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Large ungulates from the basal Oligocene of Oman: 1 - Embrithopoda

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ABSTRACT

Arsinoitheres (Embrithopoda, Mammalia) have been known to occur in the Early Oligocene of Oman since 1992, yet the fossils on which the records were based have not yet been published. This contribution rectifies this situation and provides the first secure basis for the presence of arsinoitheres in Oman, some post-cranial material previously attributed to this genus being of uncertain affinities. The Omani records and the one in the Shumaysi Formation, Saudi Arabia, extend the distribution of *Arsinoitherium andrewsi* to the northeastern extremities of the Afro-Arabian Continent.

Keywords: *Arsinoitherium*, Embrithopoda, Oligocene, Oman, biogeography.

RESUMEN

Arsinoitheres (Embrithopoda, Mammalia) se han reconocido en el Oligoceno Temprano de Oman desde 1992, aunque los fósiles en los que están basados estos registros aún no han sido publicados. Este trabajo solventa esta situación y proporciona la primera base segura de la presecia de arsinoitheres en Oman, algún material post-craneal atribuido previamente a este género de afinidades inciertas. El registro de Oman y el de la Formación Shumaysi, Arabia Saudi, extiende la distribution of *Arsinoitherium andrewsi* a las extremidades del noroeste del Continente Afro-Arabia.

Palabras clave: *Arsinoitherium*, Embrithopoda, Oligoceno, Oman, biogeografia.

1. INTRODUCTION

The genus *Arsinoitherium* was first recorded in Oman by Thomas *et al*. (1992) and Roger *et al*. (1993, 1994), but the fossils were not described, featuring only in a faunal list. The various teeth upon which basis Thomas *et al*. (1992) listed the genus *Arsinoitherium* in the Early Oligocene of Oman are described herein and the biogeographic implications of the fossils are discussed. A fossil ulna attributed to *Arsinoitherium* by Al Sayigh *et al*. (2008) is too small to belong *Arsinoitherium andrewsi* and it could represent *Omanitherium* or *Arcanotherium* (or *Numidotherium*) rather than to *Arsinoitherium*.

2. GEOLOGICAL AND PALAEOENVIRONMENTAL CONTEXTS

The fossils described herein came from two localities in the Dhofar region of Oman, Taqah (TQ) near Wadi Darbat east of Salalah, some 30 metres above sea-level, and Thaytiniti (TH) west of Salalah at an altitude of over 900 metres. Two sub-localities in Thaytiniti (TH 1 and TH 2) yielded remains of arsinoitheres (Fig. 1).

The geological and stratigraphic context of the Dhofar fossils was established by Thomas *et al*. (1989, 1992, 1999). There is general acceptance of the correlations proposed by these authors, that Thaytiniti dates from the base of the Rupelian, and Taqah from slightly later in the Rupelian (Fig. 2) Coster *et al*. (2012).

Fossil freshwater gastropods and land snails from coeval deposits in the same regions show strong African affinities (Pickford *et al*., 2014) and indicate a sub-humid savannah ecosystem interspersed with swamps and stands of dense woodland, close to the ancient sea shore. Like their Egyptian relatives, the Omani arsinoitheres lived near the sea, their remains often being found close to, or within, sediments yielding marine and brackish water molluscs and foraminifers.

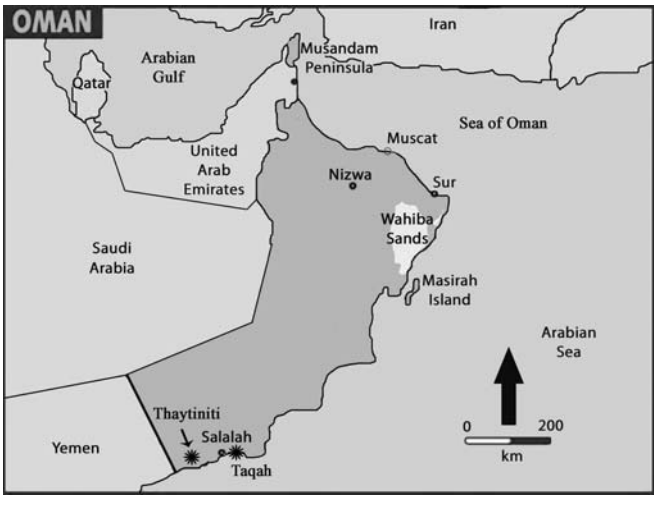

Figure 1. Location of Thaytiniti and Taqah, Oman.

