FOSSIL IMPRINT • vol. 73 • 2017 • no. 3–4 • pp. 300–321
(formerly ACTA MUSEI NATIONALIS PRAGAE, Series B – Historia Naturalis)

NATIONAL MUSEUM

LARGE MAMMALS FROM THE RUPELIAN OF OMAN – RECENT FINDS

> Animals engage in a struggle for existence; for resources,
> to avoid being eaten and to breed. Environmental factors
> influence organisms to develop new characteristics to
> ensure survival, thus transforming into new species.
> Animals that survive to breed can pass on their successful
> characteristics to offspring.
>
> Al-Jahiz, The Book of Animals, 845 CE
> (translated from the Arabic)

> تدخل الحيوانات صراعا من أجل الحياة: من
> أجل المصادر مثلا، أو بغية تجنب الافتراس
> من قبل الحيوانات الأخرى، أو من أجل التكاثر،
> بإمكان العوامل البيئية أن تؤثر على الكائنات
> الحية لتطور صفات جديدة تساعد على النجاة
> وتؤدي إلى تحولها إلى أنواع حية أخرى، إن
> الكائنات الحية التي تتمكن من البقاء تستطيع
> التكاثر؛ مما يؤدي إلى انتقال تلك الصفات
> المميزة إلى الذُّرِية

MOHAMMED AL-KINDI[1], MARTIN PICKFORD[2,*], YUSOUF AL-SINANI[3], IBRAHIM AL-ISMAILI[4], AXEL HARTMAN[5], ALAN HEWARD[6]

[1] Earth Sciences Consultancy Centre, P.O. Box 979, Nizwa, P.C. 611, Sultanate of Oman; e-mail: malkindi@gmail.com.
[2] Sorbonne Universités – CR2P, MNHN, CNRS, UPMC – Paris VI, 8, rue Buffon, 75005, Paris, France; e-mail: martin.pickford@mnhn.fr.
[3] Petroleum Development Oman LLC, P. O. Box 81, Muscat, P.C. 100, Sultanate of Oman; e-mail: Yousuf.Sinani@pdo.co.om.
[4] Vision Advanced Petroleum Solutions, L.L.C. Muscat, Sultanate of Oman; e-mail: ibrahim.ismaili@gmail.com.
[5] Shell International Exploration and Production B.V. The Hague, The Netherlands; e-mail: axel.hartman@gmail.com.
[6] 23 Croftdown Court, Malvern, The United Kingdom; e-mail: alan@midfarm.demon.co.uk.
*corresponding author

Al-Kindi, M., Pickford, M., Al-Sinani, Y., Al-Ismaili, I., Hartman, A., Heward, A. (2017): Large Mammals from the Rupelian of Oman – Recent Finds. – Fossil Imprint, 73(3-4): 300–321, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: The 2017 field survey of the Ashawq Formation, Dhofar, Oman, resulted in the collection of large mammal remains, most of which belong to Afrotheria, but with one artiodactyl lineage indicating the possibility of dispersal links with Eurasia. The new fossil remains increase our knowledge about the dental anatomy of the endemic lophodont proboscidean genus *Omanitherium*, revealing, in particular, that it possessed two pairs of lower incisors. For the first time, a palaeomastodont is recorded from the Arabian Peninsula. Additional remains of *Arsinoitherium*, a hyracoid and an anthracothere from the formation are described.

Key words: Early Oligocene, *Arsinoitherium*, *Bunohyrax*, *Omanitherium*, *Palaeomastodon*, *Bothriogenys*, Arabian Peninsula

Received: April 12, 2017 | Accepted: September 22, 2017 | Issued: December 31, 2017

Introduction

The Palaeogene fossil record of the Arabian Peninsula is of interest for several reasons, not least of which is its geographic position in the northeastern part of the Afro-Arabian land mass, south of the Tethys Seaway but not far from Asia to the northeast and from Europe to the northwest. In addition to the physical barrier of the Tethys Seaway that stood between the northern land mass and Afro-Arabia during the Eo-Oligocene, which tended to hinder dispersal of land mammals between the two continental land masses, there was a latitudinal effect which possibly played a role in restricting biotic interchanges, just as it does today, with the boreal and colder zones in the latitudes north of 30° N, and the Ethiopian sub-tropical and tropical zones to the south of 30° N. As currently understood, the affinities of the Rupelian terrestrial fauna of the Arabian Peninsula lie predominantly with those of the rest of Africa, with few signs of interchange with Eurasia having occurred, the most obvious being the influx of anthracotheres and primates into Africa from Eurasia and, in the opposite sense, the dispersal of the hyracoid *Geniohyus* ANDREWS, 1904, from Africa to Asia (Pickford 1986b).

Previous work on the large fossil mammals of the Arabian Peninsula has resulted in the description of proboscideans, arsinoitheres and anthracotheres, but the available fossils

DE G DE GRUYTER OPEN DOI 10.2478/if-2017-0017

are limited in diversity and quantity, and because of this, interpretations of the taxonomy, systematics and phylogeny of some of the taxa remain ambiguous or incomplete (Seiffert et al. 2012, Zalmout et al. 2012, Pickford 2015a, b, c). Medium-sized mammals are generally poorly represented in the peninsula, but include a diversity of primates (Thomas et al. 1991, Pickford and Thomas 1994, Zalmout et al. 2010) and hyracoids (Pickford et al. 1994), many of which remain unidentified on account of the fact that most of the fossils comprise isolated or fragmentary teeth. Fossils of small mammals are relatively common (bats – Sigé et al. 1994; small primates – Gheerbrant et al. 1993, 1995; marsupials – Crochet et al. 1992). Insectivores and rodents are common in the deposits, but remain to be published.

Fossil mammals in the Ashawq Formation are associated with invertebrates and lower vertebrates (Mollusca – Pickford et al. 2014, Harzhauser et al. 2016; Pisces – Otero and Gayet 2001), which confirm the presence of freshwater and brackish-water palaeoecosytems in or near the regions in which the mammals lived.

Because so few Palaeogene large mammal fossils have been described from the Arabian Peninsula, recent discoveries in the Dhofar Governorate of Oman are important. The fossils were collected during fieldwork in January 2017, and are curated at the Oman Natural History Museum, Muscat.

Taphonomical aspects

The marls of the Ashawq Formation show signs of intensive trampling and other forms of bioturbation, such as gastropods burrowing through the sediment. A consequence of this biotic activity is that many of the gastropod shells and other fossils are broken, and mammalian remains are scattered and generally isolated from each other. It is not possible to determine whether the mammal specimens were transported post-mortem, because there has been alteration of the surface of the bones and teeth by gypsum-attack. During the various surveys, no rich concentration of bones and teeth were identified, although some patches of sediment yielded quite a few vertebrate fossils. Many outcrops are devoid of mammalian remains, even where there are abundant gastropods.

At the *Omanitherium* type locality, the fossil mammals occur in gypsiferous marls, and as a result, many of the dental specimens have been damaged by gypsum growth, which has partly destroyed the enamel and dentine.

When the mammal fossils erode out of the sediments, they tend to break into fragments, due to daily cycles of temperature change (repetitive thermal shocks), and they obtain a glossy surface (desert varnish), which can make them difficult to distinguish from stones covered in similar varnish.

Geological and stratigraphic contexts

The study area is located in the southern part of the Governorate of Dhofar, in South Oman. It is located on the northern side of what is known as Jebel al Qamar (“Moon” Mountain). The al Qamar Mountain is a broad monoclinal plateau that dips gently between 10° and 15° to the NNW. Palaeogene and Neogene deposits of primarily whitish bioclastic or biomicritic limestone and yellow or green marl cover most of the area (Text-figs 3–5). These facies were deposited in alternating mixed carbonate shelf and lagoonal environments. Older Mesozoic and Palaeozoic sediments are exposed along the eastern edge of the plateau, along a 1,000 m tall fault scarp that faces south towards the Indian Ocean, forming a sharp boundary between land and sea. The fault is parallel to the Gulf of Aden’s spreading ridge and its subsidiary parallel faults, and has likely been active since the end of the Palaeogene, following the opening of the Gulf of Aden. Ever since, this part of Oman has formed a passive margin of the rift system in the Gulf of Aden.

The area of interest for Palaeogene mammals comprises the north-western zone of Jebel al Qamar (Text-figs 1, 2). This area is known as Aidum (also spelled Aydim), and it includes a network of wadis that drain towards the north, including Wadi Ashawq. It is an arid desert with a few small settlements, such as Thaytiniti.

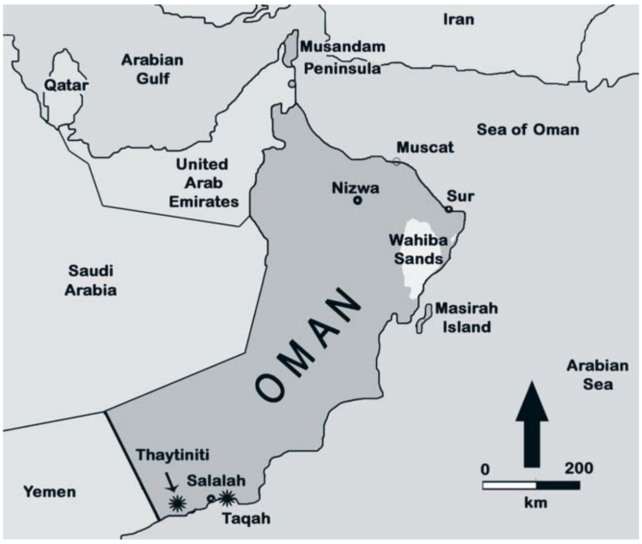
Numerous trans-tensional faults, trending NE-SW, bisect the area (Roger et al. 1989, Lepvrier et al. 2002). These were probably mostly active during the Late Palaeogene and Early Neogene, during the opening of the Gulf of Aden, as only minor faulting is observed to affect the Middle Miocene and Pliocene outcrops in the area (Platel and Roger 1992, Thomas et al. 1992, 1999).

On the basis of the molluscan faunas, Pickford et al. (2014) demonstrated that the Rupelian deposits at Taqah (25 m a.s.l., east of Salalah) and Thaytiniti (970 m a.s.l., west of Salalah) accumulated near sea-level, and that subsequent tectonic activity in the Dhofar Region uplifted the deposits in the Aydim area, leaving the deposits on the downthrown side of the fault at Taqah near sea-level. This evidence constrains the age of the Jebel al Qamar escarpment fault activity: most of the relief must be due to post-Rupelian tectonic activity.

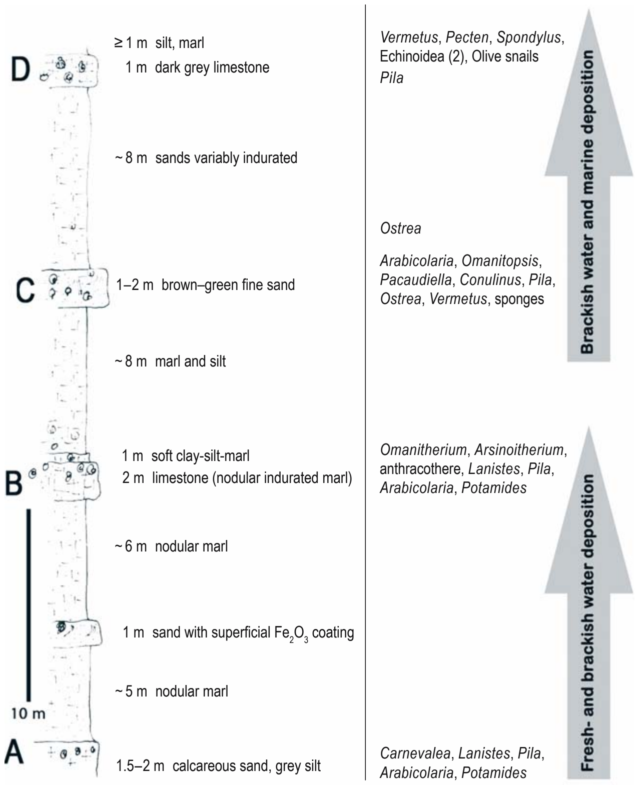
The fossils described in this study were found in the lower sections of the Early Oligocene to Middle Oligocene Ashawq Formation, which comprises the middle formation of the Dhofar Group, between the underlying Zalumah Formation and the overlying Mughsayl Formation. The Ashawq Formation is subdivided into two members which have different lithologies. The lower one is known as the Shizr Member (also spelled Shizar). Shizr is dominated by thick white to greenish units of marl, silt and sand interbedded with thinner beds of biomicritic limestone, deposited in alternating supratidal, lagoonal and tidal flat environments. In contrast, the overlying Nakhlit Member is comprised predominantly of well-bedded and massive white limestone that represents shallow-marine shelf carbonates, often rich in *Nummulites*. Overall, the Ashawq Formation was most likely deposited in a transgressive system tract, with more continental deposits in the lower part and more marine influence in the upper part of the section.

There is general agreement that the mammal-bearing deposits in the Thaytiniti area and at Taqah are Early Oligocene (Rupelian), on the basis of the marine micro- and macrofaunas associated with subjacent strata (Thomas et al. 1992, 1999, Seiffert 2010), but there are slight differences of opinion concerning correlations to strata in the Fayum, Egypt, (Pickford et al. 1994, Seiffert 2010), where correlations to the stratigraphic column are based on marine faunas, radioisotopic dates on basalts and palaeomagnetism. Sanders et al. (2010b) correlated Thaytiniti to the Late Eocene (Priabonian), and estimated the age of the Shizr Member to be 33.7–33.3 Ma (Seiffert 2006). However, the differences of opinion are not important in the context of the present study. It is noted, however, that the fossil mammals in the Ashawq Formation occur at various stratigraphic levels within the unit; the Thaytiniti site excavated by Thomas et al. (1992), for example, being ca. 40 metres higher in the succession than the *Omanitherium* type locality.

