Diversity in the later Paleogene proboscidean radiation: a small barytheriid from the Oligocene of Dhofar Governorate, Sultanate of Oman

Erik R. Seiffert, Sobhi Nasir, Abdulrahman Al-Harthy, Joseph R. Groenke, Brian P. Kraatz, Nancy J. Stevens & Abdul Razak Al-Sayigh

Springer

Springer

ORIGINAL PAPER

Diversity in the later Paleogene proboscidean radiation: a small barytheriid from the Oligocene of Dhofar Governorate, Sultanate of Oman

**Erik R. Seiffert · Sobhi Nasir ·
Abdulrahman Al-Harthy · Joseph R. Groenke ·
Brian P. Kraatz · Nancy J. Stevens ·
Abdul Razak Al-Sayigh**

Abstract Despite significant recent improvements to our understanding of the early evolution of the Order Proboscidea (elephants and their extinct relatives), geographic sampling of the group's Paleogene fossil record remains strongly biased, with the first ~30 million years of proboscidean evolution documented solely in near-coastal deposits of northern Africa. The considerable morphological disparity that is observable among the late Eocene and early Oligocene proboscideans of northern Africa suggests that other, as yet unsampled, parts of Afro-Arabia might have served as important centers for the early diversification of major proboscidean clades. Here we describe the oldest taxonomically diagnostic remains of a fossil proboscidean from the Arabian Peninsula, a partial mandible of *Omanitherium dhofarensis* (new genus and species), from near the base of the early Oligocene Shizar Member of the Ashawq Formation, in the Dhofar Governorate of the Sultanate of Oman. The molars and premolars of *Omanitherium* are morphologically intermediate between those of *Arcanotherium* and *Barytherium* from northern Africa, but its specialized lower incisors are unlike those of other known Paleogene proboscideans in being greatly enlarged, high-crowned, conical, and tusk-like. *Omanitherium* is consistently placed close to late Eocene *Barytherium* in our phylogenetic analyses, and we place the new genus in the Family Barytheriidae. Some features of *Omanitherium*, such as tusk-like lower second incisors, the possible loss of the lower central incisors, an enlarged anterior mental foramen, and inferred elongate mandibular symphysis and diminutive P_2, suggest a possible phylogenetic link with Deinotheriidae, an extinct family of proboscideans whose origins have long been mysterious.

E. R. Seiffert (✉) · J. R. Groenke
Department of Anatomical Sciences, Health Sciences Center T-8,
Stony Brook University,
Stony Brook, NY 11794-8081, USA
e-mail: erik.seiffert@stonybrook.edu

S. Nasir · A. Al-Harthy · A. R. Al-Sayigh
Department of Earth Sciences, College of Science,
Sultan Qaboos University,
P.O. Box 36, Al-Khod 123,
Muscat, Sultanate of Oman

B. P. Kraatz
Department of Anatomy, Western University of Health Sciences,
Pomona, CA 91766, USA

N. J. Stevens
Department of Biomedical Sciences,
Heritage College of Osteopathic Medicine, Ohio University,
228 Irvine Hall,
Athens, OH 45701, USA

Introduction

Recent fossil discoveries in the Paleocene (Gheerbrant 2009) and early Eocene (Gheerbrant et al. 2002) of northwest Africa have established that the order Proboscidea—a formerly diverse clade that is now represented solely by African and Indian elephants—likely arose a few million years after the K–Pg (Cretaceous–Paleogene) boundary in Afro-Arabia

(Sanders et al. 2010). Over the course of the subsequent 35 million years, primitive proboscideans diversified in isolation on that island continent, and by the earliest Oligocene (~34 million years ago), derived "elephantiform" proboscideans such as *Phiomia* and *Palaeomastodon* already displayed a series of specialized morphological features that they shared exclusively with Miocene-to-Recent elephantoids (Andrews 1906; Osborn 1936). More distantly related forms such as deinotheriids, moeritheriids, and the remaining basal "plesielephantiforms" (Sanders et al. 2010) present more perplexing combinations of primitive and derived cranial and postcranial features that have complicated attempts to resolve their positions on the earliest branches of the proboscidean family tree (Court 1995; Gheerbrant et al. 2005; Seiffert 2007; Delmer 2009).

At present the early fossil record of non-elephantiform proboscidean evolution is almost entirely restricted to northern Africa. Here we describe a new genus and species of primitive proboscidean on the basis of a partial lower jaw that was recovered from near the base of the early Oligocene Shizar Member of the Ashawq Formation (Roger et al. 1993; Seiffert 2006), a succession that outcrops extensively north of Al-Mughsayl and Rakhyut in the Dhofar Governorate of southwestern Oman (Fig. 1). Previous paleontological work at the nearby Thaytiniti locality, also at the base of the Shizar Member, which was undertaken between 1986 and 1992 by joint French-Omani expeditions, led

Fig. 1 Location of DPP-2010-1, type locality for *Omanitherium dhofarensis*

to the recovery of three enigmatic isolated proboscidean incisor and premolar teeth that were identified as "cf. Barytherioidea" by Thomas et al. (1989). It is unclear whether these specimens belong to the new genus and species described here, which not only represents the first significant record of a non-elephantiform proboscidean from the Paleogene of the Arabian Peninsula but also from any region outside of northern Africa. The specimen described here was discovered and partially collected by a local civilian, who reported the finding to the Office of Adviser to His Majesty the Sultan for Cultural Affairs. A subsequent visit to the locality by E.R.S., S.N., and A.A.-H. in 2010 led to the recovery of additional parts of the same individual as well as fragmentary teeth of another individual. No other mammalian taxa were recovered from the site. The new genus, *Omanitherium*, suggests that there was a much more diverse radiation of early proboscideans in Afro-Arabia during the Oligocene than has been documented thus far in the relatively well-known fossil deposits of northern Africa, and once again raises the possibility that barytheriids are a source group for Deinotheriidae (Harris 1978; Mahboubi et al. 1984), an enigmatic clade that originated in the Paleogene of Afro-Arabia, became widespread in Africa and Eurasia during the Miocene, and made its last appearance in the Pleistocene of Africa (Behrensmeyer et al. 1995).