3. MATERIALS AND METHODS

The fossils described herein are curated at the Oman Natural History Museum, Muscat, Oman (ONHM). Comparisons were made with fossils stored at the Natural History Museum, London (NHMUK) and the Muséum National d'Histoire Naturelle, Paris (MNHN).

Specimens were measured with sliding calipers to the nearest 0.1 mm. Images were acquired with a Sony Cybershot 16.1 megapixel camera and treated with Photoshop Elements 3 to increase contrast and to remove unwanted background. Scale bars were added manually as it has been found that a combination of parallax and digital effects can result in inaccurate scaling based on scales included with the fossil at the time of image acquisition.

Dental nomenclature of arsinoithere teeth was defined by Court (1992a). Upper teeth are identified by capital letters P – premolar, M – molar, lower teeth are in lower case letters p – premolar, m – molar. In addition, in order to avoid misprints or typographic errors, the upper teeth have a forward slash (which represents the occlusal surface) after the merisitic position (P4/ - upper fourth premolar, M1/ - upper first molar), for the lower teeth the slash is before the meristic position (p/1 – lower first premolar; m/3 – lower third molar).

3.1. Fossil arsinoithere dental elements from Oman described in this paper

Thaytiniti - ONHM TN 1992-3, lingual half of right P4/; ONHM TN 1992-1, distal half of left lower molar; ONHM TH 7 - distal enamel of a left M3/.

Taqah - ONHM TQ 1992-1, left m/3; ONHM TQ 1992-2, right M1/ heavily worn; ONHM TQ 1992-3, left p/1.

4. SYSTEMATIC PALAEONTOLOGY

Order EMBRITHOPODA Andrews, 1906
Family **Arsinoitheriidae** Andrews, 1904
Genus *Arsinoitherium* Beadnell, 1902a

