.

(0) premolariform: protocristid reduced and oblique with respect to the transversal axis, no entolophid: *Phosphatherium escuilliei*.

(1) semi-bilophodont: protocristid transversal, entolophid incipient but distinct: *Daouitherium rebouli*, *Numidothierium koholense*, *Numidothierium savagei*, *Barytherium grave*.

Comments: p3 has also an incipient trace of an entolophid in *Daouitherium*, *Numidothierium savagei* and possibly *Barytherium*; this is absent in *N. koholense* and *Phosphatherium*. The primitive outgroup condition is 5(0). Primitive pantomesaxonians, anthracobunids and *Moeritherium* have a molariform p4 with a transversal protolophid, but it is not bilophodont (no trace of an entolophid).

Feature 6. Paraconid of p3–4.

(0) small but clearly distinct: *Daouitherium rebouli*.

(1) reduced to absent: *Phosphatherium escuilliei*, *Numidothierium koholense*, *Numidothierium savagei*, *Barytherium grave*.

Comments: The polarity of the states of this feature may be questionable. However, primitive pantomesaxonians and phenacodontids show a differentiated paraconid (6(0)). Anthracobunids have a large paraconid in p3–4 (larger and higher in p3) (6(0)). *Moeritherium* has also a well developed paraconid especially on p2–3 (6(0)).

Feature 7. Occlusal outline of the premolars (especially p2–3).

(0) mesio-distally extended: *Phosphatherium escuilliei*, *Daouitherium rebouli*, *Numidothierium koholense*.

(1) more compressed mesio-distally (trigonid shortened) and rounded: *Numidothierium savagei*, *Barytherium grave*.

Comments: The outgroup condition may be 7(0) as in many “condylarths”. Anthracobunids are rather 7(0) for p2–3.

Moeritherium is variable for this feature, but it seems to have a shorter p3–4 and with a more rounded occlusal outline resulting especially from a more inflated labial flank; p2 is labio-lingually compressed as in *Daouitherium*.

Feature 8. Relative size of p3 and p2.

(0) Length of p3 > p2: *Phosphatherium escuilliei*, *Daouitherium rebouli*, *Numidothierium savagei*, *Barytherium grave*.

(1) Length of p3 < p2: *Numidothierium koholense*.

Comments: The primitive outgroup condition is 8(0). It is also generalized in tethytherians (e.g., anthracobunids and *Moeritherium*).

Feature 9. Enamel development in the premolars.

(0) restricted to above the cervix (crown): *Phosphatherium escuilliei*, *Numidothierium koholense*?, *Numidothierium savagei*?, *Barytherium grave*?

(1) extended basally (below the cervix) on the labial flank of the mesial root: *Daouitherium rebouli*.

Comments: The outgroup very generalized eutherian condition is 9(0). *Numidothierium koholense* may have a construction related to 9(1) in the wear pattern of the labial flank of mesial root of p2; in the parsimony analysis it is processed as unknown for this feature until more data is available; *N. savagei* and *B. grave* are probably primitive in this feature. Anthracobunids and *Moeritherium* are 9(0).

Feature 10. Roots of premolars p3–4.

(0) 2 roots, generally expanded transversally: *Phosphatherium escuilliei*, *Daouitherium rebouli*, *Numidothierium koholense*, *Numidothierium savagei*.

(1) the two roots of p3–4 are subdivided (four alveoli for each tooth): *Barytherium grave*.

Comments: The primitive outgroup condition known in “condylarths” such as phenacodontids is 10(0) or 2 roots not significantly expanded transversally (primitive eutherian condition). Anthracobunids and *Moeritherium* are 10(0).

Feature 11. Roots of premolar p2.

(0) 2 roots in all premolars: *Daouitherium rebouli*, *Numidothierium koholense*, *Barytherium grave*.

(1) one root for p2: *N. savagei* (Court 1995: roots fused), *Phosphatherium escuilliei* (loss of one root or roots fused).

Comments: 11(0) is the primitive eutherian condition. Anthracobunids and *Moeritherium* are 11(0). Desmostylians are 11(1).

Feature 12. Molar cristid obliqua.

(0) weakly oblique: weak angle with respect to the longitudinal axis, and joining the trigonid significantly labially: *Phosphatherium escuilliei*.

(1) moderately oblique lingually but more than *Phosphatherium* and less than *Numidothierium*: *Daouitherium rebouli*.

(2) well oblique lingually, ending mesially against the trigonid mid-width: *Numidothierium koholense*, *N. savagei*, *Barytherium grave*.