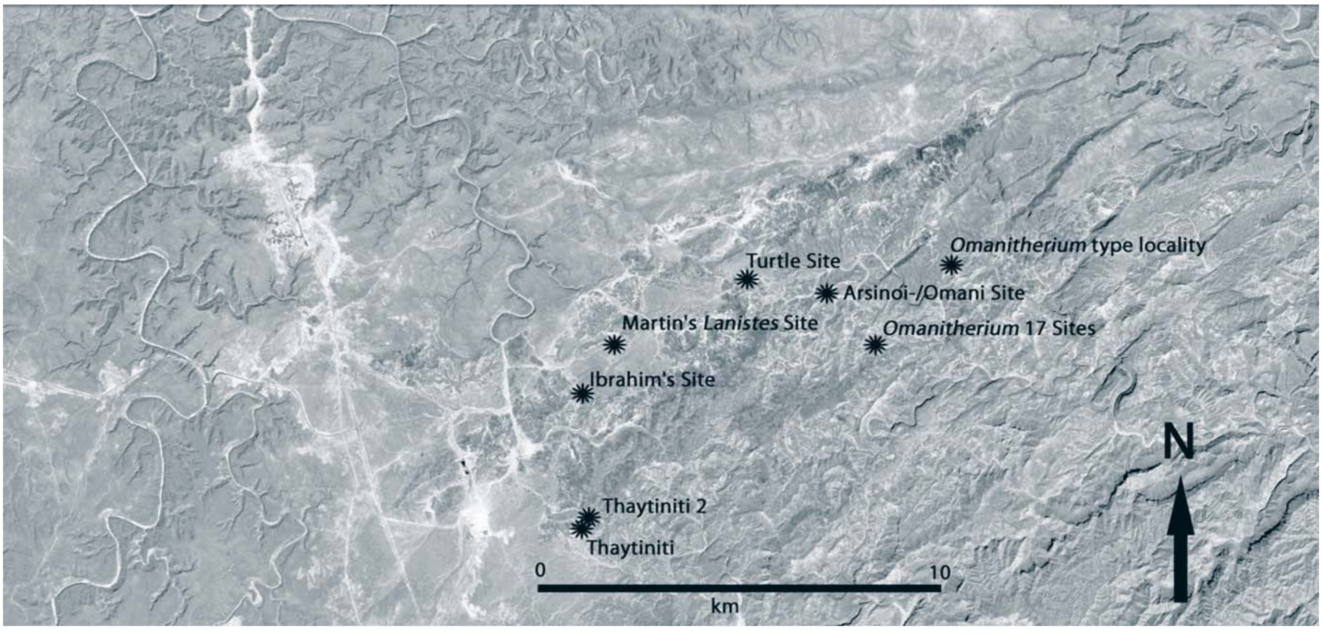
The Shizr Member has been a focus of palaeontological research in past years, primarily because of the rich and diverse macrofaunal remains that accumulated during the



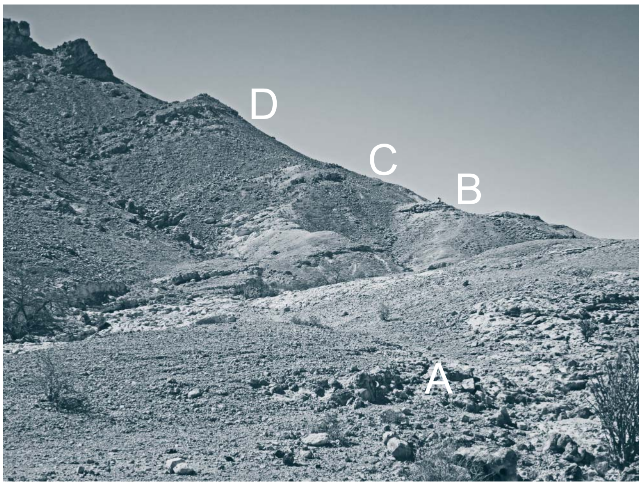
Text-fig. 1. Location of fossiliferous localities in the Ashawq Formation in south-western Oman (the star labelled Thaytiniti shows the area depicted in Text-fig. 2).



Text-fig. 3. Stratigraphic section through part of the Ashawq Formation at the *Omanitherium* type locality, Dhofar Governorate, Oman. Beds A–D are indurated cliff-forming strata identified in the accompanying field photographs (Text-figs 4, 5). Note the increase in marine influence as one ascends through the section, the fauna in Beds A and B being dominated by freshwater molluscs and land snails, with few brackish water specimens, whereas the biota in Bed D is frankly marine with a single specimen of the freshwater snail *Pila*. Bed C yielded *Vermetus*, oysters and sponges, but also contains abundant land snails and a low diversity of freshwater gastropods.



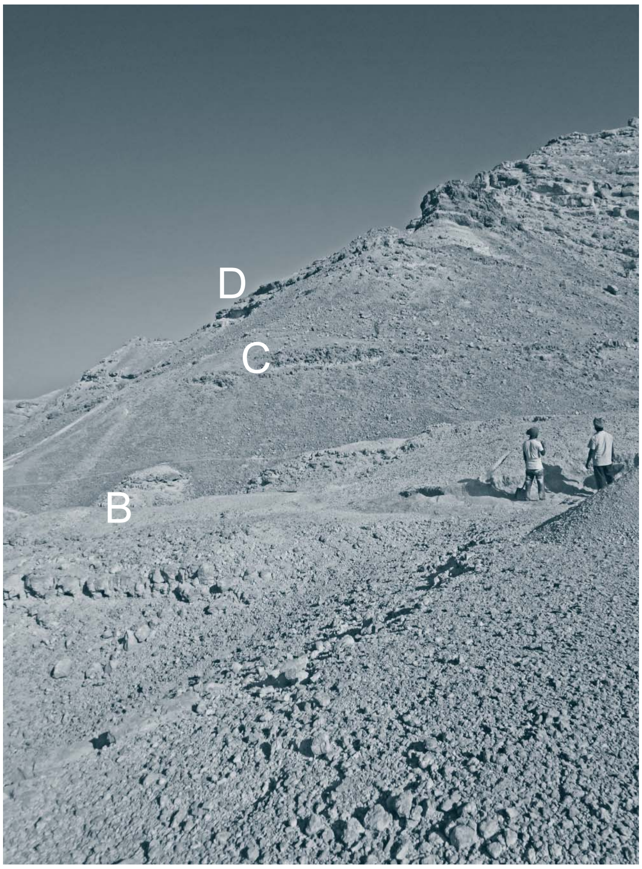
Text-fig. 2. Fossiliferous localities in the Ashawq Formation north and north-east of Thaytiniti, Dhofar Governorate, Oman (for latitude, longitude and altitude, see App. 1). The large white area either side of the north-south road is the village of Aydim (map modified from Google Earth).



Text-fig. 4. **Measured section at the *Omanitherium* type locality. A–D are indurated beds highlighted in the stratigraphic section (figure seated on outcrop B provides a scale) (see Text-fig. 3).**

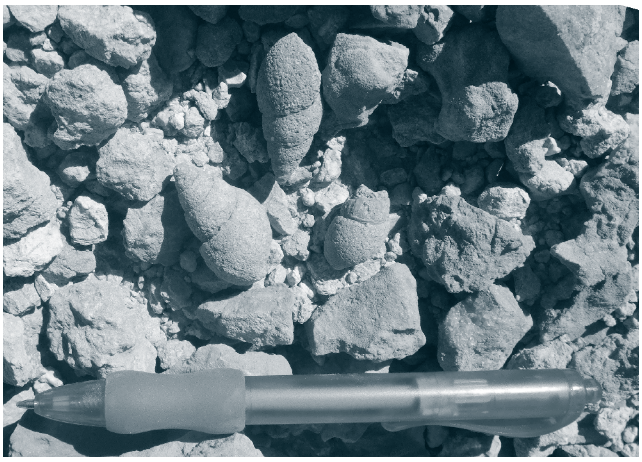
transgression event of the Ashawq Formation (Platel and Roger 1992, Roger et al. 1992, 1994a, b). The alternating sequences of clastic and carbonate beds of the formation contain *Nummulites*, and numerous types of gastropods (Text-figs 6, 7), bivalves, echinoids, sponges, corals, fish remains and other vertebrate bones, the latter including turtles, crocodiles, proboscideans, primates, anthracotheriids, *Arsinoitherium*, hyracoids, bats and rodents (e.g. Thomas et al. 1989, 1991, Roger et al. 1993, Otero and Gayet 2001, Al-Sayigh et al. 2008, Seiffert et al. 2012, Pickford 2015a, b, c, Sigé et al. 1994).

The research done on the Oligocene mammals and other vertebrates in the Dhofar area has provided new understanding of the evolution of these Oligocene mammals and the environment in which they lived. The area continues to yield fossils of a diversity of macro- and microfaunas, and several new richly fossiliferous sites have been discovered (App. 1, 2).



Text-fig. 5. **Upper part of the stratigraphic section at the *Omanitherium* type locality. B–D correspond to the beds identified in the stratigraphic section (Text-fig. 3). The workers are excavating at the type locality.**

Text-fig. 6. **Shells of the sinistral, flat-topped, freshwater ampullariid *Carnevalea thaytinitiensis* in indurated sandy marl, Bed A in the stratigraphic section (the pen is 14.5 cm long).**



Text-fig. 7. **Steinkerns of the land snail *Arabicolaria omanensis* eroding from indurated dark green-brown sands of Bed C above the *Omanitherium* type locality (the pen is 14.5 cm long).**

Appendix 2 lists the fossils collected at the various sites in the Ashawq Formation during the 2017 field survey. It is noted that the large mammals described herein are intimately associated with land snails, freshwater molluscs, chelonians, crocodiles, lung fishes, and rare brackish-water molluscs (*Potamides*). It is concluded that the large mammals lived close to the coast.

Abbreviations and curation

Fossils mentioned in this paper are housed at several institutions:

MNHN – Muséum national d'Histoire naturelle, Paris
NHMUK – Natural History Museum of the United Kingdom, London
ONHM – Oman Natural History Museum, Muscat
SQU – Sultan Qaboos University, Muscat

For teeth, the following abbreviations are employed (see Pickford 2016, for dental nomenclature):

C/c – upper/lower canine, D/d – upper/lower deciduous cheek teeth, I/i – upper/lower incisor, M/m – upper/lower molars.

Systematic palaeontology

Order Embrithopoda Andrews, 1906
Family Arsinoitheriidae Andrews, 1904

Genus *Arsinoitherium* Beadnell, 1902a

Arsinoitherium andrewsi Lankester, 1903

Material. ONHM TN 2017-04, right p/2; ONHM TN 2017-06, right p/4; ONHM TN 2017-03, right m/3.

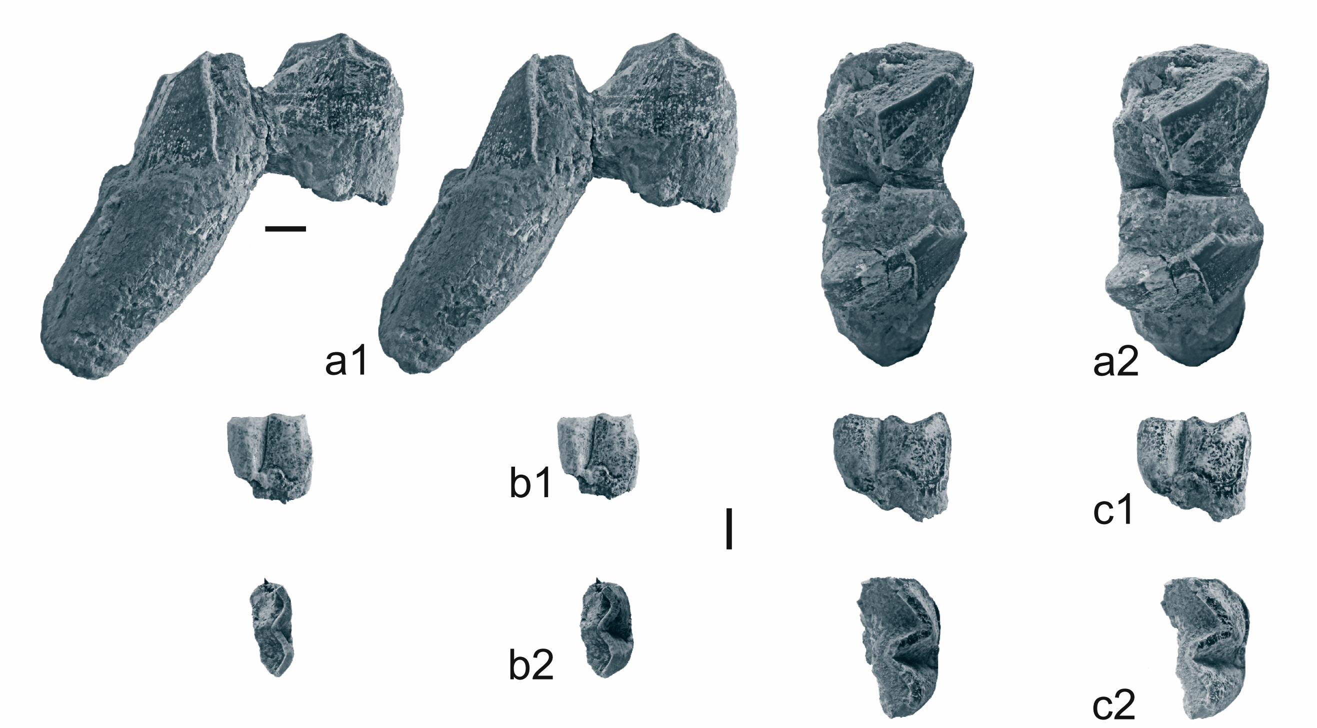
Description. Three embrithopod lower teeth were collected at the *Omanitherium* type locality (Tab. 1, Text-fig. 8). The moderately worn right p/2 and p/4 preserve only the ectolophids, which are w-shaped, with the central valley closer to the distal end than to the mesial end, the lingual sides of the teeth and the roots having been destroyed by gypsum crystal growth. On the buccal side of the tooth, there is a mesial cingulum that rises from the cervix towards the occlusal surface. The buccal valley slants distally as it descends from the occlusal surface towards the cervix. The roots are broken off.

Table 1. Measurements (in mm) of the teeth attributed to *Arsinoitherium andrewsi* from the *Omanitherium* type locality, Dhofar Governorate, Oman.

Catalogue n° and tooth	Mesio-distal length
ONHM TN 2017-04, right p/2	21.0
ONHM TN 2017-06, right p/4	29.0
ONHM TN 2017-03, right m/3	54.0

The right m/3 is heavily worn and lacks the lingual half as well as the mesial root, also damaged by gypsum growth. The distal root is massive and slants strongly to the rear, indicating that the tooth is the third molar. The crown is composed of two angular crescents with a deep central valley on the buccal side. The talonid is broken off, but its root base is preserved as a small shelf behind the distal lophid.

Discussion. There has been a long-standing tradition by which all the arsinoitheres from the Fayum, Egypt, have been interpreted to comprise a single species, *Arsinoitherium zittelli* Beadnell, 1902a (Beadnell 1902a, b, Sanders et al. 2010a), with the large range of variation being interpreted as a case of sexual dimorphism (Sanders et al. 2004). However, Pickford (2015a) considered that the range of morphological



Text-fig. 8. Lower teeth of *Arsinoitherium andrewsi* from the *Omanitherium* type locality, Ashawq Formation, Oman. a) ONHM TN 2017-03, right m/3, (a1 – stereo buccal view, a2 – stereo occlusal view); b) ONHM TN 2017-04, right p/2 (b1 – stereo buccal view, b2 – stereo occlusal view); c) ONHM TN 2017-06, right p/4 (c1 – stereo buccal view, c2 – stereo occlusal view) (scale bar 10 mm).