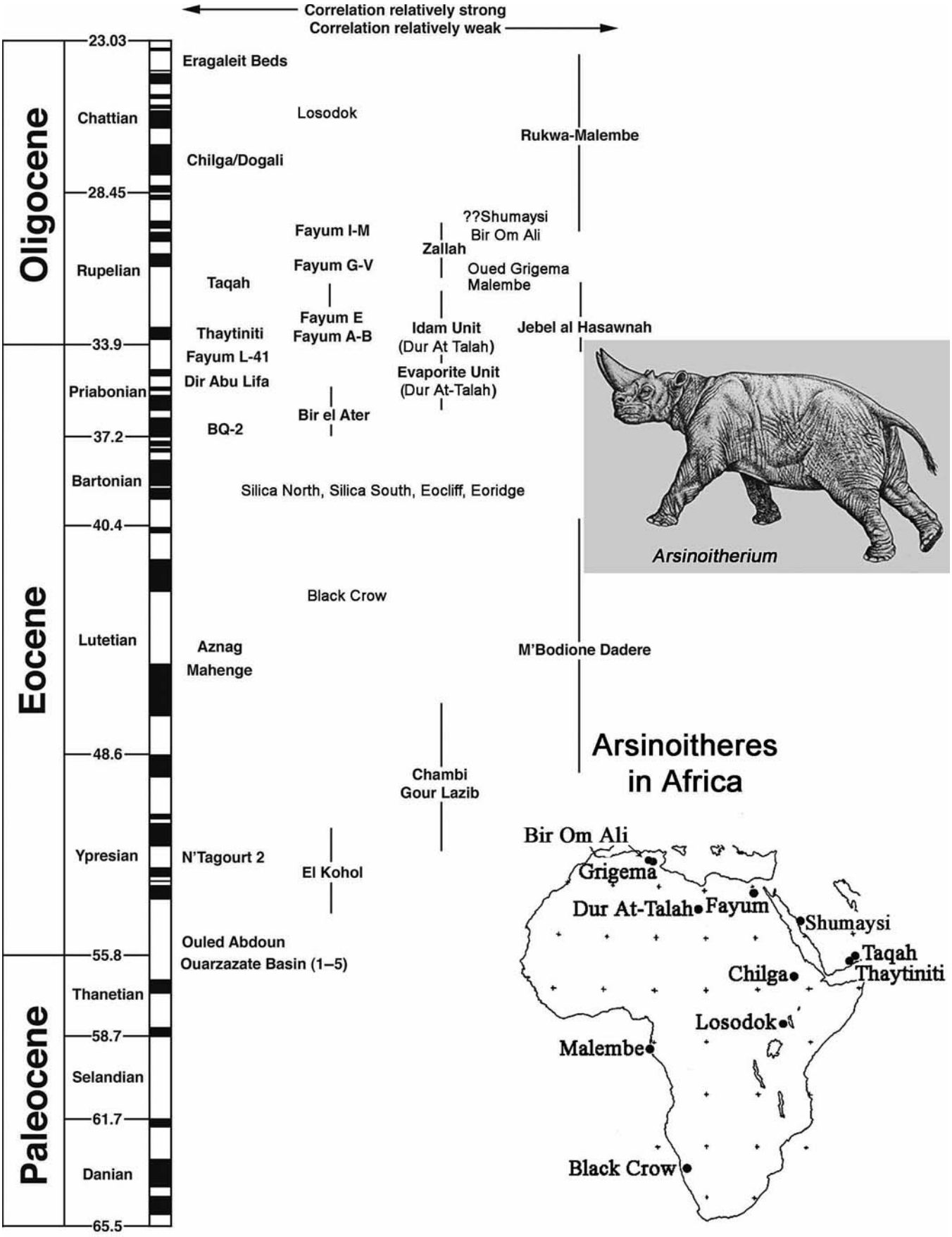

Figure 2. Geographic and stratigraphic distribution of arsinoitheres in Afro-Arabia. Shumaysi Early Oligocene (Zalmout *et al*., 2012). Time scale is from Seiffert (2010) with new content added.

Genus diagnosis. For genus diagnosis of *Arsinoitherium*, see Sanders *et al*. (2010).

Arsinoitherium andrewsi Lankester, 1903

Species diagnosis. Large species of *Arsinoitherium* in which the upper premolars show the medifossette opening lingually and closed distally, and the m/3 exhibits a distinct and well-developed hook-like talonid behind the distal lophid.

Description.

Upper dentition. P4/ is represented by a moderately worn tooth lacking the ectoloph (ONHM TN 1992-3) (Fig. 3.1). The mesial cingulum extends across the front of the tooth from the parastyle. There is a deep valley between this cingulum and the protocone, which is a large rounded bulbous cusp, decapitated by wear. There is a distinct waist between the protocone and the paracone + parastyle marked by the protocone-paracone groove. Behind the protocone there is a valley, which separates it from the hypocone. Buccal to the hypocone is the metacone from which it is separated by a waist, corresponding to the groove on the anterior aspect of the hypocone and metacone. The fossette (here termed the medifossette) between the protoloph (parastyle + paracone + protocone) and the distoloph (mesostyle + metacone + hypocone) is capacious and deep and opens lingually at the lingual notch. There are three roots on the lingual side.

The right M1/ (ONHM TQ 1992-2) is deeply worn, leaving little detail of the crown morphology (Fig. 4.2). Nevertheless, the deep valley between the parastyle and mesostyle is evident, as are the depths of the fossettes in front of and behind the protocone, the one in front being bordered anteriorly by the mesial cingulum, the one behind (the medifossette) by the hypocone.