Comments: The polarity of the states of this feature may be



Fig. 6. *Daouitherium rebouli* gen. et sp. nov. MNHN PM3, right dentary with m1–3 and p3 in occlusal view.

equivocal. The primitive eutherian condition is a cristid obliqua strongly oblique joining the metaconid (many “protheutherians” and “condylarths”), or an oblique cristid obliqua joining the trigonid in its mid-width between metaconid and protoconid (many “condylarths” including phenacodontids). The labial drift of the cristid obliqua is a derived trend in tethytherians (Tassy and Shoshani 1988; Fischer and Tassy 1993), and the cristid obliqua “entirely labial” is described as a probable synapomorphy of proboscideans s.s. (Tassy 1994). The weakly oblique (rather labial) cristid obliqua of *Phosphatherium* is indeed obviously derived with respect to the primitive eutherian (outgroup) condition. However other lophodont proboscideans seem to be characterized by a secondary lingual (more oblique) migration of the cristid obliqua (12(1) and 12(2)) with respect to *Phosphatherium*. Anthracobunids are probably primitive (or secondary derived ?) in their cristid obliqua strongly oblique lingually, joining the metaconid. *Moeritherium* is like *Numidothierium* and *Barytherium*. The alternative hypothesis would be that *Phosphatherium* is precociously specialized and that the later lophodont proboscideans (*Numidothierium* and *Barytherium*) remained more primitive in this respect.

Feature 13. Molar cristid obliqua.

(0) unreduced: *Phosphatherium escuilliei*, *Daouitherium rebouli*, *Numidothierium koholense*, *Barytherium grave*.