Materials and methods

Phylogenetic analysis

We obtained several estimates of early proboscidean phylogeny by adding the new genus described here to the combined molecular-morphological character matrix of Seiffert (2010), which samples a number of phylogenetically basal proboscideans in addition to 46 other living and extinct afrotherian relatives. The matrix is available for download at http://www.morphobank.org. A small number of codings were modified to better categorize the morphological variation observable among the proboscidean ingroup, which was further expanded by including *Arcanotherium*, based on observations on original material by E.R.S. and the descriptions of Court (1995) and Delmer (2009).

All parsimony analyses were performed in PAUP* 4.0b10 (Swofford 1998), using random addition sequence and tree bisection and reconnection across a minimum of 5,000 replicates. The matrix of Seiffert (2010) was analyzed in three ways: with some multistates ordered and scaled, some multistates ordered and unscaled, or with all characters unordered. Clade support was estimated by bootstrap analysis of the data set using PAUP* 4.0b10 (1,000 pseudoreplicates). Three additional analyses (with the same treatments of certain multistate characters) were performed in which molecular data
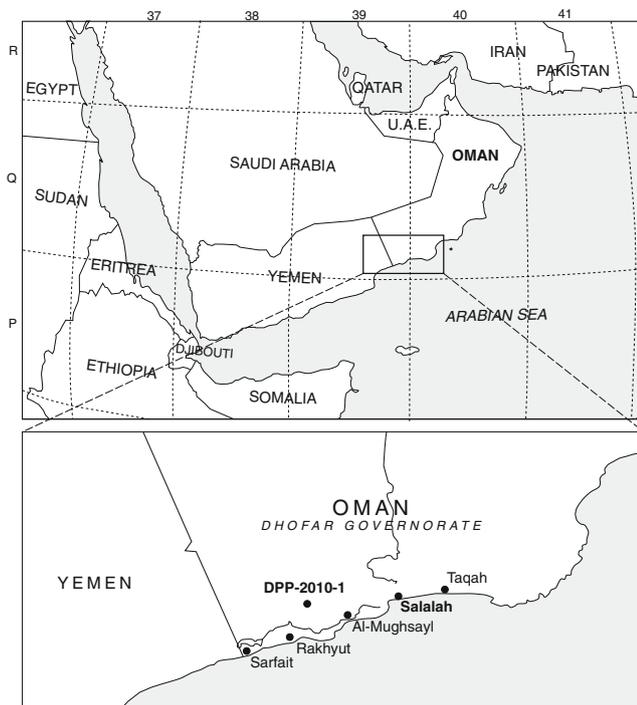
were excluded and the relationships of extant taxa were constrained by a molecular scaffold that enforced the monophyly of Afroinsectivora (Macroscelidea+Afrosoricida), Afroinsectiphillia (Tubulidentata+Afroinsectivora), and Atlantogenata (Afrotheria+Xenarthra) following the results of Murphy et al. (2001, 2007).

Abbreviations

BL=buccolingual; DPP=Dhofar Paleontological Project; I=incisor; M=molar; MD=mesiodistal; P=premolar; SQU=Sultan Qaboos University, Department of Earth Sciences collection; UTM=Universal Transverse Mercator coordinate system.

Results

Systematic Paleontology

Class Mammalia Linnaeus, 1758
    Placentalia Owen, 1837
    Cohort Paenungulata Simpson, 1945
    Order Proboscidea Illiger, 1811
    Family Barytheriidae Andrews, 1906
    Omanitherium, new genus
    Type species Omanitherium dhofarensis, new species

Etymology From the country of origin, the Sultanate of Oman, combined with *therion*, Greek for wild animal or beast.

Distribution Earliest Oligocene (earliest Rupelian) of southwestern Oman.

Diagnosis Differs from early Eocene *Numidotherium koholense* (Mahboubi et al. 1986; Noubhani et al. 2008) in being relatively large [M_1 area (length×width) of ~1,270 mm^2 in *O. dhofarensis*, compared to a mean (Noubhani et al. 2008) of ~432 mm^2 in *N. koholense*], and in combining the following features: a conical and tusk-like I_2; a relatively small P_2; a large metaconid on P_3 and entoconids on P_{3-4}; a more rectangular P_4 with no hypolophid, a relatively narrow talonid, and a centrally placed hypoconid; relatively broad and four-rooted lower molars that have relatively tall metaconids, cusps that show more basal inflation, trigonid and talonid cusps that are more equal in height, relatively distinct precingulids, no entocristids or premetacristids, and more basally inflated buccal margins; an M_3 with a relatively short hypoconulid lobe; a mediolaterally constricted symphyseal region, with a relatively long diastema between I_2 and P_2; and a relatively low coronoid process and more anteriorly positioned origin of the vertical ramus. Differs from *Arcanotherium savagei* (Court 1995; Delmer 2009) in exhibiting the following combination of features: a relatively small P_2; relatively tall P_{3-4} hypoconids; no P_4 premetacristid; a P_4 with no hypolophid or premetacristid, a relatively narrow talonid, and a