ONHM TH 7 was compared with teeth in situ in skulls housed in the NHMUK, London, and the MNHN, Paris, and is compatible with the distal enamel surface of a left third upper molar (Fig. 3.2). It is close in morphology and dimensions to *Arsinoitherium andrewsi* and *Arsinoitherium zitteli* from the Fayum, Egypt (Tables 1 and 2). The enamel is concave on the lingual part of the distal loph and convex on the buccal side. On this basis the Thaytiniti specimen is likely to be from the left side. The specimen is moderately worn, the remaining crown height being 74 mm, compared with an unworn crown height on 106.5 mm in NHMUK M 8825. Even with this crown height, the Thaytiniti arsinoithere is exceptionally hypsodont, a feature that distinguishes *Arsinoitherium* from other embrithopods such as *Namatherium* (Pickford *et al*., 2008). The enamel surface is very lightly rugose, with clear alternating stripes of enamel typical of arsinoitheres (von Koenigswald, 2013). Enamel is thin (1.7 mm at the occlusal surface) as in the Egyptian species.

Table 1. Measurements (in mm) of arsinoithere M3/s from Oman and Egypt.

Catalogue	Tooth	Height of distal enamel
NHML M 8825	Right M3/ unworn	106.5
NHML M 8802	Right M3/ lightly worn	94.5
ONHM TH 7	Left M3/ medium worn	74

Table 2. Measurements (in mm) of the teeth of Omani *Arsinoitherium andrewsi*.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
ONHM TQ 1992-1	Left m/3	70.7	41.8
ONHM TQ 1992-2	Right M1/	52.0	50.0
ONHM TQ 1992-3	Left p/1	17.7	18.0
ONHM TN 1992-1	Left m/2 rear lophid	--	34.6
ONHM TN 1992-3	Right P4/	36.1	--

Lower dentition. The p/1 from Taqah (ONHM TQ 1992-3) is well preserved with moderate wear (Fig. 4.1). The single root marks this tooth as the anterior premolar, the other premolars being double-rooted (Andrews, 1906; Court, 1992a). The buccal wall of the tooth has a prominent groove running from the apex towards the root but stopping short of the cervix. The lingual side of the tooth has strong, sharp, preparaconid and postentoconid cristids descending towards the short lingual cingulum; and there is a metaconid crest opposite the buccal groove. The enamel extends much further rootwards buccally than lingually, but mesially and distally the profiles of the cervix are the same.

The transversely oriented distal lophid of the lower molar, probably a second lower molar (ONHM TN 1992-1) has a prehypocristid which is directed mesiolingually from the midline of the tooth towards the lingual side of the median transverse valley (Fig. 3.3). There is a strong distal cingulum which descends in altitude from the lingual to the buccal side of the tooth. The cervix is thus considerably higher on the lingual side than it is on the buccal side.

The Taqah m/3 (ONHM TQ 1992-1) is bilophodont with a well-developed talonid positioned to the lingual side of the midline of the crown and well separated from the distal lophid (Fig. 4.3). The talonid is narrower bucco-lingually than the two anterior lophids. The preprotocristid descends mesio-buccally to fuse with the mesial cingulum. The premetacristid descends mesially and only slightly buccally, joining the mesial cingulum quite close to the lingual margin of the crown. The mesial lophid is slightly obliquely oriented such that the protoconid is more anteriorly positioned than the metaconid. The second lophid shows a similar slightly oblique arrangement between the hypoconid and the