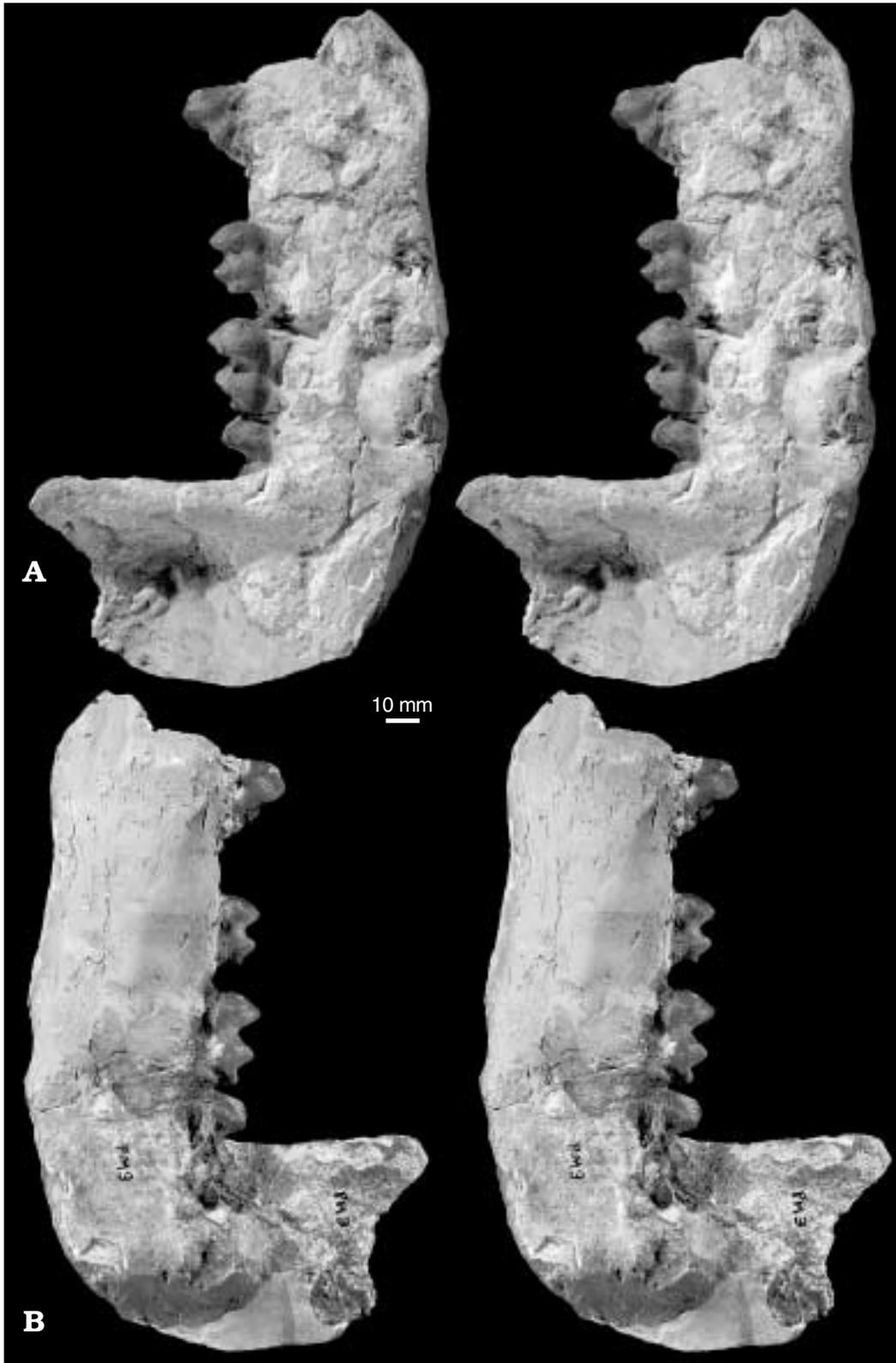


Fig. 7. *Daouitherium rebouli* gen. et sp. nov. MNHN PM3, right dentary with with ascending ramus and m1–3, p3. in labial (A) and lingual (B) views.

(1) mesial part reduced (vanished), in relation with the development of the interlophid: *N. savagei*.

Comments: 13(0) corresponds to the primitive eutherian con-

dition. Anthracobunids and *Moeritherium* have well developed cristid obliqua (13(0)), with some specializations (long and sharp in the former and inflated as a protoconulid and a mesoconid in the latter).



Fig. 8. *Daouitherium rebouli* gen. et sp. nov. CPSGM MA6, left p4 in occlusal stereo-view. Anterior is up.

Feature 14. Molar entocristid.

(0) more or less longitudinal and straight: *Phosphatherium escuilliei*.

(1) concave labially or oblique mesio-labially: *Daouitherium rebouli*.

(2) very oblique mesio-labially and significantly convergent mesially with the cristid obliqua: *Numidothierium koholense*, *N. savagei*, *Barytherium grave*.

Comments: 14(0) corresponds to the generalized eutherian condition known in many “condylarths”. Anthracobunids are derived in the reduction of the entocristid (large talonid notch), as are several phenacodontids. *Moeritherium* also has a reduced entocristid.

Feature 15. Cusps developed in the distal cingulid of lower molars (postentoconulid).

(0) hypoconulid distinct, postentoconulid variably distinct: *Phosphatherium escuilliei*.

(1) hypoconulid distinct, postentoconulid absent: *Daouitherium rebouli*, *Numidothierium koholense*, *N. savagei*, *Barytherium grave*.

Comments: The primitive eutherian (outgroup) condition known in many “condylarths” such as phenacodontids is the absence of a postentoconulid. A variable, incipient or small postentoconulid is known at least in the m3 of primitive tethytheres, phenacolophids such as *Minchenella* (small entoconulid close to hypoconulid which remains central), desmostyles, and sirenians. Anthracobunids such as *Pilgrimella* have a well developed postentoconulid on m3. *Moeritherium* has a variable more or less distinct postentoconulid. True lophodont bilophodont proboscideans seem to have reduced secondarily the postentoconulid: the reduction of the postentoconulid in *Daouitherium*, *Numidothierium* and *Barytherium* may be derived with respect to *Phosphatherium*. Trilophodont proboscideans have a postentoconulid.

Feature 16. Horizontal ramus (mandibular corpus) of the dentary.

(0) not high: *Phosphatherium escuilliei*.

(1) high (deep): *Daouitherium rebouli*, *Numidothierium koholense*, *Numidothierium savagei*, *Barytherium grave*.

Comments: 16(0) is the generalized outgroup eutherian condition from which many ungulates including anthracobunids, sirenians, *Moeritherium* and other proboscideans have departed.

Feature 17. Ascending ramus of the dentary.

—■— *Daouitherium rebouli* (CPSGM MA4)
 -◆- *Numidothierium koholense**
 -▲- *Numidothierium savagei**

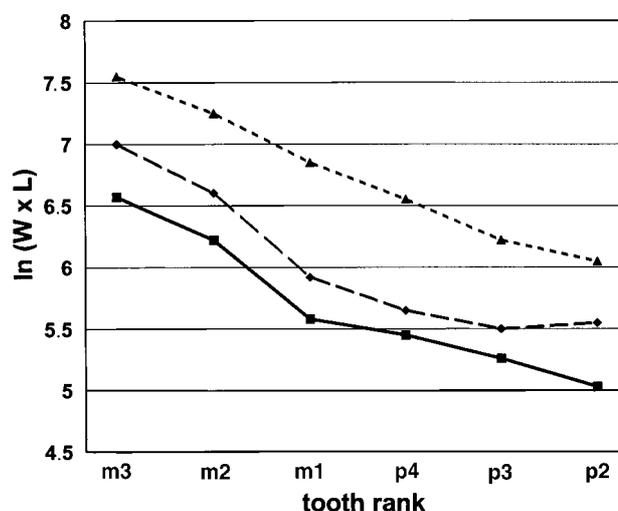


Fig. 9. Log transformed plot comparing the relative size (length \times width) of the jugal teeth of *Daouitherium* and *Numidothierium*. After Court (1995: fig. 1). Note the slightly smaller size of *Daouitherium* and the strong size difference between m1 and m2. *N. koholense* is probably specialized in its large p2 with respect to p3 (feature 7).