centrally placed hypoconid; relatively weak buccal cingulids; and relatively broad lower molars (particularly M_{2-3}) with more basally inflated cusps and buccal margins and no entocristid or premetacristid crests. Differs from *Barytherium grave* (Andrews 1906) in being much smaller [M_2 area of ~1,960 mm^2 in *O. dhofarensis* compared to ~5,500 mm^2 (Andrews 1906) in *B. grave* from Fayum, Egypt], and in having a relatively small P_2; two-rooted P_{2-4}; P_4 with no premetacristid or hypolophid, a relatively narrow talonid, and a centrally placed hypoconid; and lower molars with more basally inflated buccal margins, and no entocristids or premetacristids. Differs from *Moeritherium* (Andrews 1906; Matsumoto 1923; Delmer et al. 2006) in having a conical and tusk-like I_2 that lacks serrations; a relatively small P_2; P_{3-4} with distinct entoconids, no paraconids, and relatively large metaconids; a more rectangular P_4 with a protolophid, no premetacristid or hypolophid, a relatively narrow talonid, and a centrally placed hypoconid; lower molars with four roots, relatively small hypoconulids, no postentoconulids, weak buccal cingulids, more basally inflated buccal margins; and a significant "step" from the occlusal surfaces of the cheek teeth down to the dorsal aspect of the mandibular symphysis, which only extends back to P_3 (as opposed to~P_4). Differs from early deinotheriids such as *Prodeinotherium* (Harris 1973) in lacking a tritolophid on M_1 and a well-developed entoconid and hypolophid on P_4, and in having anteriorly directed lower incisors and no ventral curvature of the mandibular symphysis.

Omanitherium dhofarensis, new species
Etymology For the Dhofar region of Oman where the type specimen was found.
Holotype SQU-290, mandible with right I_2, P_3–M_2, and partial M_3, and left P_4–M_2 and erupting M_3.
Type locality DPP-2010-1; UTM coordinates 39Q, 767804.80 m E, 1878508.74 mN
Formation and age Shizar Member of the Ashawq Formation, earliest Oligocene in age.
Diagnosis As for genus.

Description

SQU-290 consists of three major parts (Fig. 2)—a left tooth row with erupted P_4–M_2, erupting M_3, and the coronoid process; a right tooth row with erupted P_3–M_2 and the trigonid of an erupting M_3; and a symphyseal fragment with erupting partial left and complete right incisors, which we provisionally interpret as I_2s. The bases of both corpora are missing, but the walls of the right corpus are tightly curved in the coronal plane and approach each other ventrally just behind M_2, suggesting a corpus depth of ~53 mm at this point. This measurement suggests that the corpus was quite shallow (i.e., corpus depth at M_2 would have been only about 1.35 times the width of M_2), though depth might have increased with age.
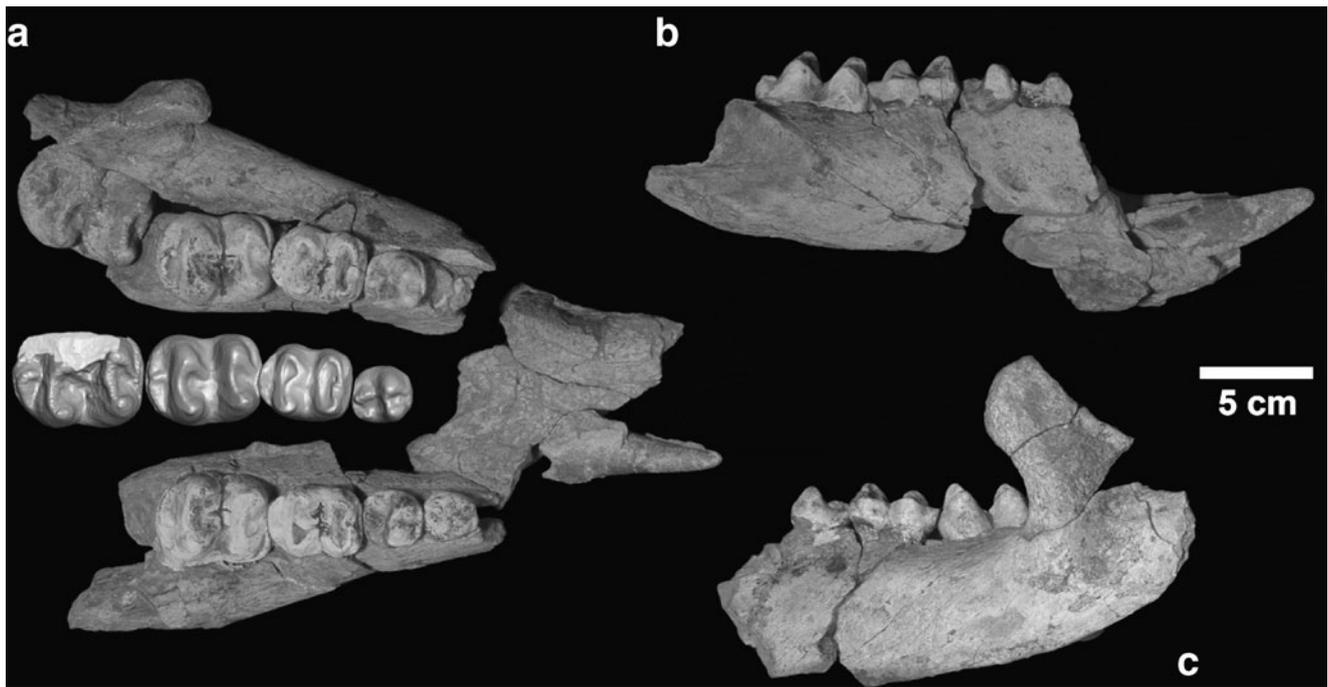
Fig. 2 SQU-290, holotype of *Omanitherium dhofarensis*, new genus and species. **a** Occlusal view, showing roots of left P₃, crowns of left P₄–M₂, left M₃ in crypt, erupting right I₂, erupted P₃–M₂, and 3D reconstruction of left P₄–M₃ based on a CT scan of a polyester cast; **b** lateral view of right side; **c** lateral side of left side

A broken surface on the right and posterior aspect of the symphyseal fragment matches a complementary surface on the anteroventral aspect of the right mandibular corpus; this contact reveals that there was a significant "step" from the occlusal surface of P₂ down to the dorsal surface of the symphyseal region. This configuration is also indicated by the morphology of the dorsal bony ridge surrounding the lingual aspect of the erupting left I₂, which curves dorsally to form the anterior part of the mesial P₂ alveolus. The symphysis is fully fused and extends back to the level of P₃.