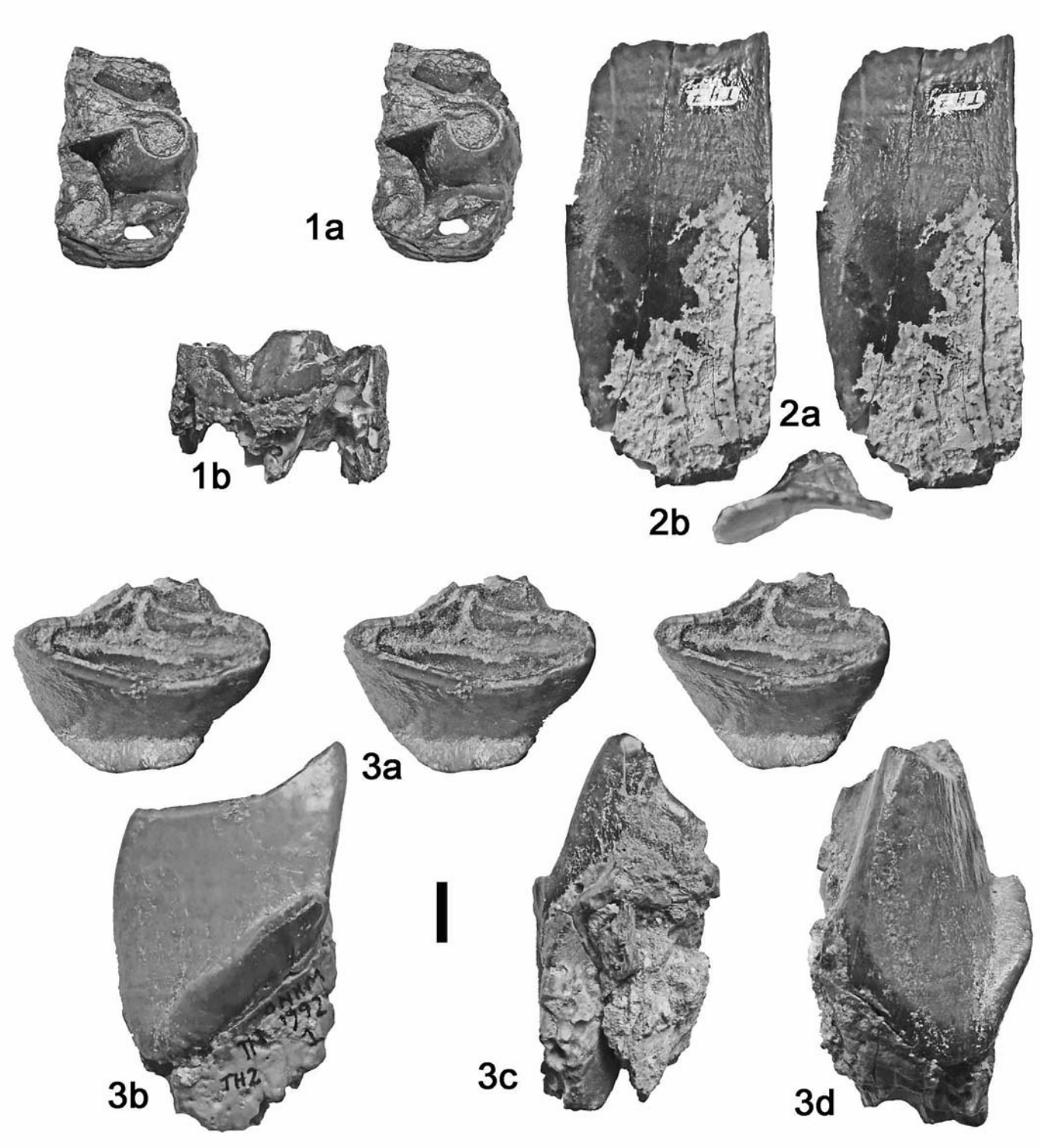

Figure 3. *Arsinoitherium andrewsi* from Thaytiniti, Oman. **1)** ONHM TN 1992-3, lingual portion of a right P4/, **(1a)** stereo occlusal view, **(1b)** lingual view. **2)** ONHM TH 7, part of the rear loph of a left M3/, **(2a)** distal stereo view, **(2b)** occlusal view to show thin enamel and concavo-convex curvature of the distal surface. **3)** ONHM TN 1992-1, distal lophid of a left lower molar (probably m/2) from locality TH 2, **(3a)** stereo triplet of the occlusal view, **(3b)** distal view, **(3c)** lingual view, **(3d)** buccal view (scale: 10 mm).

entoconid. The prehypocristid departs from the midline of the tooth towards the lingual side of the median transverse valley blocking its lingual end. There is a strong wear facet along this cristid. The hook-like talonid is prominent, is well separated from the second lophid, is about half the height of the other cusps, and about half the breadth of the tooth.

5. DISCUSSION

Sanders *et al*. (2010) concluded that there was a single species of *Arsinoitherium* in the Fayum sequence. However, there are two upper premolar morphotypes and two m/3 morphotypes in the available samples, indicating the presence of two taxa, the differences noted being outside the usual range of variation related to sexual dimorphism.