(0) its mesial flank arises at the level of m3 or more posteriorly: *Phosphatherium escuilliei*, *Numidothierium koholense*, *Daouitherium rebouli*.

(1) its mesial flank arises more anteriorly than m3: *Numidothierium savagei* (m2–3), *Barytherium grave* (m2).

Comments: The mesial flank of the ascending ramus of the dentary arises posterior to m3 (17(0)) in anthracobunids and primitive eutherians (outgroup condition), with respect to *Moeritherium* and derived proboscideans (17(1)). 17(1) is generally associated with a mesial inclination (and labial shift) of the ascending ramus in proboscideans, a feature which is only incipient in *Daouitherium*.

Feature 18. Articular condyle of the dentary.

(0) relatively low above the dental row: *Phosphatherium escuilliei*.

(1) very high above the dental row: *Daouitherium rebouli*, *Numidothierium koholense*, *Barytherium grave*.

Comments: 18(0) corresponds to the primitive outgroup eutherian condition, from which many ungulates have departed, including most proboscideans (incl. *Moeritherium*). This feature is unknown in *Numidothierium savagei*.

Feature 19. Body size.

(0) small: *Phosphatherium escuilliei*.

(1) large (up to the tapir size): *Daouitherium rebouli*, *Numidothierium koholense*, *Numidothierium savagei*.

(2) very large: *Barytherium grave*.

Comments: Outgroup generalized eutherian condition is 19(0).

Discussion

The Ouled Abdoun material described here illustrates a new, well characterized genus and species (see diagnosis above) of primitive proboscidean (traditional concept) which is named *Daouitherium rebouli*.

Some proboscidean features of *Daouitherium*, which should be noted are the development of a probable enlarged lower incisor (as exemplified by the most anteriorly preserved alveolus of the holotype), the true lophodont molar morphology, which is distinctive with respect to anthracobunids and sirenians (Gheerbrant et al. 1996, 1998), the molar cristid obliqua located labially, and the large body size. Striking features of *Daouitherium* previously unknown (primitive) in proboscideans are the absence of diastema in the anterior dentition and the retention of two additional anterior teeth, i3 and/or c1, c1 and/or p1.

The lower jugal dentition of *Daouitherium rebouli* and especially the molar series is strikingly similar to *Numidothierium koholense* Jaeger, 1986 from the early/middle Eocene of El Kohol (Mahboubi et al. 1984, 1986), *N. savagei* Court, 1995 from the late Eocene of Dor El Talha, and *Barytherium grave* Andrews, 1901b from the late Eocene and early Oligocene of Dor El Talha and Fayoum, suggesting close relationships at least within the same proboscidean suborder Barytherioidea. It is also similar to that of *Phosphatherium escuilliei* Gheerbrant, Sudre, and Cappetta, 1996, as is shown by the new material of this species, and especially in the molar morphology. Actually, the morphology of the lower molars of *Daouitherium* is virtually identical to that of *Numidothierium* and their size is close to that of *N. koholense* (Fig. 10). The morphology of the upper premolar CSGPM MA6 referred to *Daouitherium rebouli* is also similar to that of *Numidothierium* and *Barytherium* (Fig. 11).

Daouitherium also shares with *Numidothierium* and *Barytherium* the very high position of the articular condyle of the dentary, the deep horizontal ramus of the dentary, molarization of the lower premolars (but simplified in *N. koholense*), the p4 semi-bilophodont (entolophid weak but differentiated), and the entocristid concave labially or oblique mesio-labially. These features are probably derived, especially with respect to *Phosphatherium* which is also a much smaller form.

Daouitherium, however, differs strongly from *Numidothierium* and *Barytherium* in its anterior lower dentition: it is short mesio-distally, without any distinct diastema, and it preserves several additional teeth as exemplified by the occurrence of four dental alveoli in front of p2 (see the description for their interpretation). In contrast, *Numidothierium* and *Barytherium* show the occurrence of only two incisors (i1 and i2) separated from p2 by a large diastema. The short anterior lower dentition of *Daouitherium*, lacking a diastema, indicates a rather brevirostrine morphology of the head as opposed to the derived longirostrine morphology of *Numidothierium* and *Barytherium*.