Text-fig. 9. Fragmentary left m/3 with reconstructed outline of a bunodont hyracoid from the Ashawq Formation. a) lingual view, b) stereo occlusal view (scale bar 10 mm).

variation in the available samples was too great to be encompassed by a single species, and he accordingly resurrected the species *Arsinoitherium andrewsi* Lankester, 1903, to which the Omani fossils show a strong resemblance (large talonid in the m/3, morphology of the P4/). The new fossils described herein accord with this interpretation, the form of the ectolophs of the lower premolars resembling those in the lower jaw attributed to *Arsinoitherium andrewsi* by Andrews (1906), and the probable presence of a talonid behind the second lophid of the m/3 (broken off but leaving a small shelf-like process above the root), which agrees with this species.

Order Hyracoidea Huxley, 1869
Family Geniohyidae Andrews, 1906

Genus cf. *Bunohyrax* Schlosser, 1910

Material. Isolated m/3 fragment (currently without accession number).

Description. A left m/3 fragment of a large hyracoid was found in the Ashawq Formation by the Thomas Expedition, but was never described. The specimen preserves a small part of the protoconid, the rear half of the metaconid, the complete entoconid, part of the hypoconulid, and the lingual half of the hypoconid (Text-fig. 9). The tooth would originally have been about 25.3 mm long by about 14.6 mm broad at the second lophid.

The entoconid has a pre-entocristid that leads mesially into the median transverse valley, separated at its termination from the end of the pre-hypocristid. The latter cristid is directed mesio-lingually from the apex of the hypoconid, and ends in the midline of the tooth. The entoconid has a second cristid reaching buccally towards the hypoconid, where it joins a short cristid leading lingually from the apex of the hypoconid. The post-entocristid is short and directed distally. There is a short cristid in the bucco-distal corner of the entoconid, which joins the post-hypocristid, closing off a shallow foveid between the entoconid and hypoconid. The pre-hypoconulid cristid reaches towards the end of the post-hypocristid, ending at its base. The enamel in the floor of the valley between the hypoconulid and the entoconid is coarsely wrinkled, whereas that covering the mesial walls of the metaconid and entoconid is lightly wrinkled. The mesial walls of the tooth are almost vertical.

Discussion. Among Hyracoidea, the tooth is morphologically closest to members of the family Geniohyidae, *Geniohyus* Andrews, 1904 and *Bunohyrax* Schlosser, 1910. In particular, the presence of four cristids in the entoconid, the presence of a fovea between the hypoconid and entoconid, and the wrinkled enamel all fit with members of this family. The steepness of the lingual wall of the crown pleads for affinities with *Bunohyrax* rather than with *Geniohyus*. The latter genus has sloping, slightly convex, lingual walls in the lower molars.

The Ashawq specimen is considerably smaller than *Geniohyus adiposum* (Forster-Cooper, 1924) from Bugti, Pakistan (Pickford 1986b). It has comparable dimensions to the Fayum, Egypt, species *Geniohyus mirus* Andrews, 1904 (Matsumoto 1926), *Bunohyrax fajumensis* Andrews, 1904, and *Bunohyrax affinis* Matsumoto, 1926 (the latter is likely a synonym of *Bunohyrax fajumensis*). Pickford (1986a) described a similar specimen from Malembe (5°19’S : 12°01’E) in Angola.

Pickford et al. (1994) listed three hyracoid taxa from Thaytiniti: an unidentified medium-sized species based on some upper molar fragments, and two small species, cf. *Saghatherium bowni* Rasmussen et Simons, 1991, and cf. *Thyrohyrax meyeri* Rasmussen et Simons, 1991, based on isolated teeth. The specimen described above could well represent the same taxon as the unidentified upper molar fragments from Thaytiniti.

The same authors listed two species of hyracoids from Taqah, east of Salalah: a medium-sized species similar to an un-named species from Quarry L41 in the Fayum, Egypt, and a smaller species, *Thyrohyrax meyeri*, also known at Quarry L41.

Order Proboscidea Illiger, 1811
Superfamily Numidotherioidea Shoshani et Tassy, 1992 new rank

Genus *Omanitherium* Seiffert, Nasir, Al-Harthy, Groenke, Kraatz, Stevens et Al-Sayigh, 2012

Omanitherium dhofarense Seiffert et al., 2012

Material. See Table 2.

Description. The fossils attributed to *Omanitherium* comprise 21 specimens out of 89 catalogue entries in the 2017 field catalogue (Tab. 2, Appendix 2), indicating that among the large mammals, this genus is dominant. Many of the specimens are broken pieces of mandibles and maxillae, and limb bone fragments, which yield little morphological information. There are also many enamel fragments. The following descriptions deal only with the more complete dental elements, comprising some rather complete lower incisors, and a reasonable sample of upper cheek teeth, which were poorly represented in previously available samples (Seiffert et al. 2012, Pickford 2015b).

ONHM TN 2017-19 is a damaged left i/1 with apical wear (Text-fig. 10). The section of the tooth is a compressed rectangle. The labial surface is almost complete and shows a shallow groove near the apex, positioned about one third of the distance from the mesial edge towards the distal margin. The labial surface is shallowly convex, almost flat; the mesial surface is at right angles to the labial one and measures about

8 mm from labial to lingual. The lingual surface is damaged, but remnants of enamel are preserved along the distal half, which shows that the lingual surface was originally covered in enamel, which is appreciably thinner than that on the labial side. The distal edge is damaged. The cervix is distinct labially, and rises towards the apex on the mesial side and then extends across the lingual side. The apex is somewhat damaged, so the exact shape of the wear facet cannot be determined.

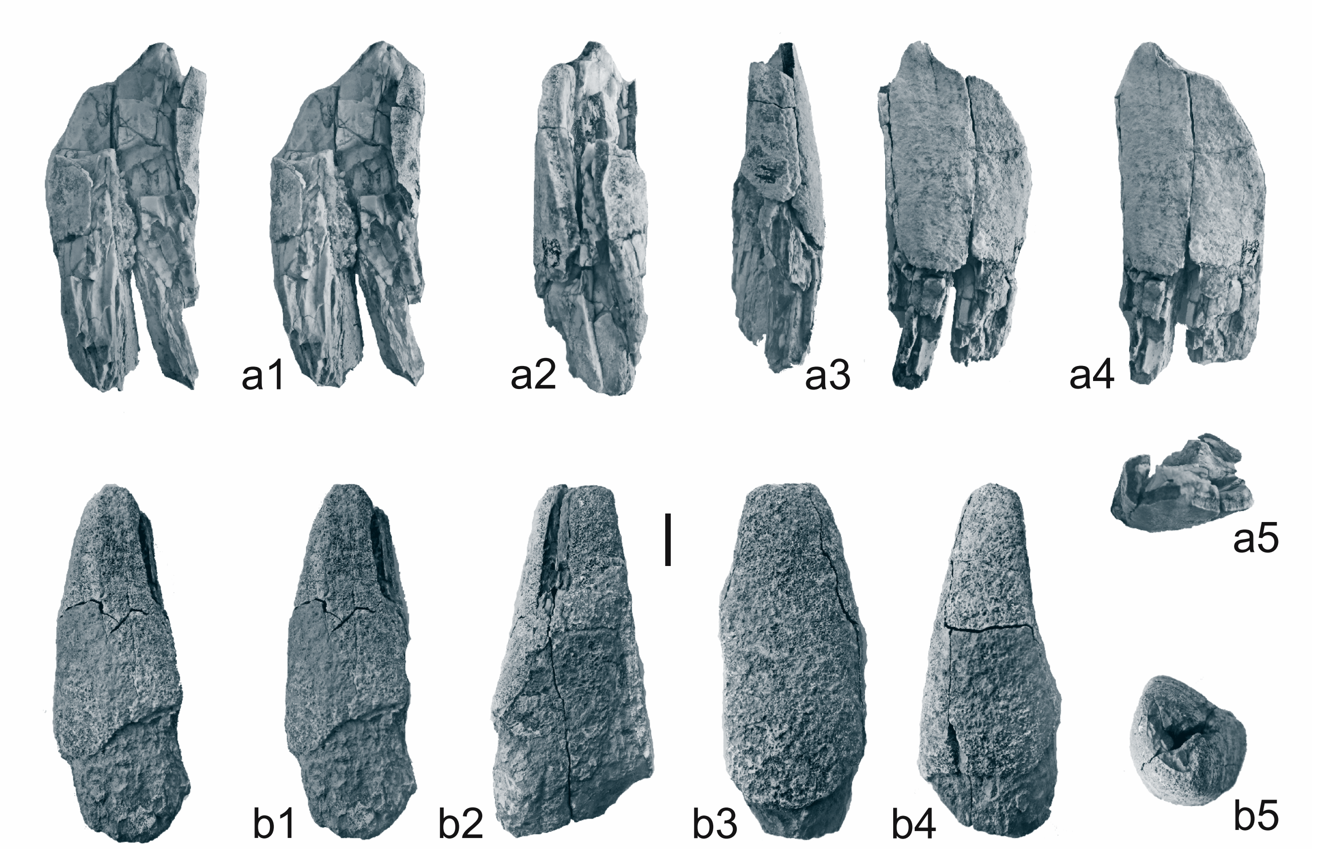
ONHM TN 2017-51 is a complete, lightly worn right i/1 crown with part of the root preserved (Text-fig. 11). The tooth has a rectangular section, much broader mesio-distally than the labio-lingual diameter. The labial surface has a subtle groove that extends from the apex towards the root, fading out as it goes. This groove is positioned about 1/3 of the distance between the mesial and distal margins of the crown. The mesial side of the tooth is almost flat, with a complete cover of thin enamel. The distal margin of the tooth is curved apically, but for most of its height it is parallel to the mesial margin. The mesial side of the tooth is flat and at right angles to the labial side. The wear facet is straight and at right angles to the long axis of the crown.

ONHM TN 2017-43 is a left i/2 with a wear facet at its apex. The section is ovoid, such that the mesio-distal diameter is slightly greater than the labio-lingual diameter. The labial surface is uniformly curved, but the lingual side is more angular. The cervix is far from the apex on the labial side, but rises a long way towards the apex mesially, before descending rootwards again. The wear facet is flat and at right angles to the long axis of the tooth.

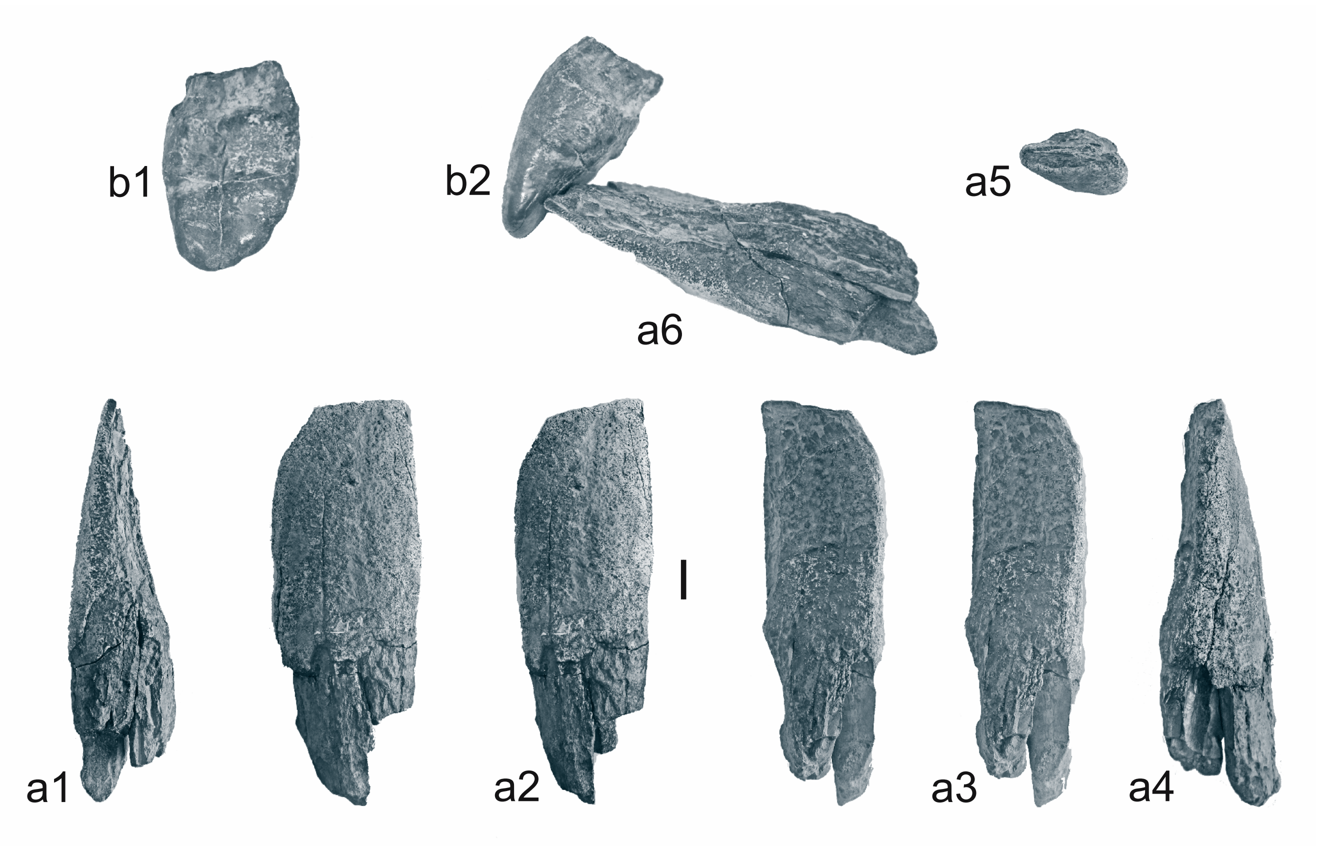
ONHM TN 2017-50 is the distal lophid of an unworn lower molar, probably m/2 on the basis of its dimensions (Text-fig. 12). The crest of the lophid has a mamellated appearance, with no central sulcus. The precristids are well-developed, in particular the one on the buccal cusp. The distal cingulum is broken off, but the posterior accessory tubercle is preserved, and lies in line with the pre-cristid of the buccal cusp, as in other specimens of the species (Text-fig. 13).

ONHM TN 2017-16 is an unworn left P3/ crown. It has a prominent protocone, which is separated by a sulcus from the buccal cusp, which is comprised of closely fused paracone and metacone. The parastyle is bordered on either side by a cingulum, which is prominent near the parastyle, but fades out buccally and lingually. The distal cingulum is prominent in the centre-line of the tooth, but diminishes buccally and lingually. The pre-protocrista reaches mesio-buccally towards the pre-paracrista, thereby forming a loph-like wall with a shallow notch between the two cristae.