Much of the crown of the left I₂ is missing, but the right I₂ is complete. It is clear that both teeth were completely unerupted because bone still adheres to the mesiobuccal surface of the right I₂ crown, and a thick layer of bone (maximum thickness of ~13 mm at the broken margin) that covers the lingual surface of the left I₂ extends far anteriorly and likely would have completely surrounded the crown of that tooth (see Online Resource 1 of the Electronic supplementary material). This dental eruption pattern matches that which has been documented in *Moeritherium*, in which the I₂ erupts at about the same time as the M₃ (Andrews 1906; Tassy 1987). The tooth is essentially conical but somewhat compressed mesiodistally (MD length 24 mm, BL width 29.80 mm), differing from the more lanceolate form of the I₂ in some early proboscideans; the crown is completely surrounded by smooth enamel that lacks crenulations or serrations. In lateral view, the long axis of the crown is almost parallel to the occlusal surface of the cheek teeth

(Fig. 2, b). Because the I₂s are completely unerupted in SQU-290, adult *Omanitherium* individuals must have had fairly elongate mandibular symphyses. We estimate that symphyseal length in SQU-290 would have been at least two thirds the length of its premolar–molar toothrow (Fig. 3), and possibly much longer.

The P₂ crown is not known, but an alveolus for the tooth's distal root is present anterior to the mesial root of the P₃ on the right side, and the anterior part of the alveolus for the mesial root of the left P₂ is present on the symphyseal fragment. The former alveolus is quite short mesiodistally (~6 mm long), and the tooth was likely considerably smaller than P₃. The P₃ crown (MD=22.40 mm, BL=20.85 mm) is
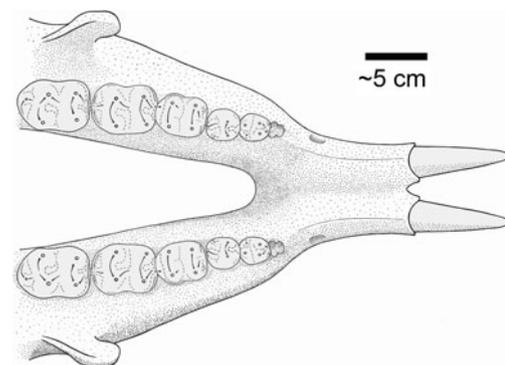

Fig. 3 Hypothetical reconstruction of the SQU-290 mandible with incisors and M₃s fully erupted, showing inferred elongate symphysis and gap between right and left I₂

only present on the right side and has a large metaconid that is approximately equal in height and volume to the proto-conid cusp; the two cusps are fused through most of their height. The talonid bears a hypoconid that is greater than half the height of the protoconid, as well as a slightly smaller entoconid that is separated from the hypoconid by a shallow sulcus. Paraconid cusps are absent on all of the lower teeth, and both P_3 and P_4 bear rounded paracristids that descend mesiolingually from the protoconids to meet mesial cingulids. The P_4 (right—MD=25.60 mm, BL=24.90 mm; left—MD=26.40 mm, BL=24.80 mm) is similar in morphology to P_3 but has taller trigonid cusps, a distinct protocristid connecting the metaconid and protoconid, and a relatively small entoconid. The hypoconid is tall and blends with a rounded cristid obliqua that terminates lingual to the apex of the protoconid.

All of the lower molars are similar in overall appearance in being fully bilophodont, with concave proto- and hypo-lophids connecting the primary mesial and distal cusps, respectively. There is a marked increase in molar size from M_1 to M_3 (dimensions in millimeters—right M_1, MD=39.85, BL=31.90; left M_1, MD=39.50, BL=32.15; right M_2, MD=50.75, BL=39.65; left M_2, MD=48.60, BL=39.30; left M_3, MD=61.70, BL=43.60). All of the molars bear short paracristids that terminate along mesial cingulids. There are no buccal cingulids. There are no premetacristid or entocristid crests on any of the lower molars, but the oblique cristids are trenchant on M_{2-3}. A small hypoconulid projects just above the distal cingulid on M_2, but is relatively large on M_3, being about half the height of the entoconid. A hypoconulid cusp might also have been present on the more worn M_1s, but none of the lower molars bear postentoconulids. The M_3 was unerupted at the time of death, with no roots formed; the buccal aspect of the tooth is covered by bone that has broken off from the lateral wall of the crypt postdepositionally. This unworn tooth bears several mammillons along the proto- and hypolophid, the para-cristid, the cristid obliqua, the mesial cingulum, and the hypocristid; it is possible that similar cuspules were originally present on M_{1-2}, but have been removed by wear.