This primitive construction of the anterior lower dentition

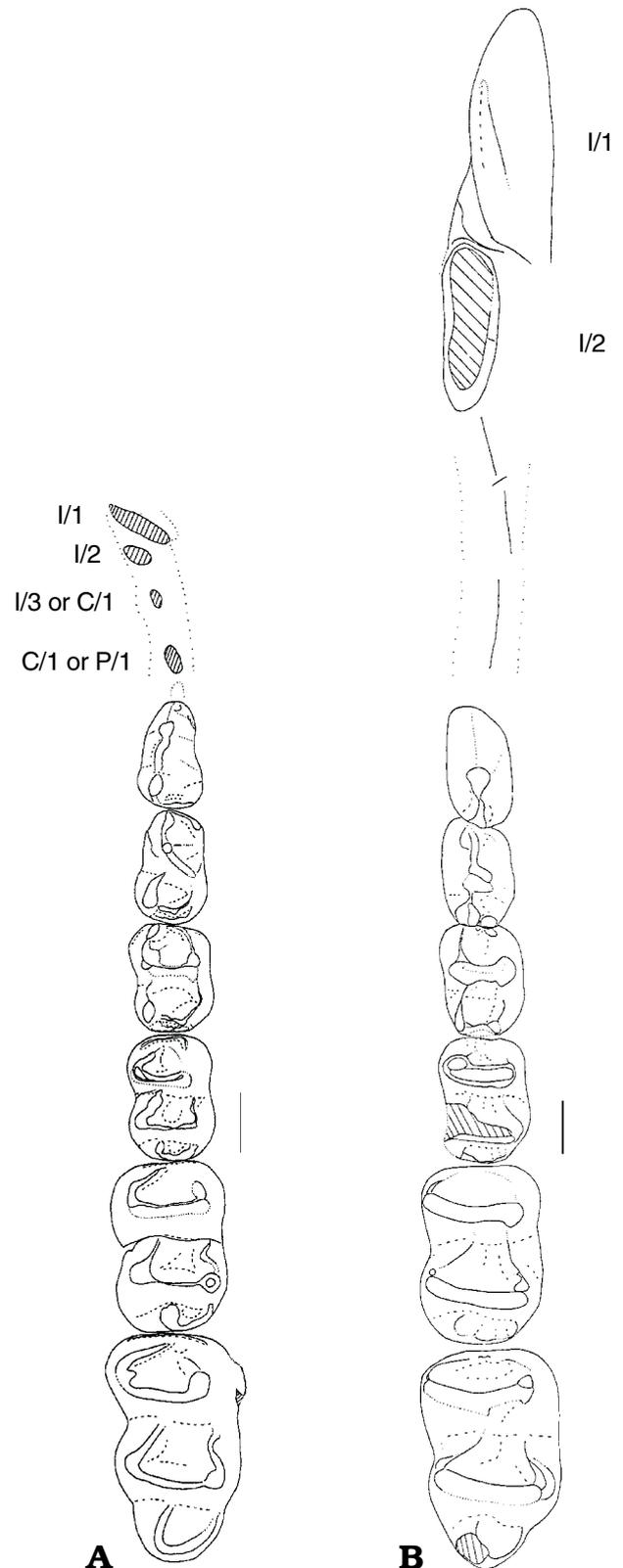


Fig. 10. Comparison of the lower jugal dentition of *Daouitherium rebouli* gen. et sp. nov. and *Numidothierium koholense*. Occlusal sketches of the teeth. A. *Daouitherium rebouli*, CPSGM MA4, left p2–4, m1–3, and alveoli for i1 or i2, i2 or i3, i3 or c1, c1 or p1. B. *Numidothierium koholense*, cast of unnumbered specimen with left i1–2, diastema, p2–4, and m1–3. Drawings not to scale; scale bars 5 mm.