The P4/ from Thaytiniti, even though incomplete, closely matches the P4/ in NHMUK M 8463 (Andrews, 1906, pl. 2; Court, 1992b, pl. 2) but is radically different from the P4/ in NHMUK M 8461 (the holotype of *Arsinoitherium zitteli*) illustrated by Andrews (1906, text-fig.6, pl. 4) and Court (1992a, fig. 2) (Fig. 4). In the former the medifossette opens lingually and is walled off distally, whereas in the latter, the medifossette opens distally and is walled off lingually. Such differences are not due to different stages of wear, and are unlikely to be due to sexual dimorphism. They reflect divergent functional occlusal relationships between the upper and lower premolars, implying different ways of mastication (Court, 1992a).

Lower third molars of arsinoitheres from the Fayum, Egypt, illustrated by Andrews (1906) and Court (1992a) show poorly developed talonids which are little more than distal cingula not projecting very far distally. A specimen curated in the MNHN, Paris, however, shows a prominent hook-like talonid in the m/3 located in the lingual half of the tooth (Mondegar Fernandez *et al*., 2008). The difference in m/3 talonid development in some specimens from the Fayum and that from Taqah is probably of taxonomic significance. The question needs to be examined in greater detail, but the morphological variability in the material currently classified in *Arsinoitherium zitteli* by Sanders *et al*. (2010) is too great for all of it to belong to a single species. The validity of a second species *Arsinoitherium andrewsi* is accepted here, and the Omani material is attributed to this second taxon.

5.1. Diversity in Fayum arsinoitheres

Sanders *et al*. (2010) considered that *Arsinoitherium andrewsi* Lankester, 1903, was a junior synonym of *Arsinoitherium zitteli* Beadnell, 1902a (1902b). However, there is significant morphological varaibility among the specimens previously identified as *Arsinoitherium zitteli*. There are two kinds of talonid in the m/3, one with an elongated hook-like talonid well separated from the posterior lophid, and positioned on the lingual side of the crown. In addition there are two kinds of P4/ in the specimens from the Fayum, one in which the medifossette opens lingually, the other in which the medifossette opens distally. On the basis of post-cranial bones, *Arsinoitherium andrewsi* is a much larger species than *A. zitteli* as demonstrated by Andrews (1906) and confirmed by Mondegar Fernandez *et al*. (2008). The Taqah and Thaytiniti embrithopod fossils are close in morphology and dimensions to specimens attributed to *Arsinoitherium* from the Fayum, Egypt (Andrews, 1906; Court, 1992a, b) but on the basis of their morphology they are considered to belong to the second form of arsinothere represented in the Fayum, *Arsinoitherium andrewsi*. Until better material is found, some doubt will persist concerning the identification of the species present in Oman, although the balance of the available evidence (P4/ and m/3 morphology) suggests that it does not represent *A. zitteli*, in which case it is likely to belong to *A. andrewsi* or less likely to an undescribed species. Pending the recovery of additional material, the author prefers to attribute the Omani material to an existing taxon, rather than to erect a new species.

In summary it is not known whether the differences in upper premolar morphology and m/3 talonid development reflect species differences, or a peculiar form of polymorphism. If the former is the case, then the upper premolars in which the medifossette opens lingually could represent *Arsinoitherium andrewsi*. The upper premolars in which the medifossette opens distally belong to *Arsinoitherium zittelli*, as this morphotype occurs in the holotype (Andrews, 1906). The m/3 with well-developed talonid would belong to *Arsinoitherium andrewsi*, and those with only a distal cingulum would belong to *Arsinoitherium zitteli*. But to resolve the uncertainty, associated material is required.

A fossil ulna from the Dhofar region of Oman was attributed to *Arsinoitherium* Al-Sayigh *et al*. (2008). However, examination of the specimen, which is curated at the Sultan Qaboos University, Muscat, reveals that it is too small to belong to *Arsinoitherium zitteli* or *Arsinoitherium andrewsi*. It is however, compatible in dimensions with the proboscidean (barytherioid?) *Omanitherium* found in the same region (Seiffert *et al*., 2012) and it is here considered more likely to belong to this genus, or to *Arcanotherium* Delmer (2009) than to an embrithopod or to *Barytherium*.