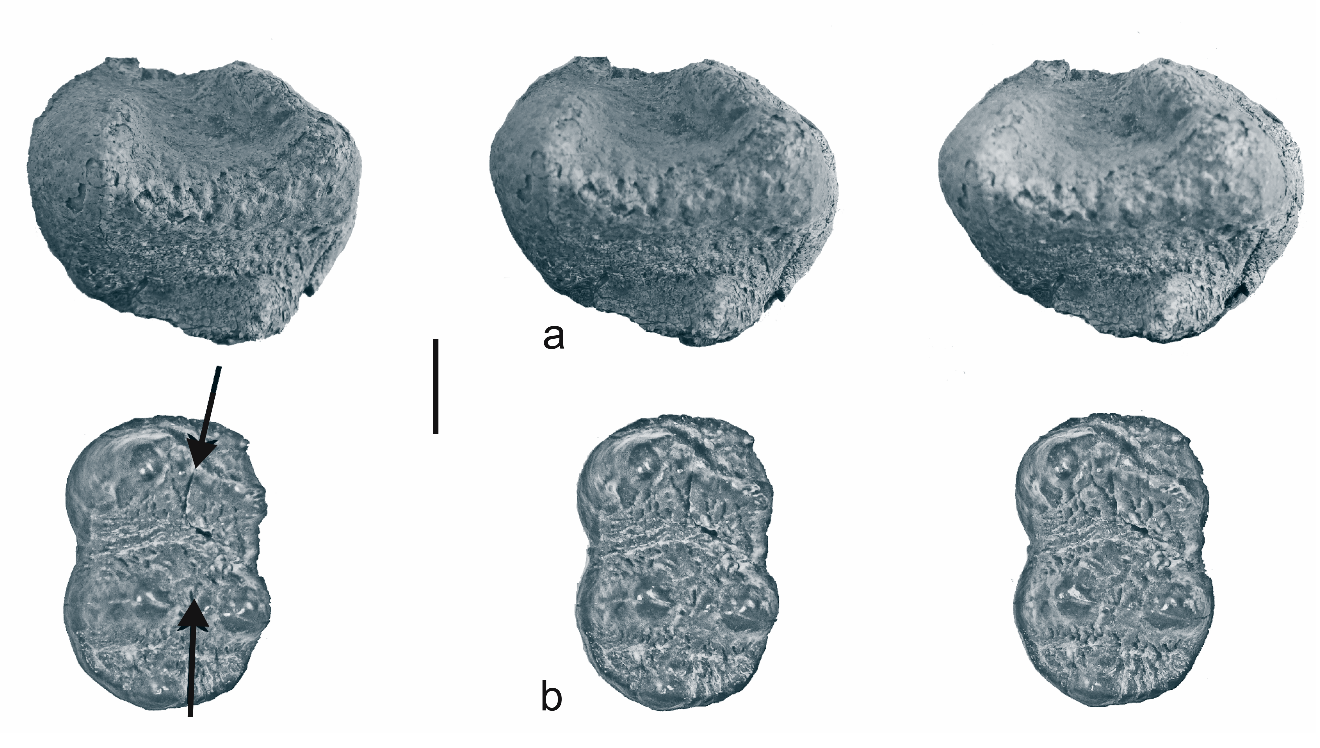
ONHM TN 2017-17 is an unworn right P4/ found close to the left P3/. It is slightly larger than the P3/, the loph is better formed and the central sulcus is broader than that in the P3/. The protocone is large, and the paracone and metacone are separated at their apices, but solidly fused at



Text-fig. 10. Lower incisors of *Omanitherium dhofarense*. a) ONHM TN 2017-19, left i/1, (a1 – stereo lingual view, a2 – distal view, a3 – mesial view, a4 – stereo labial view, a5 – apical view); b) ONHM TN 2017-43, left i/2 from Mohammed's i/2 site (b1 – stereo distal view, b2 – lingual view to show the anticlinal form of the cervix, b3 – labial view, b4 – mesial view, b5 – apical view) (scale bar 10 mm).



Text-fig. 11. Upper and lower incisors of *Omanitherium dhofarense*. a) ONHM TN 2017-51, right i/1 from Mohammed's molar site (a1 – mesial view, a2 – stereo labial view, a3 – stereo lingual view, a4 – distal view, a5 – apical view, a6 – mesial view of tooth occluded with the I1/); b) ONHM TH 6, from Thaytiniti (b1 – lingual view, b2 – mesial view of tooth occluded with the i/1) (scale bar 10 mm).



Text-fig. 12. Lower molars of (a) *Omanitherium dhofarense* and (b) *Moeritherium chehbeurameuri*. a) stereo occlusal views of ONHM TN 2017-50, posterior lophid of an unworn right lower molar, probably m/2, from Mohammed's molar site, Dhofar, Oman, b) stereo occlusal views of MNHN 1890-14, left lower molar from "Khenchella", Algeria (note the longitudinal sulcus in the centre-line of the tooth of *Moeritherium* and its absence in *Omanitherium*). Arrows show the course of the sulcus in the molar from "Khenchella" (scale bar 10 mm).

Text-fig. 13. Stereo occlusal views of SQU 290, juvenile left mandible of *Omanitherium dhofarense*, part of the holotype (scale bar 5 cm).

Table 2. Measurements (in mm) of the teeth of *Omanitherium dhofarense*.

Catalogue n°	Tooth	Mesio-distal length	Bucco-lingual breadth	Crown height
ONHM TN 2017-51	Right i/1	31.0	22.7	49+
ONHM TN 2017-19	Left i/1	29.4	–	45+
ONHM TN 2017-43	Left i/2	27.6	20.7	50+
ONHM TN 2017-85	Right i/2	32.0	23.0	56.0
ONHM TN 2017-50	Left m/2	–	37.3	–
ONHM TN 2017-16	Left P3/	22.5	24.0	–
ONHM TN 2017-17	Right P4/	22.3	29.0	–
ONHM TN 2017-44	Right P4/	24.4	30.7	–
ONHM TN 2017-18	Right M1/	31.2	–	–
ONHM TN 2017-79	Left M3/	43.7	38.3	–

their bases. The crests of the tooth are comparable to those in the P3/, but show stronger beading along their edges. The same can be said about the beading of the cingula.

ONHM TN 2017-44 is a lightly worn right P4/, similar in construction to ONHM TN 2017-17, but slightly larger (Text-fig. 14). The apices of the loph and the cingula are lightly worn, to the stage where the beading has been removed.

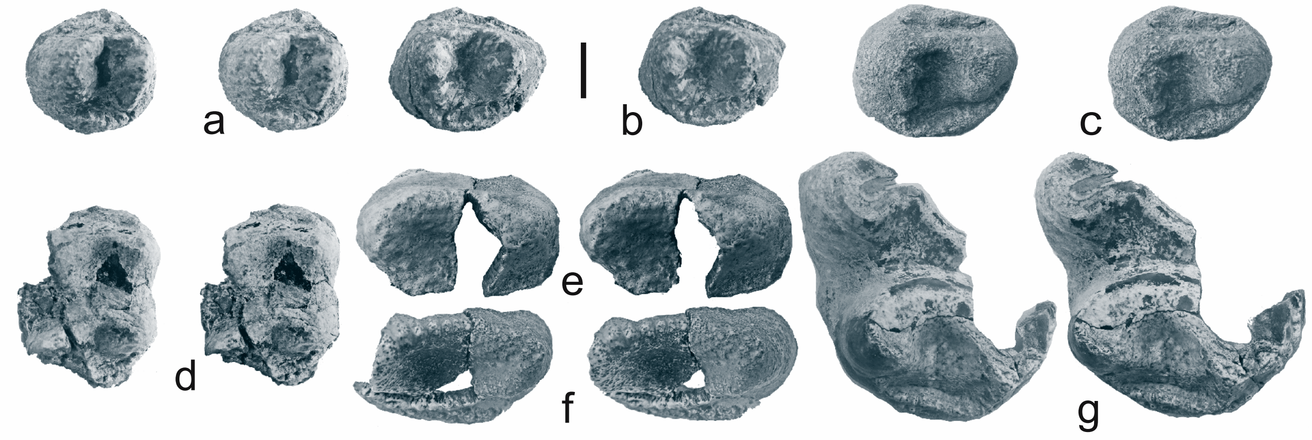
ONHM TN 2017-18 is a lightly worn right M1/, lacking the buccal part of the crown (Text-fig. 14). It was found close to the left P3/. The protocone and paracone form a clear loph, as do the hypocone and metacone behind, separated from each other by a broad central valley. There is a narrow mesial cingulum, and a broader distal one. The mesial edge of each loph is straight, but the distal side is concave, due to the way that the post-cristae are arranged.

ONHM TN 2017-45 comprises two fragments of an unworn left M2/ (Text-fig. 14). The tooth is bilophodont, with beaded apices of the lophs. The mesial cingulum is broken off, but the distal one is preserved, and shows a beaded apex. The distal cingulum blends into the post-metacrista.

ONHM TN 2017-79 is a damaged right M3/ with medium wear (Text-fig. 14). The tooth is bilophodont, but the occlusal outline is more trapezoidal than it is in the M1/ and M2/, which are rectangular. This is due to the fact that not only is the hypocone more distally positioned relative to the metacone than it is on the anterior molars, but in addition, the post-hypocrista is more voluminous than the post-metacrista. As a result of this arrangement of the main cusps, the distal cingulum is oblique to the long axis of the tooth. In other respects, the M3/ is similar to the other molars.

Discussion. The first mentions of the presence of a lophodont proboscidean at Thaytiniti were by Thomas et al. (1989, 1999), summarised as ?*Barytherium* sp. indet. ("cf. Barytherioidea") by Sanders et al. (2010b), and now known as *Omanitherium dhofarense* Seiffert et al., 2012.

When *Omanitherium* was described for the first time, Seiffert et al. (2012) reconstructed the mandible with only

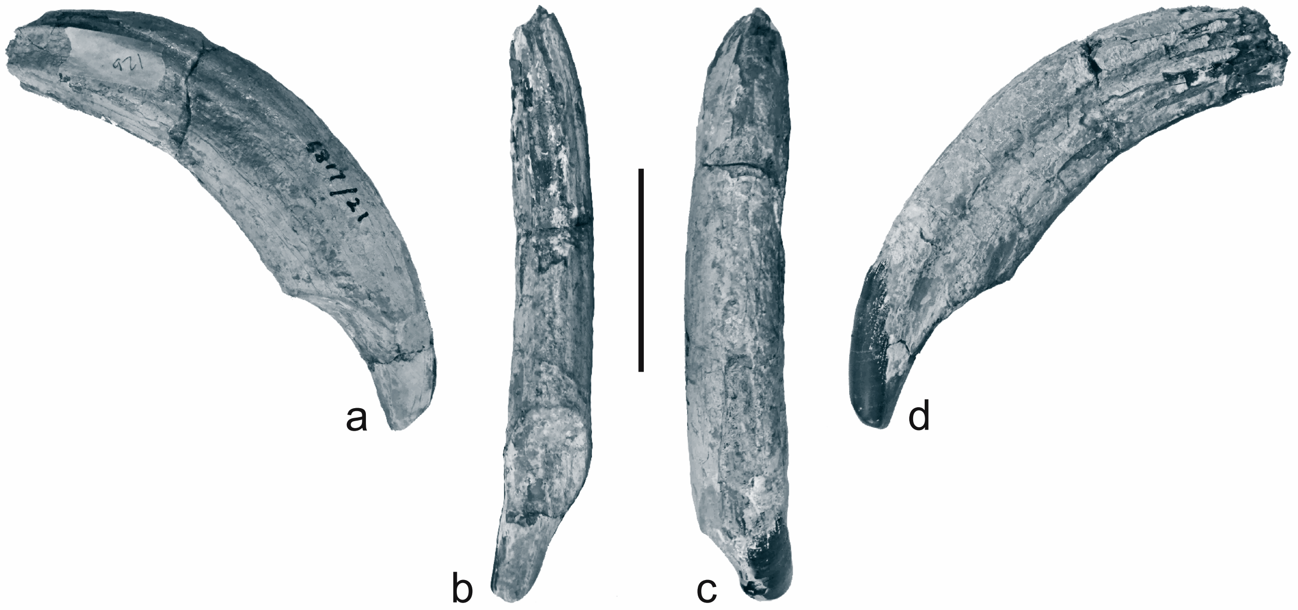


Text-fig. 14. Upper cheek teeth of *Omanitherium dhofarense*. a) ONHM TN 2017-16, left P3/, stereo occlusal view; b) ONHM TN 2017-17, right P4/, stereo occlusal view; c) ONHM TN 2017-44, right P4/, stereo occlusal view; d) ONHM TN 2017-18, right M1/ stereo occlusal view; e and f) ONHM TN 2017-45, fragments of left M2/, stereo occlusal view; g) ONHM TN 2017-79, right M3/, stereo occlusal view (scale bar 10 mm).