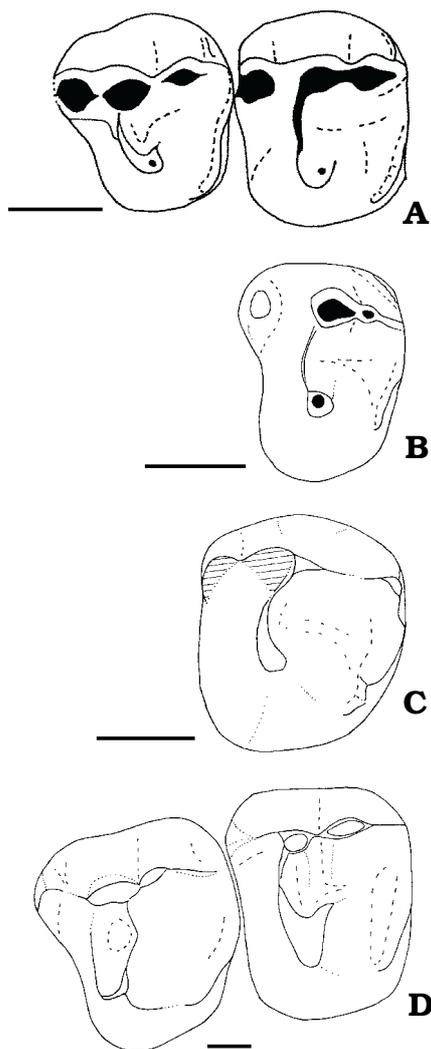


Fig. 11. Comparison of the upper premolar referred to *Daouitherium rebouli* gen. et sp. nov. with those of *Phosphatherium* and *Numidothierium*. **A.** *Phosphatherium esculliei*, holotype, P3–4. **B.** *Phosphatherium esculliei*, PM18, P4. **C.** *Daouitherium rebouli*, CPSGM MA6, P4?. **D.** *Numidothierium koholense*, P3–4, unnumbered cast. Occlusal sketches of the teeth. Drawings not proportional; scale bars 5 mm. CPSGM MA6 belongs to a noticeably small individual with respect to the hypodigm of *Daouitherium rebouli*.

of *Daouitherium* reminds that of *Phosphatherium*. It may be even more primitive than that of *Phosphatherium* in some features such as the retention of an additional dental alveolus in front of p2 (however, this difference needs to be confirmed in better preserved material), and the p2 which has two roots as in *Numidothierium koholense* and *Barytherium*. The p2 of *Phosphatherium* has most probably one root, which is by contrast a derived feature. The p2 of *N. savagei* has also only one root, probably as the result of parallelism. It should be noticed that the loss of c1 and p1 was once considered as a synapomorphic feature of proboscideans (e.g., Tassy 1981; Domning et al. 1986; Tassy 1994; Court 1995; Shoshani et al. 1996). These teeth are now known in *Daouitherium* (retention of two teeth among i3, c1 and p1) and *Phosphatherium* (retention of c1).

Other primitive features of *Daouitherium* with respect to *Numidothierium* and *Barytherium* are the distal location of the anterior margin of the coronoid process (ascending ramus; feature 17), which rises from the horizontal ramus at the level of m3, and its weak mesial inclination. *Daouitherium* is also characterized by premolars retaining a small paraconid (especially p3–4; feature 6). In addition, the premolars of *Daouitherium* show an elongated occlusal outline, which resembles that of *Phosphatherium* and *Numidothierium koholense* and which clearly differs from the shorter (trigonid very compressed mesio-distally) and more rounded occlusal outline of *N. savagei* and *Barytherium grave* (feature 7). This latter condition indicates a relative shortening of the jugal dental series in *N. savagei* and *Barytherium grave* (which contrasts strikingly with the long diastema in these species). In addition, the most anterior alveolus (i1 or less possibly i2) preserved in CPSGM MA4 is much less enlarged with respect to the central lower incisor of *Numidothierium* (here interpreted as a possible i1), and probably even with respect to that of *Phosphatherium* (i1?) (feature 3).

Comparison with other primitive proboscideans suggests that the occurrence of a very large and very labial hypoconid in the p3 and p2 of *Daouitherium*, and that the resulting characteristic triangular occlusal outline, may be autapomorphic. This might be also true for the basal extension of the enamel on the labial side of the anterior root of lower premolars (feature 9), which appears to be distinctive with respect to *Phosphatherium*, *N. savagei*, and *Barytherium* species. Instead, this feature is reminiscent of the peculiar mode of wear evidenced by Court (1993) on the labial side of the anterior root of p2 of *N. koholense*. These features seem to be more or less functionally related, although in *N. koholense* the peculiar mode of wear of p2 appears to be linked to the development of a large diastema. The condition seen in *N. koholense* could be a more derived expression of a same specialized functional trend of the premolar series already initiated in *Daouitherium*.

Some other features of *Daouitherium* are of uncertain polarity with respect to *Numidothierium* and *Barytherium*, such as the cristid obliqua being less oblique lingually (feature 12; primitive?) and the precingulid which is small (thin and not extended laterally), but distinct and curved upward in m1.