The coronoid process arises from the corpus at about the same antero-posterior level as the M_2 hypolophid, and is anteriorly inclined. The posterior surface of the coronoid process thins to a sharp edge and so appears to be complete; the most ventral point of its preserved surface is remarkably low, indicating that there was a very deep mandibular notch. Two mental foramina are present on each side of the mandible: a relatively small (~5 mm in diameter) posterior mental foramen below the distal root of P_2 and a relatively large (~1 cm in diameter) anterior mental foramen a few centimeters anterior to the P_2. This pattern differs from that in "plesielephantiforms" and *Moeritherium*, which have

relatively small, and more posteriorly placed, mental foramina, but is similar to *Prodeinotherium* and primitive elephantiforms (Ferretti and Debruyne 2011). *Barytherium* appears to have a relatively large anterior mental foramen, but it is more posteriorly placed than in *Omanitherium*, dein-otheriids, and elephantiforms, the latter of which have enlarged anterior mental foramina inferior to the large diastema between the incisors and anterior premolar.

Phylogenetic position of *Omanitherium*

Parsimony analyses of the modified matrix of Seiffert (2010) recovered different arrangements of "plesielephantiform" genera depending on how certain multistate characters were treated. When some multistates were ordered and scaled, *Omanitherium* was placed as the sister group of *Barytherium*, followed by *Arcanotherium*; this [*Arcanotherium*, (*Barythe-rium*, *Omanitherium*)] clade formed the sister group of elephantiforms (see Online Resource 2 of the Electronic sup-plementary material). When the same multistate characters were treated as ordered but were not scaled, *Moeritherium* shifted from its more basal position in the former analysis to join *Arcanotherium*, *Barytherium*, and *Omanitherium* in a clade, within which relationships were unresolved (see Online Resource 2 of the Electronic supplementary material), though the Adams consensus of the four trees places *Omanitherium* with *Barytherium*. Finally, when all characters were treated as unordered and unscaled, *Omanitherium* was again placed as the sister group of *Barytherium*, but in an unresolved position relative to other "barytherioids" and elephantiforms (Online Resource 2 of the Electronic supplementary material). The Adams consensus of all the trees recovered by the three analyses (Fig. 4) reveals that *Omanitherium* was consistently placed in a clade with *Barytherium* in all of the analyses. These results held when molecular data were excluded and the relationships of extant taxa were constrained by a molecular scaffold that enforced the monophyly of Afroinsectivora (Macroscelidea+Afrosoricida), Afroinsecti-phillia (Tubulidentata+Afroinsectivora), and Atlantogenata (Afrotheria+Xenarthra)—with one exception: when all characters were unordered the strict consensus was more resolved, with a *Barytherium*–*Omanitherium* clade recovered as sister of elephantiforms. The monophyly of "Barytherioi-dea" was never recovered, and *Arcanotherium* was never placed exclusively as a sister group of *Numidotherium*, suggesting that the former genus should be considered valid as argued by Delmer (2009).

Discussion

Within the plesielephantiform grade, some authorities have recognized a superfamily Barytherioidea that includes three
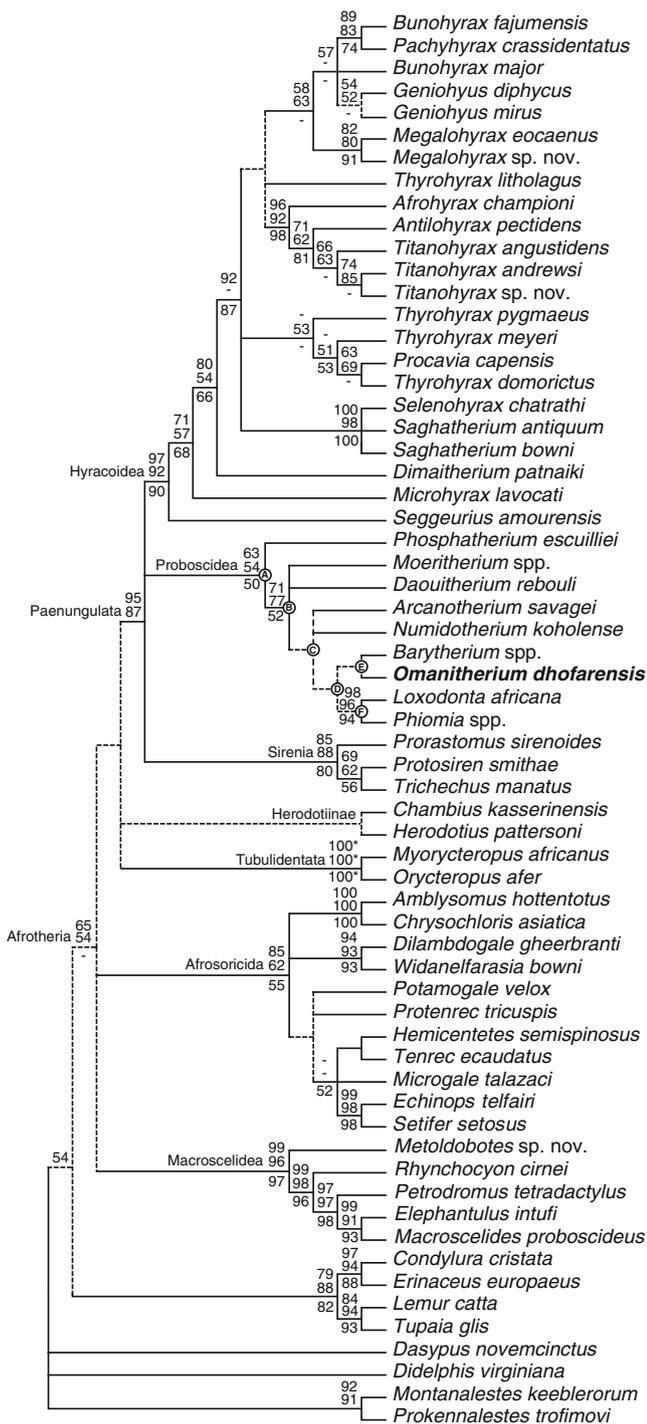
Fig. 4 Estimates of *Omanitherium*'s phylogenetic position within Proboscidea. Tree is an Adams consensus based on all trees recovered in three parsimony analyses of a modified version of the mixed molecular–morphological character matrix of Seiffert (2010), which now includes 18,369 nucleotide bases from 21 loci (three mtDNA genes and 20 nuclear genes), 10 chromosomal associations, eight SINEs, and 404 morphological and developmental characters. The complete matrix is available at www.morphobank.org. Values next to nodes represent bootstrap support (derived from 1,000 replicates) for, from *top* to *bottom*, analyses with (1) some multistate characters ordered but unscaled, (2) some multistate characters ordered and scaled, and (3) all characters unordered. *Dashes* ("–") indicate support <50%. *Dashed lines* are those that would break down in the strict consensus of trees derived from all three analyses. Morphological character support for nodes A–F is available in Online Resource 3 of the Electronic supplementary material