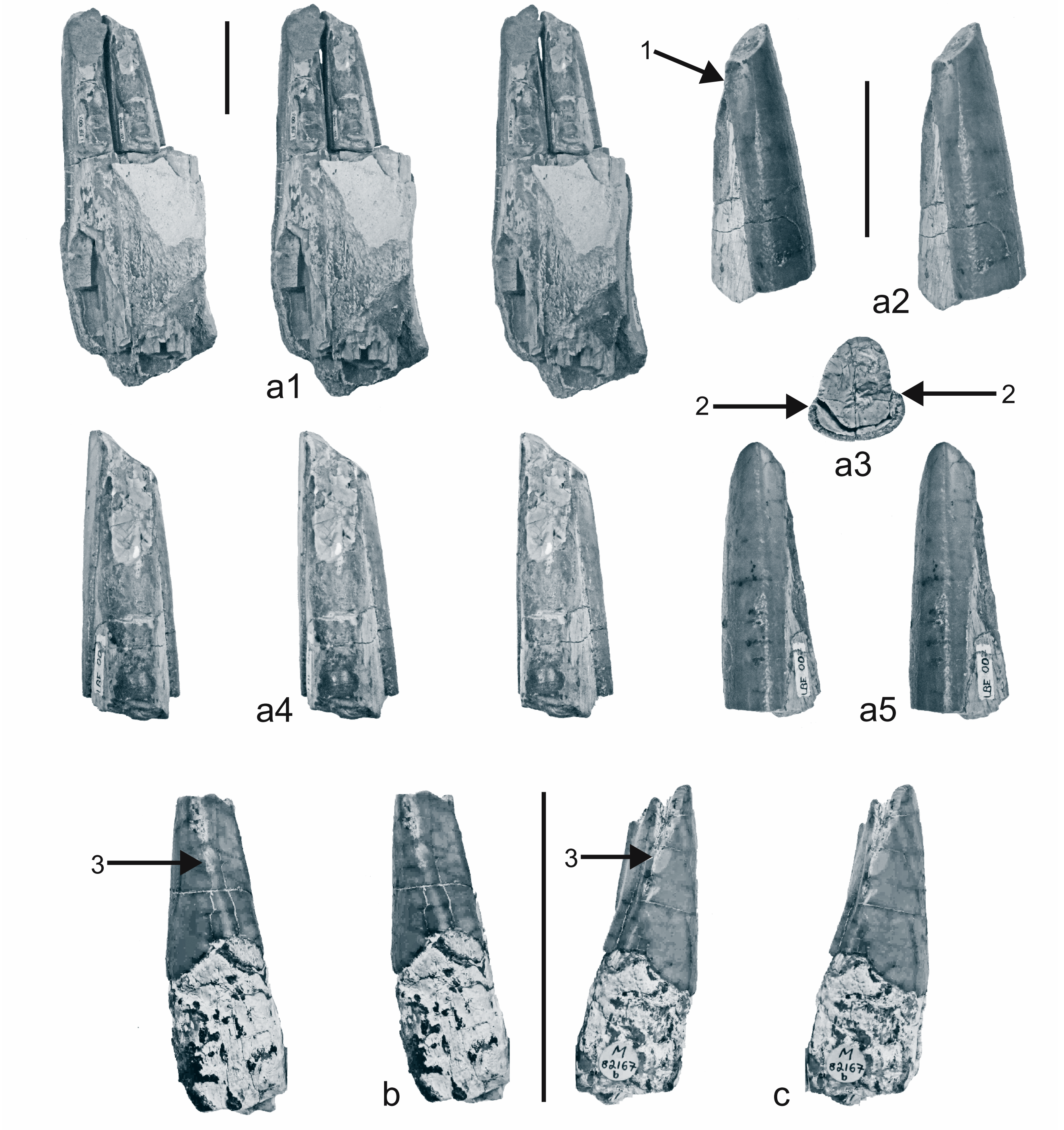
two incisors, separated from each other by a broad gap. In contrast, Pickford (2015b) thought that there would have been a pair of central incisors infilling the gap. The new fossils from the type locality and nearby sites indicate that *Omanitherium* did indeed possess four lower incisors, but instead of the central lower incisors being relatively low crowned as originally thought, they are taller. The difference of opinion is due to the fact that Pickford (2015b) used an upper central incisor as a proxy for the lower incisor.

The meristic position (upper central incisor) and orientation (steeply inserted in the premaxilla) of ONHM TH 6 inferred from the wear facet and general form of the tooth is confirmed by the discovery of two skulls of the closely related taxon, *Arcanotherium savagei* from Dor el Talha, Libya (classified as *Numidotherium savagei* by Jaeger et al. 2012).

The difference in crown height between the upper and lower central incisors of *Omanitherium dhofarense* is illustrated in Text-fig 11. The upper central incisor is not only lower crowned than the lower incisor, but it has an undulating distal margin and thick enamel on the lingual surface, whereas the lower central incisor has no sign of undulations on its distal margin, and the lingual enamel is thin. Furthermore, the crown of the upper incisor is labio-lingually compressed, and the wear facet is confined to the lingual surface of the tooth, where it forms a broad surface ending at a step about half way between the apex and the cervix, whereas the wear facet on the lower incisor is apical. This conformation indicates that the upper central incisor was steeply inserted in the jaw, whereas the lower incisor was procumbent, almost horizontal.



Text-fig. 15. NHMUK 17/2189, upper left central incisor (probably female) of *Barytherium* from Dor el Talha, Libya. a) mesial, b) lingual, c) labial, d) distal views (scale bar 10 cm).



Text-fig. 16. a) MNHN LBE 007, symphysis with left and right i/1 of *Barytherium* sp. from Dor el Talha, Libya. (a1 – superior stereo views of the symphysis, a2 – stereo distal view of right i/1 (arrow 1 shows the interstitial contact facet close to the apex caused by abrasion against the right i/2), a3 – section of right i/1 viewed from the radicular end to show the extent of the enamel cover (below the arrows 2) and the dome-shaped dentine mass on the lingual aspect (above the arrows), a4 – stereo occlusal views of right i/1 (note the orientation of the apical wear facet), a5 – stereo mesial view) (scale bar 5 cm); b–c) NHMUK M 82167b, distal stereo views of lower central incisors of *Arcanotherium savagei* from Dor el Talha, Libya, to show the interstitial wear facets near cervix caused by abrasion against the i/2s (b – left i/1, c – right i/1) (scale bar 10 cm).

In *Barytherium* Andrews, 1901a, from Dor el Talha (also spelled Dur at Talha), Libya, in contrast to *Omanitherium dhofarense*, the upper central incisor is tusk-like, with a uniformly curved root and crown, compressed mesio-distally rather than labio-lingually, with a longitudinal groove on the distal aspect of the root and shallow grooves on the lingual side of the root (Text-fig. 15). There is a lingual wear facet that extends onto the root, and there is abrasional wear all over the exposed part of the tooth, probably caused by rubbing against vegetation during acquisition of food (for example, debarking trees, or reaching upwards to high branches to draw them downwards towards the mouth). The upper central incisor of *Barytherium* evidently occluded with both the lower central and lateral incisors. An I1/ of

Barytherium from Dor el Talha housed in the NHMUK, London (Text-fig. 15), is considered to represent a female individual, because its crown and root are relatively gracile. A second specimen housed in the MNHN, Paris, has a much enlarged crown base and a huge root (broken off just beneath cervix), and is interpreted to represent a male individual.

As concerns the second lower incisor, the holotype specimen of *Omanitherium dhofarense* is unworn, so it is not possible to determine its occlusal relationships to the upper incisors. The new fossils available from the Ashawq Formation indicate that the second incisors also experienced apical wear. The significance of the new data is that it strengthens the affinities of the Omani proboscidean with the Libyan genus *Arcanotherium*, as deduced by Pickford (2015b), but it distances these two genera from *Barytherium*, and even more so, from *Deinotherium* Kaup, 1829.

The original sample of *Omanitherium* did not have any elements of upper dentition. Pickford (2015b) described some upper premolars and part of an upper molar, which revealed that the species was similar in many respects to *Arcanotherium savagei* (Court, 1995) from Dor el Talha, Libya. Amongst the premolars attributed to *Omanitherium* by Pickford (2015b), there was a P4/ that turned out to belong to a different proboscidean taxon, probably a palaeomastodontoid (see below). The removal of the P4/ previously attributed to *Omanitherium*, and its replacement by a new specimen from the type locality, strengthens the affinities with *Numidotherium* (Mahboubi et al. 1986, Noubhani et al. 2008, Adnet et al. 2010), *Phosphatherium* (Gheerbrant et al. 1998, 2005) and *Daouitherium* (Gheerbrant et al. 2002).

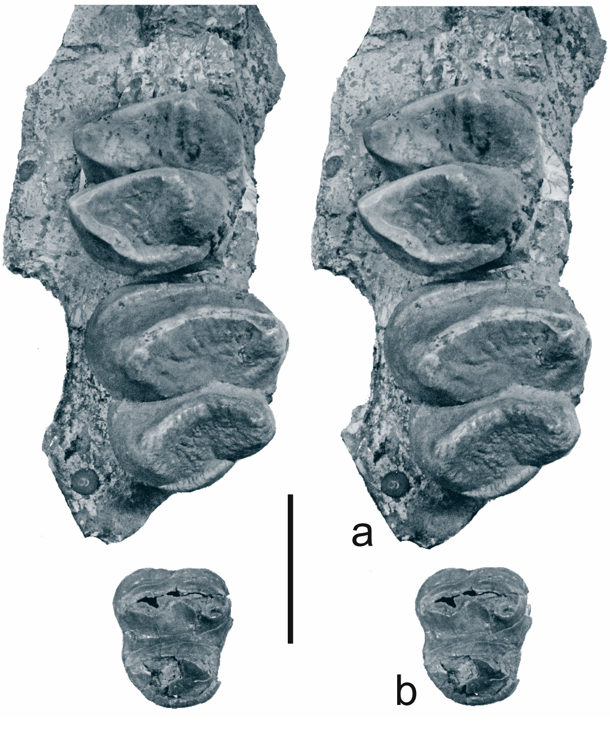
The 2017 sample of *Omanitherium* teeth from Dhofar includes upper premolars as well as molars, all of which lessen residual doubts that might still exist concerning the systematic relationships of this species. Interestingly, the lower central incisors of *Omanitherium* have thinner enamel on the lingual surface than on the labial side, whereas in the second incisors, the enamel is thick all around, but lingually there is a tall anticline in the cervix, which means that on the lingual side of the crown, the enamel of the i/2 covers only half the height of the tooth compared with the enamel on the labial side.

The large barytherioid, *Barytherium*, in contrast, shows no enamel at all on the lingual surfaces of the i/1 and i/2 (Pickford 2015b) (Text-fig. 16). Not only that, but lingual doming of the dentine, best appreciated in the section, is vast, comprising the bulk of the volume of the tooth, providing a major contrast with the almost flat or even slightly concave lingual surface of the i/1 in *Omanitherium* and *Arcanotherium*. The wear facet at the apex of the tooth in *Barytherium* is more inclined distally than it is in *Omanitherium*, suggesting that the upper central incisor was oriented differently in the two genera.

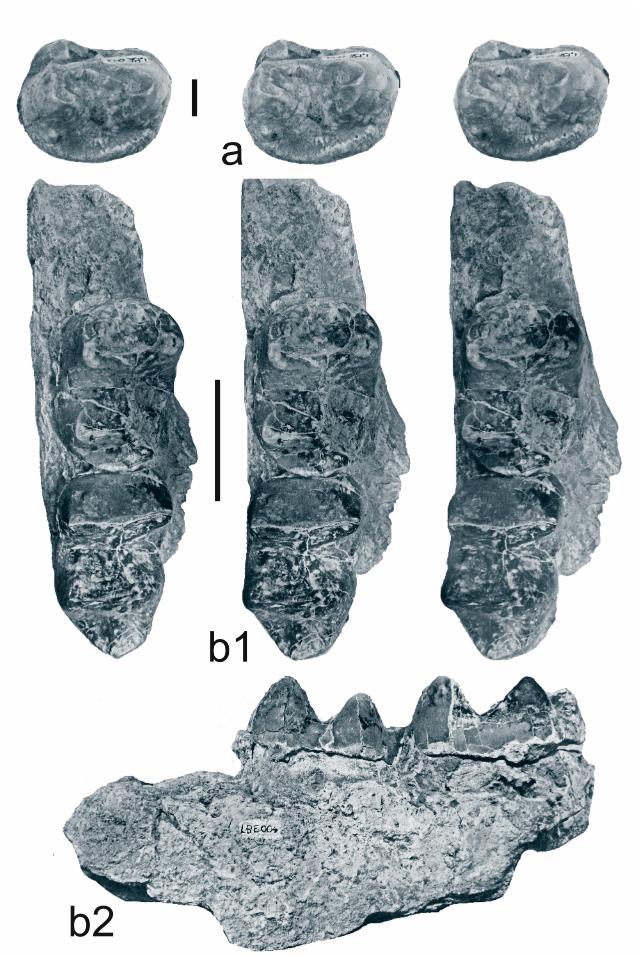
Near its apex, the lower first incisor of *Barytherium* shows an interstitial contact facet on its distal margin caused by abrasion against the i/2 (Text-fig. 16a2). In *Arcanotherium* and *Omanitherium*, the interstitial wear facet of the lower incisors is not near the apex, but is well towards the cervix (Text-fig. 16b, c), indicating that the two lower incisors were separated at their apices, unlike *Barytherium*, in which the two incisors were in contact at their apices, and for quite a distance towards the cervix. The i/2 in *Barytherium* is poorly represented in the fossil record, but judging from its alveolus, it is highly compressed, being mesio-distally short and bucco-lingually broad, and its crown would have been almost as tall as that of the i/1. Note also the mammelated distal margin of the i/1 in *Arcanotherium*, and the non-mammellated margin in *Barytherium*. In *Omanitherium*, the distal margin of the i/1 is not mammelated (Text-figs 10, 11), in strong contrast to the distinct mammelae present in *Arcanotherium* (Text-fig. 16b, c).

In contrast to *Barytherium*, the i/1 and i/2 of *Omanitherium* and *Arcanotherium* show no contact near their apices, even though their roots are close together. *Arcanotherium* shows an interstitial facet on its distal margin close to the base of the crown, caused by contact with i/2 (Text-fig. 16b, c). Orientations of the lower incisors in *Barytherium* and *Omanitherium* were different, implying divergent occlusal relationships with the upper incisor battery. *Arcanotherium* and *Omanitherium* are much more similar to each other and to the older genera, *Numidotherium*, *Phosphatherium* and *Daouitherium*, than they are to *Barytherium*. This new evidence concerning lower incisor morphology in barytheres (sensu lato) does not resolve the issue of relationships between them and deinotheres (Sanders et al. 2010b), but it means that a close relationship is unlikely.

The upper teeth of *Omanitherium* now available reveal that it is substantially smaller than *Arcanotherium savagei* (Text-figs 17, 18). The M3/ of the latter species (Delmer 2009: fig. 3D), for example, measures 51 × 45 mm (length × breadth), which compares with 43.7 × 38.3 mm in



Text-fig. 17. Upper molars of a) *Barytherium* sp. and b) *Arcanotherium savagei* from Dor el Talha, Libya. a) stereo occlusal view of MNHN LBE 002, left maxilla containing M2/ and M3/, b) stereo occlusal view of MNHN LBE 020, left M3/ (scale bar 5 cm).



Text-fig. 18. *Barytherium* sp. from Dor el Talha, Libya. a) MNHN LBE 13, right upper premolar, stereo occlusal views (scale bar 1 cm) and b) MNHN LBE 004, right mandible containing m/2 and m/3 (b1 – stereo occlusal views, b2 – lingual view) (scale bar 5 cm).

Omanitherium dhofarense.