Daouitherium is closer to *Numidothierium koholense* than to *N. savagei* and *Barytherium grave* in size (smaller), the elongated occlusal outline of its premolars, the two-rooted premolars (p2: roots fused in *N. savagei*; p3–4: four roots in *Barytherium* resulting from the subdivision of the two transverse roots), and the unreduced anterior part of entocristid and cristid obliqua (interlophid poorly differentiated). However these resemblances may be symplesiomorphic and *Numidothierium koholense* differs by its more simplified p2–3 (primitive), the jugal teeth broader and significantly more bunodont (probably primitive), the absence of entolophid in p3 (primitive), and the p2 slightly longer than p3 (derived, possibly autapomorphic).

Phylogenetic and systematic conclusions (Fig. 12)

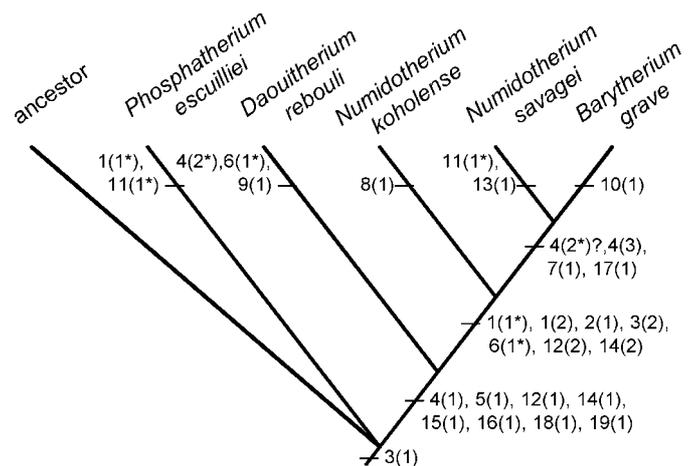
Daouitherium rebouli gen. et sp. nov. is a new, primitive large lophodont African proboscidean of basal Eocene age. A parsimony analysis (Hennig 86) of its most important features (features 1–19) produced the cladogram of Fig. 12. It shows that the phylogenetic position of *Daouitherium* with respect to other lophodont primitive proboscideans is intermediate between the primitive *Phosphatherium* and the more derived *Numidothierium* and *Barytherium*. This is supported by important features such as large body size (feature 19), the very high position of the articular dentary (feature 18), the deep horizontal ramus of the dentary (feature 16), molarization of the premolars (feature 4) and the semi-bilophodont p4 with an incipient entolophid (feature 5), among others (features 12–14).

It should be emphasized that this resulting cladogram is unrooted. The significance of *Daouitherium* for the ancestral dental morphotype of proboscideans (out of the true lophodont molars), as well as for the basal relationships of these primitive lophodont taxa with respect to other proboscideans (e.g., *Moeritherium*), to tethytherians (anthracobunids, sirenians, desmostyles) and to higher inclusive taxa such as pantomesaxonians, will be investigated together with the study of the new informative material of *Phosphatherium* (skull and lower dentition: work in preparation).

The problem of the relationships with the deinotheres will be also investigated separately in the light of the new data on *Phosphatherium* and of the extended comparisons with *Moeritherium* and Elephantiformes Tassy, 1988. *Daouitherium* itself does not add significant data to the question of the origin of deinotheres, except it shares the true lophodonty and supports that this is the probable ancestral morphotype of the Proboscidea. *Numidothierium* and especially *Barytherium* are clearly closer to deinotheres in their more derived anterior dentition (e.g., diastema, loss of several anterior teeth).

The family referral of *Daouitherium* remains difficult to establish confidently in the present state of data. *Daouitherium* is especially close to *Numidothierium*, but no special synapomorphy excluding *Barytherium* can be identified. Here, we emphasize this phenetic special resemblance of *Daouitherium* with *Numidothierium* with its provisional inclusion in the Numidothieridae. This, however, makes this family probably paraphyletic, as with the inclusion of *Phosphatherium* in this family (Gheerbrant et al. 1996, 1998). Referral of *Daouitherium* to the Numidothieridae would be more legitimate than for *Phosphatherium*, which is much more primitive as evidenced by new material in the course of study. As for *Phosphatherium*, there are indeed some striking primitive features of *Daouitherium* which raise questions about their familial numidothierid allocation. This is especially true for the anterior dentition which has no developed diastema (brevirostrine form) and which retains several teeth (i3 or c1, c1 or p1) which are lost in *Numidothierium*, i.e. corresponding to a more primitive dental formula.