teeth and mandible of *Omanitherium* are morphologically intermediate between those of *Arcanotherium* and *Barytherium*. In its size and premolar morphology, *Omanitherium* closely resembles *Arcanotherium*, a form that is still known solely from the roughly contemporaneous Dor el-Talha locality in Libya (Savage 1969; Court 1995; Delmer 2009). *Arcanotherium* was initially considered to be a small species of *Barytherium* (Savage 1969; Harris 1978), but was later reassigned to *Numidotherium* (Court 1995) before being given its own genus name (Delmer 2009). The phylogenetic analyses presented here support Delmer's (2009) contention that *Arcanotherium* is more closely related to elephantiforms than is *Numidotherium*. *Omanitherium*'s varied placement relative to *Arcanotherium* in our phylogenetic analyses suggests that the features that these taxa share are plesiomorphic among derived "plesielephantiforms" and do not support a close relationship between the two genera. The relatively broad M_{2-3} and tall lophids of *Omanitherium* are, on the other hand, clearly derived relative to those of *Arcanotherium* and *Moeritherium*, and are most similar to those of *Barytherium* and deinotheriids. We provisionally place *Omanitherium* in the family Barytheriidae because the molar and mandibular morphology of *Omanitherium* closely matches that of *Barytherium*, and a close relationship of *Barytherium* and *Omanitherium* was consistently recovered across multiple assumption sets in our phylogenetic analyses.

The most surprising feature of *Omanitherium*'s dentition is its peculiar lower incisors, which differ from those of all Paleogene proboscideans in being distinctly conical and "tusk"-like and somewhat transversely (i.e., mesiodistally) compressed, rather than being buccolingually compressed and spatulate as in *Arcanotherium*, *Moeritherium*, and elephantiforms. The two incisors preserved in SQU-290 are separated by a large gap and, judging from their long axes, also would have been separated by a gap upon full eruption (Fig. 3). Using Delmer's (2009) proposed homologies for the incisors of early proboscideans, *Arcanotherium*,

genera with strongly lophodont molars: late Eocene and possibly early Oligocene *Barytherium* from Egypt and Libya (Andrews 1906; Delmer 2005), *Arcanotherium* from Libya (Court 1995; Delmer 2009), and early Eocene *Numidotherium* from Algeria (Sanders et al. 2010). Phylogenetic analyses nevertheless consistently suggest that Barytherioidea is, like Plesielephantiformes, not a natural group (Gheerbrant et al. 2005; Seiffert 2007; Delmer 2009). The lower cheek

Moeritherium, and elephantiforms have tightly apposed I_1s with long and straight mesial edges. Based in part on the large gap between *Omanitherium*'s preserved incisors, we identify these teeth as I_2s. There is no clear evidence from the preserved symphyseal region of *Omanitherium* for alveoli that might hold intervening or underlapping incisors, but this area is, however, badly damaged. Two additional partial incisors, slightly larger than those in SQU-290, were also recovered at DPP-2010-1, and these specimens present the same morphology as the incisors preserved in the type specimen. Because more than one individual is represented at DPP-2010-1, these could be either (1) I_2s of another, slightly larger or older individual; (2) I_1s of the individual represented by SQU-290 (though they appear to be too large to be accommodated in the space separating the two pre-served incisors); or (3) they could even be upper incisors; this cannot be determined without more complete material. If *Omanitherium* enlarged its I_2s and lost its I_1s entirely, this would represent a trend parallel to that seen in *Moeritherium*, which, uniquely among Eocene proboscideans, has an I_2 that is enlarged relative to I_1 (Andrews 1906; Matsumoto 1923) (but which, importantly, does not exhibit the derived conical tusk-like morphology of *Omanitherium*).

The isolated "barytherioid" incisor from the nearby Thaytiniti locality described by Thomas et al. (1989) resembles the I_1s of other early proboscideans and could conceivably represent an I_1 of *Omanitherium*. However, the Thaytiniti specimen is not only spatulate and bears lateral serrations but is much broader than the preserved I_2s of *Omanitherium*; if this is an I_1 of *O. dhofarensis*, the species would have combined radically different incisor morphologies in the same anterior dental battery, implying a bizarre pattern unlike anything that has been documented among early proboscideans and their close living and extinct afrotherian relatives. We currently consider it more likely that this incisor belongs to some other proboscidean species that lived at the same time and place.