Doubts have been raised about the validity of *Arsinoitherium giganteum* from Chilga, Ethiopia (Mondegar Fernandez *et al*., 2008), as it appears that the main difference from *Arsinoitherium zitteli* concerns its supposedly greater dental dimensions and differences in post-cranial proportions (Sanders *et al.*, 2004). However,

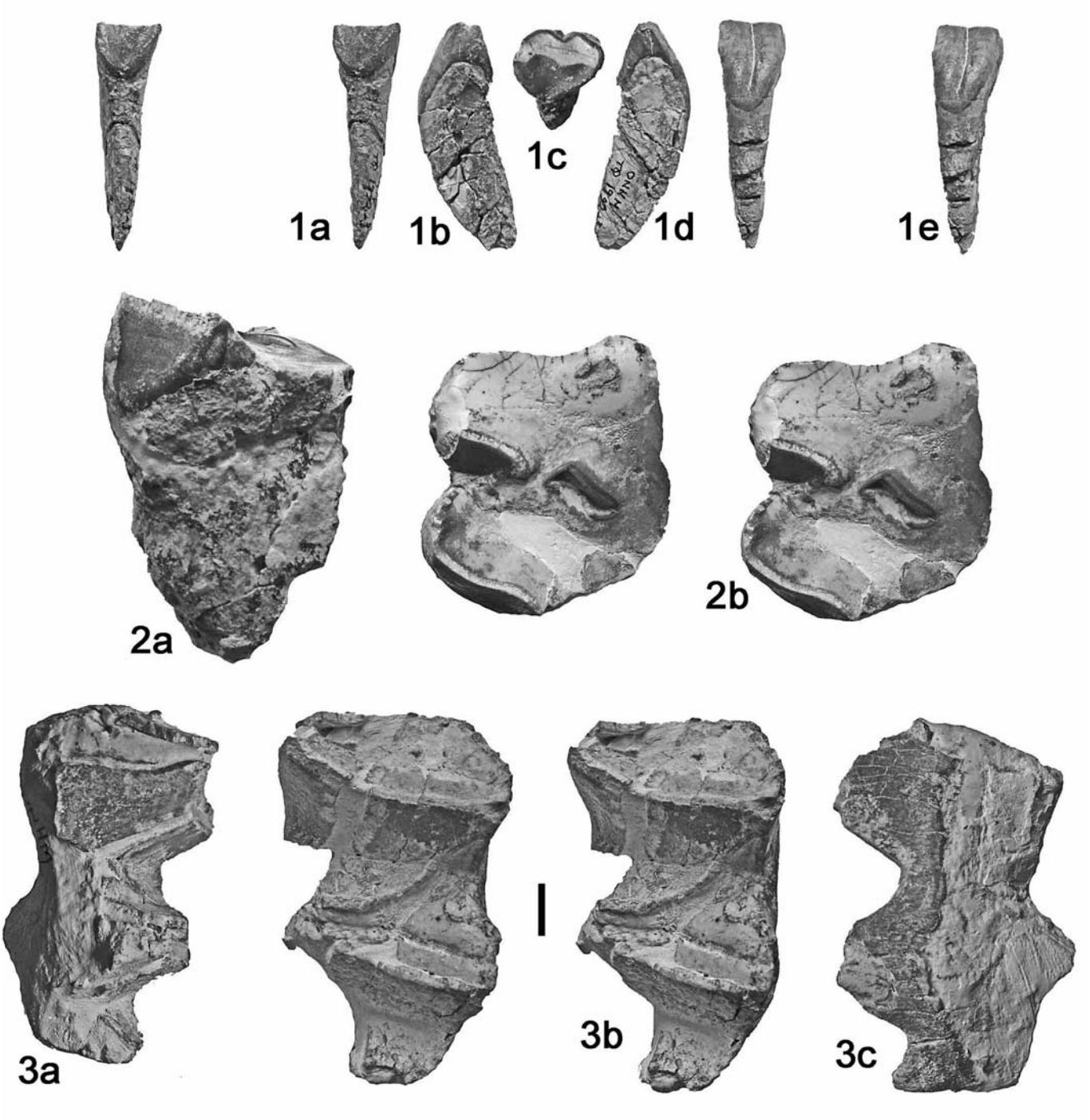

Figure 4. *Arsinoitherium andrewsi* from Taqah, Oman. **1)** ONHM TQ 1992-3, left p/1, **(1a)** stereo lingual view, **(1b)** distal view, **(1c)** occlusal view, **(1d)** mesial view, **(1e)** stereo buccal view. **2)** ONHM TQ 1992-2, deeply worn right M1/, **(2a)** distal view, **(2b)** stereo occlusal view. **3)** ONHM TQ 1992-1, left m/3, **(3a)** buccal view, **(3b)** stereo occlusal view, **(3c)** lingual view (scale: 10 mm).