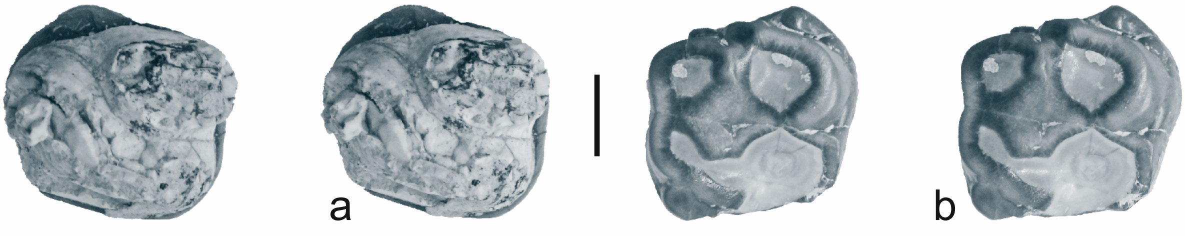
In summary, additions to the hypodigm of *Omanitherium dhofarense* collected in 2017 contribute to our understanding of its anterior dentition and upper cheek teeth, and thereby clarify its relationships to numidotheres (close) and barytheres (remote). However, there remain uncertainties, especially concerning the number of upper incisors, and the presence or absence of canines and anterior premolars. Furthermore, little is known about the skull and post-cranial skeleton of the species. In contrast, the recovery of relatively complete cranial remains of *Arcanotherium savagei* from Dor el Talha in Libya reveals that there were three pairs of upper incisors, a low-crowned spatulate central incisor with beaded distal margin, a taller, more tusk-like second incisor and a small upper third incisor and upper canine (Jaeger et al. 2012). It remains to be discerned whether *Omanitherium* conforms in this respect to *Arcanotherium*. These Omani and Libyan discoveries reveal that knowledge about incisors is essential for sorting out phylogenetic relationships of Palaeogene proboscideans, and furthermore, for resolving the long-lasting debate about the meristic position of the tusks of elephants and mastodonts. In this respect, *Omanitherium* is closer to elephants than it is to barytheres, despite the fact that the cheek teeth of numidotheres and barytheres are morphologically comparable. For these reasons, we here adopt a modified classification of the Palaeogene lophodont proboscideans, recognising Barytherioidea Andrews, 1906, as a distinct superfamily from Numidotherioidea Shoshani et Tassy, 1992 (new rank).

Superfamily Palaeomastodontoidea Andrews, 1906

Genus *Palaeomastodon* Andrews, 1901b or *Phiomia* Andrews et Beadnell, 1902

Material. ONHM TQ 15, right P4/.

Description. A heavily worn bunodont right upper fourth premolar of a proboscidean (ONHM TQ 15: length × breadth: 25.0 × 25.6 mm) was found at Taqah (Text-fig. 19). It was attributed to *Omanitherium* by Pickford (2015b) but the discovery of upper premolars of this genus at the type locality and nearby indicate that the identification was erroneous. The Taqah tooth is quadricuspidate, with low cingular remnants on the mesio-lingual corner of the protocone and the disto-buccal corner of the metacone, whereas the P4/ of *Omanitherium* is lophodont, with a weak or absent hypocone, the protocone and paracone are strongly joined together, and the paracone and metacone are linked together, signifying major differences from palaeomastodonts, in which the four cusps are distinct from each other, even in heavily worn specimens. The lingual, pretrite side of the tooth is more deeply worn than the buccal, post-trite side, as is usual in proboscideans (Tobien 1978). Interstitial wear against the P3/ and M1/ has removed a considerable amount of the mesial and distal margins of the tooth, leaving small remnants of the cingula.



Text-fig. 19. ONHM TQ 15, right P4/ of a palaeomastodontoid from Taqah, Dhofar Governorate, Oman. a) stereo radicular view, b) stereo occlusal view (scale bar 10 mm).

In the tooth from Taqah, the root beneath the protocone is contiguous with the one beneath the metacone, while the root that supports the paracone is distinct. This arrangement of the roots appears to be the usual pattern in moeritheres and palaeomastodontoids (Tassy 1981).

Discussion. The P4/, ONHM TQ 15, was attributed to *Omanitherium dhofarense* by Pickford (2015b: fig. 4b), due to its dimensions, which are compatible with the holotype mandible, and due to its morphology, which mirrored the bunodont anterior cusps of the p/4 from the type locality. However, the discovery of a fully lophodont P4/ in the Ashawq Formation not far from the *Omanitherium* type locality prompted a re-examination of the Taqah specimen, and a deeper comparison to premolars of other proboscideans from Eo-Oligocene deposits of Africa. Study of the roots reveals that the tooth is a right P4/ (Tassy 1981, Gheerbrant et al. 2005).

Appurtenance of this premolar to *Moeritherium* Andrews, 1901b, can be discounted, despite the compatibility in dimensions, because this genus has a weak to absent hypocone in the P4/ (Andrews 1906: pl. VIII). The Taqah fossil is closest in terms of its morphology, dimensions and wear pattern to specimens of *Palaeomastodon* (Andrews 1906: pl. XII) and *Phiomia* (Andrews and Beadnell 1902). Given the deeply worn condition of the crown, the identification is left open, with the balance somewhat favouring appurtenance to *Palaeomastodon* rather than to *Phiomia*.

Order Artiodactyla Owen, 1848
Family Anthracotheriidae Leidy, 1869

Genus *Bothriogenys* Schmidt, 1913

Bothriogenys gorringei (Andrews et Beadnell, 1902)

Material. ONHM TN 2017-01, first phalanx.

Description. The *Omanitherium* type locality yielded a first phalanx of an anthracothere in situ in indurated marl (Text-fig. 20). The specimen, ONHM TN 2017-01, is complete. The distal end shows a moderate central valley between the two articular surfaces, a feature of artiodactyl phalanges, which distinguishes this fossil from proboscidean phalanges that have an almost obsolete central valley (Gheerbrant et al. 2005, Delmer et al. 2006). The specimen is 41.4 mm long, and the distal end is 15.3 mm broad by ca. 9 mm tall, and is thus compatible in dimensions with the species *Bothriogenys gorringei*, which has already been recorded from the Ashawq Formation on the basis of upper and lower molars (Pickford 2015c)

Discussion. The anthracothere phalanx from the *Omanitherium* type locality proves the association of this family with fossils of the arsinoithere, *Arsinoitherium andrewsi*, and the numidotherioid, *Omanitherium dhofarense*. This association was already noted at the Thaytiniti locality excavated by the Thomas Expedition of 1992 (Pickford 2015c).

Sileem et al. (2015, 2016) and Sallam et al. (2016) extended knowledge of *Bothriogenys* and other anthracotheres in the Fayum deposits of northern Egypt, in particular regarding stratigraphic distribution of various taxa, reporting specimens from the Late Eocene Qasr el Sagha Formation and the Jebel Qatrani Formation. The results of this work agree with the Omani record, which, it must be admitted, is still rather sparse. It suggests that the Ashawq Formation is close in age to Quarry L41 in the Jebel Qatrani Formation (Rupelian) (Seiffert 2006), although a correlation to the earlier Qasr el Sagha Formation (Priabonian) cannot be discounted (Sileem et al. 2016).

Text-fig. 20. ONHM TN 2017-01, anthracothere 1st phalanx in situ in indurated marl at the *Omanitherium* type locality.

The fossil record of anthracotheres in the Arabian Peninsula is filling in, but there are still long gaps in the stratigraphic representation of the family. The next youngest anthracotheres following the Ashawq records (Pickford 2015c) and those from the Usfan and Shumaysi Formations, Western Saudi Arabia (Zalmout et al. 2012) of Early Oligocene age, are those from the Early Miocene deposits at Wadi Sabya, southwestern Saudi Arabia (*Brachyodus* Depéret, 1895, at 17°12’46.3”N : 42°47’08.8”E 79 m a.s.l. – Madden et al. 1983) and Ghaba, Oman (*Afromeryx zelteni* Pickford, 1991 – Roger et al. 1994a).

Biogeography

The mammals from the Ashawq Formation comprise predominantly lineages of African affinities (bats, arsinoitheres, palaeomastodonts, numidotherioids, hyracoids), but there are some groups (primates, anthracotheres) that originated in Eurasia and dispersed to Afro-Arabia during the Palaeogene (Text-fig. 21). The fact that the bats from Taqah show strong African affinities (Sigé et al. 1994), with little influence from Eurasia, is of interest, as these flying mammals are not usually hindered in their dispersal by ocean barriers such as that which separated Arabia and Iran. This evidence suggests that there was more than the physical barrier of the Tethys Seaway keeping the Eurasian and African chiropteran faunas distinct, which in turn pleads for a latitudinal climatic effect, similar to the one that keeps the Boreal and Ethiopian faunas largely distinct even today, when there is no effective physical barrier to their dispersal.

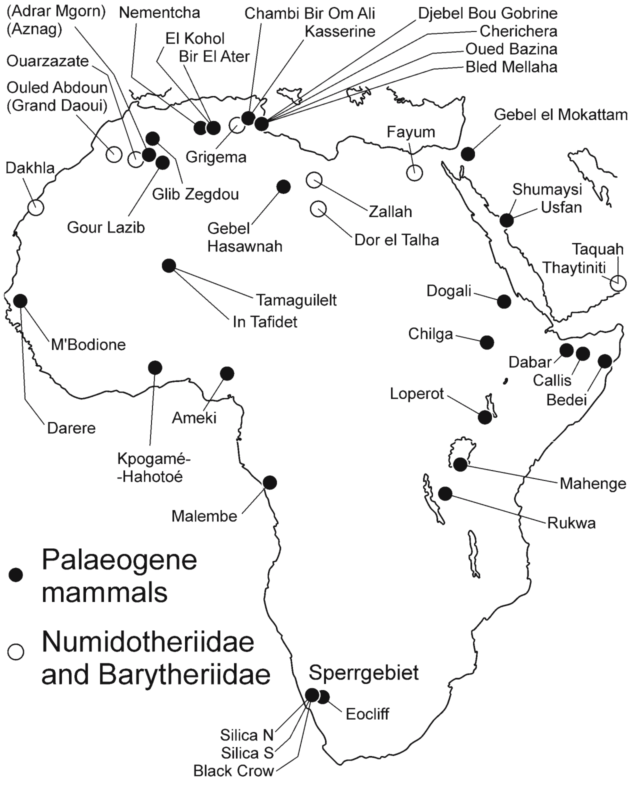
Pickford et al. (2014) studied non-marine molluscs from the Thaytiniti region and noted strong affinities with African molluscan faunas. In contrast, Harzhauser et al. (2016)

considered that several of the Omani non-marine molluscan species had closer affinities with lineages from mid-latitude Europe and Asia than with Africa.

Pickford (1990) and Pickford and Morales (1994) argued that animal adaptations to Boreal and Tropical palaeoenvironments have an ancient pedigree, with breeding in the middle and high latitudes (30°–90°) being triggered predominantly by changes in day-length, combined with cold-warm seasonality, whereas in the tropics and sub-tropics (0°–30° of latitude), breeding is triggered mainly by wet-dry seasonality, day-length changes being minimal in the equatorial belts of the globe. If this is so, then it is suggested that the Ashawq faunas were adapted to tropical to sub-tropical biogeographic conditions.

That this may be so is supported by the similarities of the bulk of the Ashawq faunal elements to faunas from other sites in Afro-Arabia. Even the mammalian lineages that originated in Eurasia (primates and anthracotheres) are well represented in African Palaeogene localities as far south as the Sperrgebiet, Namibia (Pickford 2015d).

The available evidence from Dhofar thus indicates that the Afro-Arabian Rupelian mammalian fauna was distinct from that of the more Boreal landmass, Eurasia, even though a few lineages had managed to disperse to Africa before the Rupelian (primates, anthracotheres), and at least one lineage had dispersed from Africa to Eurasia during the Rupelian (the hyracoid, *Geniohyus*) (see Pickford 1986b for a summary). It was only during the latest Oligocene and basal Miocene that many lineages of mammals dispersed between the two land masses, indicating the establishment of relatively easy passage in both N-S and S-N directions. Low sea-levels during the Oligocene may have facilitated these dispersals, but climatic change may also have played a decisive role, since it is clear that mid-latitude Eurasia became warmer and more humid during the Early and Middle Miocene than it was during the Eocene and Oligocene, thereby facilitating survival of tropically adapted lineages in areas where they were previously excluded by climatic and ecological factors.



Text-fig. 21. Palaeogene fossil mammal localities of Africa and the Arabian Peninsula, highlighting the distribution of *Omanitherium* and other numidotheres and barytheres.

Conclusions

Fossils collected from the Early Oligocene Ashawq Formation, Dhofar, Oman, reveal that the numidotherioid afrothere *Omanitherium dhofarense* possessed four lower incisors, rather than two as originally published (Seiffert et al. 2012), a finding that indicates closer relationships to *Arcanotherium* from Libya (Jaeger et al. 2012), and *Numidotherium* from Algeria (Noubhani et al. 2008) and Moroccan Sahara (Adnet et al. 2010), than to *Barytherium* (Seiffert et al. 2012). Relationships of *Omanitherium* to *Barytherium* are more distant than previously reported (Seiffert et al. 2012), the upper and lower incisors being radically different, not only in their morphology, but also in the orientation of the apical wear facet in the lower central incisor, which implies divergent incisor battery occlusal relationships. For this reason, we adopt the view that there are two distinct superfamilies of Palaeogene lophodont proboscideans, Barytherioidea and Numidotherioidea, the latter of which is closer to extant elephants than is the former. The new data support the view that *Omanitherium* and *Arcanotherium* are valid genera, distinct from *Numidotherium* (Delmer 2009, Pickford 2015b). At the same time, they increase the phylogenetic distance between numidotheres and deinotheres, which renders unlikely the classification by Shoshani and Tassy (2005), in which deinotheres are positioned within Plesielephantiformes, next to Barytheriidae and Numidotheriidae.

Additional fossils of hyracoids and arsinoitheres from the Ashawq Formation are described, and an upper premolar previously thought to belong to *Omanitherium* (Pickford 2015b) is attributed to a palaeomastodontoid, the first record of this group of proboscideans from the Arabian Peninsula.

Additional remains of anthracotheres from the Ashawq Formation, even though limited, strengthen the overall affinities of the Dhofar mammal fauna with those from the Fayum, Egypt, suggesting that they belonged to a single biogeographic province and are close in age to each other.

The results of the 2017 palaeontological field survey in Dhofar are encouraging, and indicate that surveys should continue. The full palaeopotential of the Aydim region is waiting to be realised.

Acknowledgements

We gratefully acknowledge financial support from the Ministry of Culture and Heritage in Oman. Support of the study by H. E. Salim al Mahruqi, Undersecretary of the Ministry of Culture and Raya al Kindi, acting director of Museums Department, is greatly appreciated. We are anxious to thank the Ministry of Defence in Oman for providing accommodation and board during the course of the field work in South Dhofar. Representatives from the office of the Public Authority of Mining in Dhofar participated in the field work. We thank Christine Argot (MNHN) and Pip Brewer and Roula Pappa (NHMUK) for providing access to fossils in their care.

References

Adnet, S., Capetta, H., Tabuce, R. (2010): A new Eocene vertebrate fauna (selachians and mammals) from southwestern Morocco: preliminary report: age and palaeobiogeographical implications. – Geological Magazine, 147: 860–870.
https://doi.org/10.1017/S0016756810000348

Al-Jahiz, Abu ‘Uthman (1960): Kitab al-Hayawan [The Book of Animals] (edited by Abdesselam Mohamed Harun, 2nd Edition). – Mustapha Halabi, Egypt, 2072 pp. (in Arabic) (critical edition of manuscript from 845 CE).