Among non-elephantiform proboscideans for which the anterior dentition has been described, *Omanitherium*'s lower incisors most closely resemble those of Miocene deinotheriids such as *Prodeinotherium*, which are similarly conical and "tusk"-like, but differ in being distinctly curved (ventrally concave). This similarity is intriguing because the downturned condition seen in the earliest deinotheriids is unambiguously autapomorphic for that clade and logically must trace back to an anteriorly projecting condition similar to that seen in *Omanitherium*. *Barytherium*'s incisors have never been adequately figured and described, but the reconstruction of *B. grave* published by Sanders et al. (2010), based on Delmer's (2005) study of that material, suggests that its I_2 was probably lingually flattened and not conical as in *Omanitherium* and deinotheriids. Obviously, the lower incisors represent only one character complex that should be

considered for phylogenetic inference; the broad and lopho-dont molars of *Omanitherium* are fully consistent with a link to deinotheriids, but, importantly, *Omanitherium* differs from known deinotheriids and elephantiforms in displaying primitive features such as less molarized premolars and no tritolophid on M_1. For *Omanitherium* to be more closely related to deinotheriids than to elephantiforms, additional fossil evidence would be required to demonstrate that the latter two features were acquired convergently in these lineages. *Omanitherium*'s very reduced P_2 (judging from the size of the P_2 alveoli) and enlarged and anteriorly placed anterior mental foramen are additional derived features that might place the genus closer to the deinotheriid–elephantiform clade than *Moeritherium*.

The discovery of *Omanitherium* in the earliest Oligocene of the southern Arabian Peninsula, combined with the results of our phylogenetic analyses, clearly complicates the already controversial picture of elephantiform and dein-otheriid origins. The emerging consensus among students of early proboscidean evolution (Court 1995; Delmer 2009; Gheerbrant and Tassy 2009; Sanders et al. 2010) is that the highly specialized late Eocene/early Oligocene genus *Moeritherium* is more closely related to the deinotheriid–elephantiform clade than are any "barytherioids", whereas previously *Moeritherium* was considered to be quite basal in proboscidean phylogeny, and barytherioids were afforded a more central role in elephantiform and/or deinotheriid origins (Mahboubi et al. 1984, 1986; Domning et al. 1986). The hypothesis of a more nested position for *Moeritherium* is based in part on the recognition that the lophodonty of bar-ytherioids is primitive within Proboscidea (Gheerbrant et al. 2005), and that a *Moeritherium*–elephantiform–deinotheriid clade might trace back to a "bunolophodont" ancestor (Sanders et al. 2004). However, the oldest described *Moeritherium* specimens are more lophodont than later species (Delmer et al. 2006), suggesting that evolution of bunolophodonty in the *Moeritherium* lineage might have occurred in parallel with that in elephantiforms. The auditory features that appear to link *Moeritherium* to elephantiforms to the exclusion of *Numidotherium* (Court 1994) are not yet known in barytheriids.

The nested position proposed for *Moeritherium* also poses a temporal paradox. The highly distinctive cranial and postcranial morphology of *Moeritherium*, which differs dramatically from that of the oldest elephantiforms and deinotheriids, has now been documented at the 37 Ma Locality BQ-2 in the Fayum region of northern Egypt, suggesting an extensive prior phase of independent evo-lution for the *Moeritherium* lineage that would surely extend back well into the middle Eocene (if not much earlier). In strong contrast, the oldest elephantiforms do not appear until the early Oligocene, while deinotheriids are not known until the late Oligocene (Sanders et al.

2004; but see Delmer 2009; Rasmussen and Gutierrez 2009); if the deinotheriid–elephantiform clade's closest known relative is *Moeritherium*, then a considerable ghost lineage is implied, also stretching back well into the middle Eocene. In light of these considerations, we suggest that barytheriids—which are now known to have been distributed broadly across northern Afro-Arabia through the later Paleogene—should once again be seriously considered as a possible source group for deinotheriids. This hypothesis is consistent with the basal position for *Moeritherium* recovered in most of our analyses of the Seiffert matrix (2010) following addition of *Arcanotherium* and *Omanitherium* (Fig. 4, a). The situation should be further clarified by analysis of the entire *Barytherium* sample from Dor el-Talha, and analysis and description of new *Barytherium* and *Moeritherium* material from the 37 Ma Birket Qarun localities in Egypt (Sanders et al. 2010).

The *Omanitherium*-bearing sediments that are preserved at the base of the Shizar Member document deposition in near-shore tidal and subtidal environments during an early Oligocene transgressive phase, and are similar to those that have yielded remains of *Barytherium* and *Moeritherium* in older deposits that occur along the southern rim of the Tethys Sea in northern Africa. The tooth enamel of *Barytherium* and *Moeritherium* show low and restricted $\delta^{18}O$ values that are consistent with these taxa having been at least semi-aquatic (Liu et al. 2008; Clementz et al. 2008), while their $\delta^{13}C$ values and dental functional morphology suggest that these forms consumed freshwater plants (Liu et al. 2008). Judging from the very similar molar morphology of *Barytherium* and *Omanitherium*, it is likely that these forms had similar feeding habits, while the depositional environment of the Shizar Member is at least consistent with the possibility that *Omanitherium* was also an amphibious form. A larger sample of *Omanitherium* remains will be required to further test the intriguing hypothesis that basal proboscideans were ancestrally amphibious (Liu et al. 2008).