Daouitherium and *Numidothierium* seem to exemplify an



Character matrix of <i>Daouitherium</i>						
Feature n°	00000	00001	11111	1111		
	12345	67890	12345	6789		
Ancestor	00000	00000	0000?	0000		
<i>P. escuilliei</i>	10100	10000	10000	0000		
<i>D. rebouli</i>	00?21	00010	01011	1011		
<i>N. koholense</i>	21211	10170	02021	1011		
<i>N. savagei</i>	21231	11000	12121	11?1		
<i>B. grave</i>	21231	11001	02021	1112		
Weight	32222	12122	21111	3232		

Fig. 12. Character matrix of *Daouitherium* and other primitive lophodont proboscideans (see text: features 1–19) and most parsimonious cladogram resulting from parsimony analysis with Hennig86 program, with distribution of the derived features. Length = 56; CI = 85; RI = 82. This cladogram is unrooted. The significance of *Daouitherium* for the ancestral morphotype of proboscideans and the basal relationships of lophodont proboscidean taxa with respect to other proboscideans (e.g., *Moeritherium*, deinotheres) and tethytherians will be investigated separately with the study of the new material of *Phosphatherium* (work in preparation). Analysed features are additive and are weighted according to their relative importance (see matrix); however an analysis of this matrix without weighting the features does not change the resulting topology. Several reversions that are possible according to the algorithm have been discounted as being anatomically unlikely (features 1, 3, 4). Asterisk indicates convergent feature.

early radiation of basal Barytherioidea. *Daouitherium* is indeed included in Barytherioidea, following the initial systematic position adopted for *Numidothierium* (Mahboubi et al. 1986). However, formally such a concept of the Barytherioidea is paraphyletic. *Phosphatherium*, *Daouitherium*, *Numidothierium*, *Barytherium* and the Deinotheriidae correspond actually to successive plesions belonging to the stem-group Proboscidea.

The antiquity (early Ypresian) and primitive morphology of *Daouitherium* with respect to *N. koholense* would be in accordance with their hypothesized ancestral-descendant relationship. Clearly, this is a better supported hypothesis than the possible filiation of *Phosphatherium* and *N. koholense* discussed by Gheerbrant et al. (1996, 1998): the mandibular and dental anatomy of *Daouitherium* is much closer to those

of *N. koholense*. However, there are no special synapomorphies of *Daouitherium* and *N. koholense* supporting a peculiar lineage of primitive lophodont proboscideans. In addition *Daouitherium* has some derived features with respect to *N. koholense*: the p3–4 more molarized, the enamel extended basally on the anterior root of premolar (feature 9; however the peculiar mode of wear of p3 in *N. koholense* may be reminiscent of this feature in *Daouitherium*: see above), and the jugal teeth less bunodont. These specializations seem, conversely, to exclude *Daouitherium* from the direct ancestry of *N. koholense*.

General implications of the new Ypresian Ouled Abdoun mammal

Daouitherium rebouli gen. et sp. nov. adds to the faunal list of the mammals described from the Ouled Abdoun Basin which includes *Abdounodus hamdii* (Gheerbrant et al., 2001), *Ocepeia daouiensis* (Gheerbrant et al., 2001), and *Phosphatherium escuilliei*, as well as several other undescribed new species. Compared to *Phosphatherium escuilliei*, *D. rebouli* is a rare mammal species in the Ouled Abdoun Phosphate sites.

Daouitherium rebouli represents a new lineage of primitive lophodont proboscideans which is well distinguished from *Phosphatherium* and *Numidotherium*. Along with *Phosphatherium* and possibly *Khamsaconus* (Ouarzazate Basin), it is actually the earliest known proboscidean. It is also the earliest known large mammal from Africa. The discovery of such a large and distinctive proboscidean associated with the much more primitive and smaller *Phosphatherium* in the same earliest Eocene fossiliferous beds of the Ouled Abdoun Basin is quite surprising. This, and the fact that *Daouitherium* and *N. koholense* might belong to different lineages, are first elements emphasizing an unexpected precocious diversity of proboscideans in Africa. This is especially striking with respect to the modest diversity which characterizes the order throughout the Paleogene (8–7 Eocene–Oligocene genera, of which four recently described ones are the earliest known: *Khamsaconus*?, *Phosphatherium*, *Daouitherium*, *Numidotherium*, *Moeritherium*, *Barytherium*, *Palaeomastodon*, *Phiomia*). Such an early diversity and the significant evolutive divergence exemplified by *Phosphatherium* and *Daouitherium*, are new and strong arguments for an old age of the order in Africa, of at least Paleocene roots. This adds to the evidence seen in the primitive morphology of *Phosphatherium* (Gheerbrant et al. 1996, 1988; work in preparation) for the probable African origin of the order Proboscidea s.s. The old origin of the order Proboscidea in Africa supported here fits well with the molecular hypotheses of Paenungulata and Afrotheria (Madsen et al. 1997, 2001; Murphy et al. 2001; Springer et al. 1997; Stanhope et al. 1998; Van Dick et al. 2001).

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