Al-Sayigh, A. R., Nasir, S., Schulp, A. S., Stevens, N. J. (2008): The first described *Arsinoitherium* from the Upper Eocene Aydim Formation of Oman: Biogeographic implications. – Palaeoworld, 17: 41–46.
https://doi.org/10.1016/j.palwor.2007.07.005

Andrews, C. W. (1901a): A new name for an ungulate. – Nature 64: 577.
https://doi.org/10.1038/064577d0

Andrews, C. W. (1901b): Über das Vorkommen von Proboscidiern in untertertiären Ablagerungen Aegyptens. – Tagesblatt des V Internationalen Zoologischen-Kongresses, Berlin, 6: c4–c5.

Andrews, C. W. (1904): Further notes on the mammals of the Eocene of Egypt, part II. – Geological Magazine, Series 5, 1: 157–162.
https://doi.org/10.1017/S0016756800119491

Andrews, C. W. (1906): A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. – British Museum of Natural History, London, 342 pp.

Andrews, C. W., Beadnell, H. J. L. (1902): A preliminary note on some new mammals from the upper Eocene of Egypt. – Egypt Survey Department, Public Works Ministry, Cairo, pp. 1–9.
https://doi.org/10.5962/bhl.title.77312

Beadnell, J. (1902a): A preliminary note on *Arsinoitherium zitteli* Beadnell, from the upper Eocene strata of Egypt. – Survey Department, Public Works Ministry, Cairo, National Printing Department, pp. 1–4.

Beadnell, J. (1902b): Note on *Arsinoitherium*. – Geological Magazine, 10: 529.

Court, N. (1995): A new species of *Numidotherium* (Mammalia: Proboscidea) from the Eocene of Libya and the early phylogeny of the Proboscidea. – Journal of Vertebrate Paleontology, 15: 650–671.
https://doi.org/10.1080/02724634.1995.10011254

Crochet, J.-Y., Thomas, H., Sen, S., Roger, J., Gheerbrant, E., Al-Sulaimani, Z. (1992): Découverte d’un Péradectidé (Marsupialia) dans l’Oligocène inférieur du Sultanat d’Oman: Nouvelles données sur la paléobiogéographie des Marsupiaux de la plaque arabo-africaine. – Comptes Rendus de l’Académie des Sciences, Paris, 314: 539–544.

Delmer, C. (2009): Reassessment of the generic attribution of *Numidotherium savagei* and the homologies of lower incisors in proboscidens. – Acta Palaeontologica Polonica, 54(4): 561–580.
https://doi.org/10.4202/app.2007.0036

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(2): 421–434.
https://doi.org/10.1111/j.1475-4983.2006.00548.x

Depéret, C. (1895): Über die Fauna von miocänen Wirbelthieren aus der ersten Mediterranstufe von Eggenburg. – Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-naturwissenchaftliche Klasse, Abteilung 1, Mineralogie, Biologie, Erdkunde, 104(4): 395–416.

Forster-Cooper, C. (1924): The Anthracotheriidae of the Dera Bugti deposits in Baluchistan. – Memoir of the Geological Survey of India, Palaeontologia Indica, 8(2): 1–59.

Gheerbrant, E., Sudre, J., Cappetta, H., Bignot, G. (1998): *Phosphatherium escuillei* du Thanétien du bassin des Ouled Abdoun (Maroc); plus ancien proboscidien (Mammalia) d’Afrique. – Geobios, 32: 247–269.
https://doi.org/10.1016/S0016-6995(98)80041-7

Gheerbrant, E., Sudre, J., Cappetta, 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 Palaeontologica Polonica, 47: 493–506.

Gheerbrant, E., Sudre, J., Tassy, P., Amaghzaz, M., Bouya, B., Iarochène, M. (2005): Nouvelles données sur *Phosphatherium escuillei* (Mammalia, Proboscidea) de l’Éocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. – Geodiversitas, 27(2): 239–333.

Gheerbrant, E., Thomas, H., Roger, J., Sen, S., Al-Sulaimani, Z. (1993): Deux nouveaux primates dans l’Oligocène inférieur de Taqah (Sultanat d’Oman): premiers adapiformes (?Anchomomyini) de la Peninsule Arabique? – Palaeovertebrata, 22: 141–196.

Gheerbrant, E., Thomas, H., Sen, S., Al-Sulaimani, Z. (1995): Nouveau primate Oligopithecinae (Simiiformes) de l’Oligocène inférieur de Taqah, Sultanat d’Oman. – Comptes Rendus de l’Académie des Sciences, Paris, série 2, 321: 425–432.

Harzhauser, M., Neubauer, T., Kadolsky, D., Pickford, M., Nordsieck, H. (2016): Terrestrial and lacustrine gastropods from the Priabonian (upper Eocene) of the Sultanate of Oman. – Paläontologische Zeitschrift, 90(1): 63–99. https://doi.org/10.1007/s12542-015-0277-1

Huxley, T. H. (1869): An Introduction to the Classification of Animals. – John Churchill and Sons, London, viii + 147 pp.

Illiger, C. (1811): Prodromus systematis mammalium et avium additis terminis zoographicis utriudque classis. – C. Salfeld, Berlin, xviii + 301 pp.

Jaeger, J.-J., Salem, M. J., Abolhassan Bilal, A., Benammi, M., Chaimanee, Y., Duringer, P., Marandat, B., Marivaux, L., Métais, E., Schuster, M., Valentin, X., Viriot, L., Hammuda, O., Brunet, M. (2012): Dur at Talah Vertebrate locality revisited: New data on its stratigraphy, age, sedimentology and mammalian fossils. – In: Salem, M. J., Elbakai, M. T., Abuturruma, Y. (eds), Geology of Southern Libya, Volume 1. Gutenberg Press, Malta, pp. 241–258.

Kaup, J. (1829): *Deinotherium giganteum*, eine Gattung der Vorwelt aus der Ordnung der Pachydermen, aufgestellt und beschreiben. – Isis, 22: 401–404.

Lankester, E. R. (1903): A new extinct monster. – Sphere, London, 1903: 238.

Leidy, J. (1869): The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. – Journal of the Academy of Sciences of Philadelphia, Series 2, 7: 1–472.

Lepvrier, C., Fournier, M., Bérard, T., Roger, J. (2002): Cenozoic extension in coastal Dhofar (southern Oman): implications on the oblique rifting of the Gulf of Aden. – Tectonophysics, 357: 279–293. https://doi.org/10.1016/S0040-1951(02)00372-4

Madden, C., Schmidt, D. L., Whitmore, F. C. (1983): *Masritherium* (Artiodactyla, Anthracotheriidae) from Wadi Sabya, southwestern Saudi Arabia: an earliest Miocene age for the continental rift-valley volcanic deposits of the Red Sea margin. – United States Geological Survey, Open File Report 83-488, 24 pp. Prepared for the Ministry of Petroleum and Mineral Resources of the Kingdom of Saudi Arabia.

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, A, 192: 15–49.

Matsumoto, H. (1926): Contribution to the knowledge of the fossil Hyracoidea of the Fayum, Egypt, with description of several new species. – Bulletin of the American Museum of Natural History, 56: 253–350.

Noubhani, A., Hautier, L., Jaeger, J.-J., Mahboubi, M., Tabuce, R. (2008): Variabilité dentaire et crânienne de *Numidotherium koholense* (Mammalia, Proboscidea) from El Kohol: Eocene, Algeria. – Geobios, 41: 515–531. https://doi.org/10.1016/j.geobios.2007.09.002

Otero, O., Gayet, M. (2001): Palaeoichthyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: Palaeoecological and palaeobiogeographical implications. – Palaeogeography, Palaeoclimatology, Palaeoecology, 165: 141–169. https://doi.org/10.1016/S0031-0182(00)00158-9

Owen, R. (1848): Description of teeth and portions of jaw of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. – Quarterly Journal of the Geological Society of London, 4: 103–141. https://doi.org/10.1144/GSL.JGS.1848.004.01-02.21

Pickford, M. (1986a): Première découverte d'une faune mammalienne terrestre paléogène d'Afrique sub-saharienne. – Comptes rendus de l'Académie des sciences, Paris, Série II, 302: 1205–1210.

Pickford, M. (1986b): Première découverte d'un Hyracoïde paléogène en Eurasie. – Comptes rendus de l'Académie des sciences, Paris, Série II, 303: 1251–1254.

Pickford, M. (1990): Dynamics of Old World biogeographic realms during the Neogene: implications for biostratigraphy. – In: Lindsay, E., Fahlbusch, V., Mein, P. (eds), European Neogene Mammal Chronology (NATO ASI Series, Series A: Life Sciences, vol. 180). Plenum Press, New York, London, pp. 413–442. https://doi.org/10.1007/978-1-4899-2513-8_24

Pickford, M. (1991): Revision of the Neogene Anthracotheriidae of Africa. – In Salem, M. J., Hammuda, O. S., Eliagoubi, B. A. (eds), Geology of Libya, Volume 4. Elsevier, Amsterdam, pp. 1491–1525.

Pickford, M. (2015a): Large Ungulates from the Basal Oligocene of Oman: 1 – Embrithopoda. – Spanish Journal of Palaeontology, 30(1): 139–148.

Pickford, M. (2015b): Large Ungulates from the Basal Oligocene of Oman: 2 – Proboscidea. – Spanish Journal of Palaeontology, 30(2): 33–46.

Pickford, M. (2015c): Large ungulates from the basal Oligocene of Oman: 3 – Anthracotheriidae. – Spanish Journal of Palaeontology, 30 (2): 257–264.

Pickford, M. (2015d): *Bothriogenys* (Anthracotheriidae) from the Bartonian of Eoridge, Namibia. – Communications of the Geological Survey of Namibia, 16: 215–222.

Pickford, M. (2016): Revision of European Hyotheriinae (Suidae) and Doliochoeridae (Mammalia). – Münchner Geowissenschaftliche Abhandlungen, A, 44: 1–270.

Pickford, M., Gheerbrant, E., Sen, S., Roger, J., Al-Sulaimani, Z. (2014): Palaeogene non-marine molluscs from Oman: implications for the timing of uplift of the Dhofar Plateau and the opening of the Red Sea and Gulf of Aden. – In: Rollinson, H. R., Searle, M. P., Abbasi, I. A., Al-Lazki, A., Al-Kindi, M. H. (eds), Tectonic Evolution of the Oman Mountains. Special Publications, Geological Society, London, 392: 89–102. http://dx.doi.org/10.1144/SP392. https://doi.org/10.1144/SP392

Pickford, M., Morales, J. (1994): Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. – Palaeogeography, Palaeoclimatology, Palaeoecology, 112: 297–322. https://doi.org/10.1016/0031-0182(94)90078-7

Pickford, M., Thomas, H. (1994): Sexual dimorphism in *Moeripithecus markgrafi* from the early Oligocene of Taqah, Oman. – In: Thierry, B., Anderson, J. R., Roeder, J. J., Herrenschmidt, N. (eds), Current Primatology, vol. 1: Ecology and Evolution. Université Louis Pasteur, Strasbourg, pp. 261–264.

Pickford, M., Thomas, H., Sen, S., Roger, J., Gheerbrant, E., Al-Sulaimani, Z. (1994): Early Oligocene Hyracoidea (Mammalia) from Thaytiniti and Taqah, Dhofar Province, Sultanate of Oman. – Comptes rendus de l'Académie des sciences, Paris, Série II, 318: 1395–1400.

Platel, J. P., Roger, J. (1992): Explanatory Notes, Geological Map of Raysut, Sheet NE 39-16C, Scale 1:100,000. – Bureau de Recherches Géologiques et Minières, Orléans, France; Sultanate of Oman, Muscat, Ministry of Petroleum and Minerals, Directorate General of Minerals, 53 pp.

Rasmussen, D. T., Simons E. L. (1991): The oldest Egyptian hyracoids (Mammalia: Pliohyracidae): New species of *Saghatherium* and *Thyrohyrax* from the Fayum. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 182: 187–209.

Roger, J., Pickford, M., Thomas, H., de Broin, F., Tassy, P., Van Neer, W., Bourdillon-de-Grissac, C., Al-Busaidi, S. (1994a): Découverte de vertébrés fossiles dans le Miocène de la région du Huqf au Sultanat d'Oman. – Annales de Paléontologie, 80: 253–273.

Roger, J., Platel, J. P., Berthiaux, A., Le Métour, J. (1992): Explanatory Notes, Geological Map of Hawf, Sheet NE 39-16, Scale 1:250,000. – Bureau de Recherches Géologiques et Minières, Orléans, France; Sultanate of Oman, Muscat, Ministry of Petroleum and Minerals, Directorate General of Minerals, 51 pp.

Roger, J., Platel, J., Bourdillon-de-Grissac, C., Cavelier, C. (1994b): Geology of Dhofar: Geology and Geodynamic Evolution during the Mesozoic and Cenozoic; Ph.D. thesis. – MS, Geological Documents, Ministry of Petroleum and Minerals, Muscat, Sultanate of Oman, 259 pp. (copy in Bureau de Recherches Géologiques et Minières, France)

Roger, J., Platel, J. P., Cavelier, C., Bourdillon-de-Grissac, C. (1989): Donneées nouvelles sur la stratigraphie et l'histoire géologique du Dhofar (Sultanat d'Oman). – Bulletin de la Société Géologique de France, 2: 265–277.

Roger, J., Sen, S., Thomas, H., Cavalier, C., Al-Sulaimani, Z. (1993): Stratigraphic, palaeomagnetic and palaeoenvironmental study of the Early Oligocene vertebrate locality of Taqah (Dhofar, Sultanate of Oman). – Newsletters on Stratigraphy, 28: 93–119.
https://doi.org/10.1127/nos/28/1993/93

Sallam, H. M., Sileem, A. H., Miller, E. R., Gunnell, G. F. (2016): Deciduous dentition and dental eruption sequence of *Bothriogenys fraasi* (Anthracotheriidae, Artiodactyla) from the Fayum Depression, Egypt. – Palaeontologia electronica, 9.3.38A: 1–17.
https://doi.org/10.26879/646

Sanders, W. J., Gheerbrant, E., Harris, J. M., Saegusa, H., Delmer, C. (2010b): Proboscidea. – In: Werdelin, L., Sanders, W. J. (eds), Cenozoic Mammals of Africa. University of California Press, Berkeley, Los Angeles, London, pp. 161–251.
https://doi.org/10.1525/california/9780520257214.003.0015

Sanders, W. J., Kappelman, J., Rasmussen, D. T. (2004): New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. – Acta Palaeontologica Polonica, 49: 365–392.

Sanders, W., Rasmussen, D. T., Kappelman, J. (2010a): Embrithopoda. – In: Werdelin, L., Sanders, W. J. (eds), Cenozoic Mammals of Africa. University of California Press, Berkeley, Los Angeles, London, pp. 115–122.
https://doi.org/10.1525/california/9780520257214.003.0012

Schlosser, M. (1910): Über einige fossile Säugetiere aus dem Oligocän von Ägypten. – Zoologische Anzeiger, 35: 500–508.