References

Andrews CW (1906) A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt; based on the collection of the Egyptian Government in the Geological Museum, Cairo, and on the collection in the British Museum (Natural History). Trustees of the British Museum (Natural History), London

Behrensmeyer AK, Potts R, Plummer T, Tauxe L, Opdyke N, Jorstad T (1995) The Pleistocene locality of Kanjera, western Kenya—stratigraphy, chronology, and paleoenvironments. J Hum Evol 29(3):247–274

Clementz MT, Holroyd PA, Koch PL (2008) Identifying aquatic habits of herbivorous mammals through stable isotope analysis. Palaios 23:574–585

Court N (1994) The periotic of *Moeritherium* (Mammalia, Proboscidea): homology or homoplasy in the ear region of Tethytheria McKenna, 1975? Zool J Linn Soc 112:13–28

Court N (1995) A new species of *Numidotherium* (Mammalia: Proboscidea) from the Eocene of Libya and the early phylogeny of the Proboscidea. J Vert Paleontol 15(3):650–671

Delmer C (2005) The first stages in the differentiation of proboscideans: the role of *Barytherium grave* from Libya (Translated from French). Ph.D., Museum National d'Histoire Naturelle, Paris

Delmer C (2009) Reassessment of the generic attribution of *Numidotherium savagei* and the homologies of lower incisors in proboscideans. Acta Palaeont Pol 54:561–580

Delmer C, Mahboubi M, Tabuce R, Tassy P (2006) A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: new perspectives on the ancestral morphotype of the genus. Palaeontology 49:421–434

Domning D, Ray CE, McKenna MC (1986) Two new Oligocene desmostylians and a discussion of tethytherian systematics. Smithson Contrib Paleobiol 59:1–56

Ferretti MP, Debruyne R (2011) Anatomy and phylogenetic value of the mandibular and coronoid canals and their associated foramina in proboscideans (Mammalia). Zool J Linn Soc 161:391–413

Gheerbrant E (2009) Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. Proc Natl Acad Sci USA 106:10717–10721

Gheerbrant E, Tassy P (2009) L'origine et l'évolution des éléphants. Comptes Rendus Palevol 8:281–294

Gheerbrant E, Sudre J, Capetta H, Iarochène M, Amaghzaz M, Bouya B (2002) A new large mammal from the Ypresian of Morocco: evidence of surprising diversity of early proboscideans. Acta Palaeont Pol 47(3):493–506

Gheerbrant E, Sudre J, Tassy P, Amaghzaz M, Bouya B, Iarochene M (2005) New data on *Phosphatherium escuilliei* (Mammalia, Proboscidea) from the early Eocene of Morocco, and its impact on the phylogeny of Proboscidea and lophodont ungulates (Translated from French). Geodiversitas 27(2):239–333

Harris JM (1973) *Prodeinotherium* from Gebel Zelten, Libya. Bull Brit Mus Nat Hist (Geol) 23:211–274

Harris JM (1978) Deinotherioidea and Barytherioidea. In: Maglio VJ, Cooke HBS (eds) Evolution of African mammals. Harvard University Press, Cambridge, pp 315–332

Liu AGSC, Seiffert ER, Simons EL (2008) Stable isotope evidence for an amphibious phase in early proboscidean evolution. Proc Natl Acad Sci USA 105(15):5786–5791

Mahboubi M, Ameur R, Crochet JY, Jaeger JJ (1984) Earliest known proboscidean from early Eocene of north-west Africa. Nature 308:543–544

Mahboubi M, Ameur R, Crochet J-Y, Jaeger J-J (1986) El Kohol (Saharan Atlas, Algeria): a new Eocene mammal locality in northwestern Africa. Palaeontographica, Abt A 192:15–49

Matsumoto H (1923) A contribution to the knowledge of *Moeritherium*. Bull Am Mus Nat Hist 48:97–139

Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, Teeling E, Ryder OA, Stanhope MJ, de Jong WW, Springer MS (2001) Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294:2348–2351

Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W (2007) Using genomic data to unravel the root of the placental mammal phylogeny. Genome Res 17:413–421

Noubhani A, Hautier L, Jaeger J-J, Mahboubi M, Tabuce R (2008) Dental and cranial variability of *Numidotherium koholense* (Mammalia, Proboscidea) from El Kohol, Eocene, Algeria. Geobios 41:515–531. doi:10.1016/j.geobios.2007.09.002

Osborn HF (1936) Proboscidea: a monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. I: Moeritherioidea, Deinotherioidea, Mastodontoidea. The American Museum Press, New York

Rasmussen DT, Gutierrez M (2009) A mammalian fauna from the late Oligocene of northwestern Kenya. Palaeontographica, Abt A 288:1–52

Roger J, Sen S, Thomas H, Cavelier C, Al Sulaimani Z (1993) Stratigraphic, paleomagnetic and paleoenvironmental study of the early Oligocene vertebrate locality of Taqah (Dhofar, Sultanate of Oman). Newsl Stratigr 28(2/3):93–119

Sanders WJ, Rasmussen DT, Kappelman J (2004) New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. Acta Palaeont Pol 49:365–392

Sanders WJ, Gheerbrant E, Harris JM, Saegusa H, Delmer C (2010) Proboscidea. In: Werdelin L, Sanders WJ (eds) Cenozoic mammals of Africa. University of California Press, Berkeley, pp 161–251

Savage RJG (1969) Early Tertiary mammal locality in southern Libya. Proc Geol Soc Lond 1657:167–171

Seiffert ER (2006) Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. Proc Natl Acad Sci USA 103:5000–5005

Seiffert ER (2007) A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. BMC Evol Biol 7:224

Seiffert ER (2010) The oldest and youngest records of afrosoricid placentals from the Fayum Depression of northern Egypt. Acta Palaeont Pol 55(4):599–616. doi:10.4202/app.2010.0023

Swofford DL (1998) PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4. Sinauer Associates, Sunderland

Tassy P (1987) A hypothesis on the homology of proboscidean tusks based on paleontological data. Am Mus Novit 2895:1–18

Thomas H, Roger J, Sen S, Boudillon-de-Grissac C, Al-Sulaimani Z (1989) Découverte de Vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). Geobios 22(1):101–120