Schmidt, M. (1913): Über Paarhufer der fluviomarinen schichten des Fajum. Odontographisches und osteologisches Material. – Geologische und Paläontologische Abhandlungen, NS, 11(3): 153–264.

Seiffert, E. R. (2006): Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. – Proceedings of the National Academy of Sciences, 103: 5000–5005.
https://doi.org/10.1073/pnas.0600689103

Seiffert, E. R. (2010): Chronology of Paleogene Mammals. – In: Werdelin, L., Sanders, W. J. (eds), Cenozoic Mammals of Africa. University of California Press, Berkeley, Los Angeles, London, pp. 19–26.
https://doi.org/10.1525/california/9780520257214.003.0002

Seiffert, E., Nasir, S., Al-Harthy, A., Groenke, J., Kraatz, B., Stevens, N., Al-Sayigh, A. (2012): Diversity in the later Paleogene proboscidean radiation: a small barytheriid from the Oligocene of Dhofar Governorate, Sultanate of Oman. – Naturwissenschaften, 99(2): 133–41.
https://doi.org/10.1007/s00114-011-0878-9

Shoshani, J., Tassy. P. (1992): Classifying elephants. – In: Shoshani, J. (ed.), Elephants. Weldon Owen, Sydney, pp. 22–23.

Shoshani, J., Tassy, P. (2005): Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behaviour. – Quaternary International, 126-128: 5–20.
https://doi.org/10.1016/j.quaint.2004.04.011

Sigé, B., Thomas, H., Sen, S., Gheerbrant, E., Roger, J., Al-Sulaimani, Z. (1994): Les chiroptères de Taqah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. – Münchner Geowissenschaftliche Abhandlungen, A, 26: 35–48.

Sileem, A. H., Sallam, H. M., Hewaidy, A. A., Gunnell, G. F., Miller, E. R. (2015): Anthracotheres (Mammalia, Artiodactyla) from the upper-most horizon of the Jebel Qatrani Formation, latest early Oligocene, Fayum Depression, Egypt. – Egyptian Journal of Paleontology, 15: 1–11.

Sileem, A. H., Sallam, H. M., Hewaidy, A. A., Miller, E. R., Gunnell, G. F. (2016): A new anthracothere (Artiodactyla) from the early Oligocene, Fayum, Egypt, and the mystery of African '*Rhagatherium*' solved. – Journal of Paleontology, 90(1): 170–181.
https://doi.org/10.1017/jpa.2016.13

Tassy, P. (1981): Le crâne de *Moeritherium* (Proboscidea, Mammalia) de l'Éocène de Dor el Talha (Libye). – Bulletin du Muséum national d'Histoire naturelle, Paris, 4ème série, 8, C (1): 87–147.

Thomas, H., Roger, J., Sen, S., Al-Sulaimani, Z. (1992): Early Oligocene vertebrates from Dhofar (Sultanate of Oman). – In: Geology of the Arab World. Cairo University, Cairo, pp. 283–293.

Thomas, H., Roger, J., Sen, S., Bourdillon de Grissac, C., Al-Sulaimani, Z. (1989): Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). – Geobios, 22: 101–120.
https://doi.org/10.1016/S0016-6995(89)80091-9

Thomas, H., Roger, J., Sen, S., Pickford, M., Gheerbrant, E., Al-Sulaimani, Z., Al-Busaidi, S. (1999): Oligocene and Miocene terrestrial vertebrates in the southern Arabian Peninsula (Sultanate of Oman) and their geodynamic and palaeogeographic settings. – In: Whybrow, P., Hill, A. (eds), Fossil Vertebrates of Arabia. Yale University Press, New Haven, pp. 430–442.

Thomas, H., Sen, S., Roger, J., Al-Sulaimani, Z. (1991): The discovery of *Moeripithecus markgrafi* Schlosser (Propliopithecidae, Anthropoidea, Primates) in the Ashawq Formation (Early Oligocene of Dhofar Province, Sultanate of Oman). – Journal of Human Evolution, 20: 33–49. https://doi.org/10.1016/0047-2484(91)90044-V

Tobien, H. (1978): The structure of the mastodont molar (Proboscidea, Mammalia), Part 3: The Oligocene Mastodont genera *Palaeomastodon*, *Phiomia* and the Eo-Oligocene Paenungulate *Moeritherium*. – Mainzer Geowissenschaftliche Mitteilungen, 6: 177–208.

Zalmout, I. S., Gunnell, G., Al-Mufarreh, Y., Ali, M., Nasser, A., Matari, A., Jamalaldeen, A., Gingerich, P. (2012): Oligocene Anthracotheriidae (Artiodactyla) from the Usfan and Shumaysi Formations, Western Saudi Arabia. – Geological Society of America Annual Meeting, Charlotte, 4–7 November, 2012, Abstracts with Programs, 44(7): 605.

Zalmout, I. S., Sanders, W. J., MacLatchy, L., Gunnell, G., Al-Muffareh, Y. A., Ali, M. A., Nasser, A.-A.H., Al-Masari, A. M., Al-Sobhi, S. A. (2010): New Oligocene primate from Saudi Arabia and the divergence of the apes and Old World monkeys. – Nature, 466(7304): 360–364 + 29 pp. https://doi.org/10.1038/nature09094

Appendix 1. GPS localisation (WGS 84 grid) of vertebrate localities in the Ashawq Formation near Aydim and Taqah, Dhofar Governorate, Oman (altitudes are from Google Earth).

Locality	Latitude : Longitude	Altitude
Omanitherium type locality	16°58'32.3"N : 53°30'55.6"E	927 m
Omanitherium I	16°58'30.9"N : 53°30'52.1"E	929 m
Thaytiniti lower site (2)	16°54'59.9"N : 53°25'38.2"E	944 m
Taqah mammal site	17°03'03.0"N : 54°27'10.7"E	25 m
Martin's *Lanistes* site	16°57'27.6"N : 53°26'09.3"E	942 m
Arsinoi-Omani site	16°58'06.6"N : 53°29'08.3"E	883 m
Ibrahim's snail site	16°56'48.4"N : 53°25'40.2"E	933 m
Omanitherium 17a (Axel's P3/)	16°57'32.1"N : 53°29'46.1"E	937 m
Omanitherium 17b (Mohammed's molar)	16°57'28.3"N : 53°29'43.3"E	935 m
Omanitherium 2nd incisor	16°57'27.4"N : 53°29'42.3"E	936 m
Turtle site	16°58'23.4"N : 53°28'04.2"E	969 m

Appendix 2. 2017 Field Catalogue, Ashawq Formation, near Aydim, Dhofar Governorate, Oman (for the stratigraphic positions of Beds A–D, see Text-figs 3, 4 and 5).

Catalogue n°	Taxon	Fossil remains	Stratigraphy and locality
TN 2017-01	Anthracothere	phalanx	Bed B, *Omanitherium* type locality
TN 2017-02	Mammal	bone fragment	Bed B, *Omanitherium* type locality
TN 2017-03	*Arsinoitherium*	m/3 and fragments	Bed B, *Omanitherium* type locality
TN 2017-04	*Arsinoitherium*	premolar	Bed B, *Omanitherium* type locality
TN 2017-05	Mammal	petrosal	Bed B, *Omanitherium* type locality
TN 2017-06	*Arsinoitherium*	premolar	Bed B, *Omanitherium* type locality
TN 2017-07	*Omanitherium*	enamel fragments	Bed B, *Omanitherium* type locality
TN 2017-08	*Omanitherium*	dentine fragments	Bed B, *Omanitherium* type locality
TN 2017-09	Mammal	bone fragments	Bed B, *Omanitherium* type locality
TN 2017-10	Chelonian	scutes	Bed B, *Omanitherium* type locality
TN 2017-11	Batoid	tooth plate	Bed B, *Omanitherium* type locality
TN 2017-12	*Pila*	shells (7)	Bed B, *Omanitherium* type locality
TN 2017-13	*Potamides*	shells (12)	Bed B, *Omanitherium* type locality
TN 2017-14	*Arabicolaria*	shell	Bed B, *Omanitherium* type locality
TN 2017-15	*Omanitopsis*	shell	Bed B, *Omanitherium* type locality
TN 2017-16	*Omanitherium*	P3/ left	Bed B, *Omanitherium* type locality
TN 2017-17	*Omanitherium*	P4/ right	Bed B, *Omanitherium* type locality
TN 2017-18	*Omanitherium*	M1/ right	Bed B, *Omanitherium* type locality
TN 2017-19	*Omanitherium*	i/1 lt	Bed B, *Omanitherium* type locality
TN 2017-20	*Omanitherium*	i/2 fragment	Bed B, *Omanitherium* type locality
TN 2017-21	*Pila*	shell	Bed A, *Omanitherium* site bottom of section
TN 2017-22	*Lanistes tricarinatus*	shells	Bed A, *Omanitherium* site bottom of section
TN 2017-23	*Carnevalea thaytinitiensis*	shells	Bed A, *Omanitherium* site bottom of section
TN 2017-24	*Potamides*	shells	Bed A, *Omanitherium* site bottom of section
TN 2017-25	*Arabicolaria*	shells	Bed A, *Omanitherium* site bottom of section
TN 2017-26	*Pila*	shells	Bed C, brown sand above *Omanitherium* site
TN 2017-27	*Arabicolaria*	shells	Bed C, brown sand above *Omanitherium* site
TN 2017-28	*Omanitopsis*	shells	Bed C, brown sand above *Omanitherium* site
TN 2017-29	*Conulinus*	shell	Bed C, brown sand above *Omanitherium* site
TN 2017-30	*Pacaudiella*	shells	Bed C, brown sand above *Omanitherium* site
TN 2017-31	Bivalves	internal moulds	Bed C, brown sand above *Omanitherium* site
TN 2017-32	*Ostrea*	shells	Bed C, brown sand above *Omanitherium* site

Appendix 2. continued.

Catalogue n°	Taxon	Fossil remains	Stratigraphy and locality
TN 2017-33	Sponge	body fossil	Bed C, brown sand above *Omanitherium* site
TN 2017-34	*Pila*	shells	Bed D, white marl above *Omanitherium* site top of section
TN 2017-35	Olive snails	shells	Bed D, white marl above *Omanitherium* site top of section
TN 2017-36	Marine snails	internal moulds	Bed D, white marl above *Omanitherium* site top of section
TN 2017-37	Bivalves	internal moulds	Bed D, white marl above *Omanitherium* site top of section
TN 2017-38	*Pecten*	shell	Bed D, white marl above *Omanitherium* site top of section
TN 2017-39	Echinoid	large specimen	Bed D, white marl above *Omanitherium* site top of section
TN 2017-40	Echinoid	small specimen	Bed D, white marl above *Omanitherium* site top of section
TN 2017-41	Sponge	body fossil	Bed D, white marl above *Omanitherium* site top of section
TN 2017-42	*Vermetus*	calcareous tube	Bed D, white marl above *Omanitherium* site top of section
TN 2017-43	*Omanitherium*	i/2 left	Mohammed’s i/2 site
TN 2017-44	*Omanitherium*	P3/ right	Axel’s P3/ site
TN 2017-45	*Omanitherium*	molar fragments	Axel’s P3/ site
TN 2017-46	Chelonian	scutes	Axel’s P3/ site
TN 2017-47	*Potamides*	shells (2)	Axel’s P3/ site
TN 2017-48	*Lanistes tricarinatus*	shells	Axel’s P3/ site
TN 2017-49	*Pila*	shells	Axel’s P3/ site
TN 2017-50	*Omanitherium*	molar fragments	Mohammed’s molar site
TN 2017-51	*Omanitherium*	i/1 right	Mohammed’s molar site
TN 2017-52	*Omanitherium*	enamel fragments	Arsinoi/Omani site
TN 2017-53	*Arsinoitherium*	tooth fragment	Arsinoi/Omani site
TN 2017-54	Mammal	bones	Arsinoi/Omani site
TN 2017-55	Mammal	bones	Arsinoi/Omani site
TN 2017-56	*Lanistes tricarinatus*	shells	Martin’s *Lanistes* site
TN 2017-57	*Carnevalea thaytinitiensis*	shells	Martin’s *Lanistes* site
TN 2017-58	*Arabicolaria*	shells	Martin’s *Lanistes* site
TN 2017-59	*Omanitopsis*	shells	Martin’s *Lanistes* site
TN 2017-60	*Carnevalea thaytinitiensis*	shells	Ibrahim’s snail site
TN 2017-61	*Lanistes tricarinatus*	shells	Ibrahim’s snail site
TN 2017-62	*Pila*	shells	Ibrahim’s snail site
TN 2017-63	*Arabicolaria*	shells	Ibrahim’s snail site
TN 2017-64	*Pacaudiella*	shells	Ibrahim’s snail site
TN 2017-65	*Potamides*	shells	Ibrahim’s snail site
TN 2017-66	*Lanistes tricarinatus*	shells	Thaytiniti shell site
TN 2017-67	*Carnevalea thaytinitiensis*	shells	Thaytiniti shell site
TN 2017-68	*Pila*	shells	Thaytiniti shell site
TN 2017-69	*Omanitopsis*	shells	Thaytiniti shell site
TN 2017-70	Chelonian	scutes	Bed B, *Omanitherium* type locality
TN 2017-71	*Pila*	shells	Bed B, *Omanitherium* type locality
TN 2017-72	*Potamides*	shells	Bed B, *Omanitherium* type locality
TN 2017-73	Chelonian	scutes	Turtle site (3)
TN 2017-74	*Omanitherium*	mandible fragments and roots	Turtle site (3)
TN 2017-75	*Omanitherium*	enamel fragments	Turtle site (3)
TN 2017-76	Anthracothere	upper molar fragment	Turtle site (3)
TN 2017-77	Polypterid	tooth plate	Turtle site (3)
TN 2017-78	Mammal	bone fragments	Turtle site (3)
TN 2017-79	*Omanitherium*	M3/ fragment and mandible pieces	Turtle site (2)
TN 2017-80	*Omanitherium*	enamel and jaw fragments	Turtle site (1)

Appendix 2. continued.

Catalogue n°	Taxon	Fossil remains	Stratigraphy and locality
TN 2017-81	*Omanitherium*	enamel fragments	Turtle site (1)
TN 2017-82	*Arsinoitherium*	enamel fragments	Turtle site (1)
TN 2017-83	Chelonian	scutes	Turtle site (1)
TN 2017-84	Vertebrate	coprolites containing snails	Turtle site (1)
TN 2017-85	*Omanitherium*	i/2 right	Thaytiniti lower site (2)
TN 2017-86	*Omanitherium*	enamel fragments	Thaytiniti lower site (2)
TN 2017-87	Mammal	bones	Thaytiniti lower site (2)
TN 2017-88	Crocodile	scute fragments	Thaytiniti lower site (2)
TN 2017-89	*Omanitherium*	symphysis fragment and bones	Mohammed’s i/2 site