the reported differences in dimensions of the teeth could be due to different ways of measuring the teeth related to the peculiar style of hypsodonty and crown curvature that typify teeth of this genus which results in very divergent occlusal length/breath proportions at different wear stages.

5.2. Biogeography and Biochronology

Arsinoitheres have been recorded from localities in northern, equatorial and southern Africa ranging in age from Middle Eocene to Late Oligocene (Pickford *et*

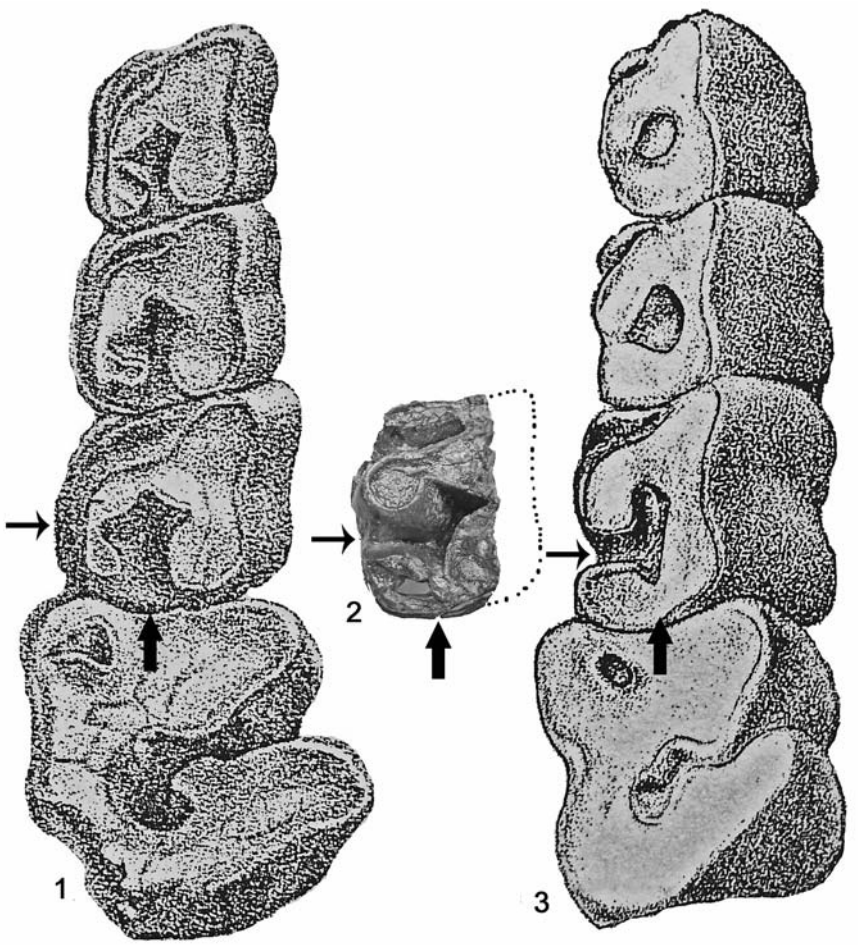

Figure 5. Comparison of left upper cheek teeth of *Arsinoitherium* from the Fayum, Egypt and Thaytiniti, Oman. **1)** NHMUK M 8461, left P2/-M1/ (holotype of *Arsinoitherium zitteli*). **2)** ONHM TN 1992-3, right P4/ (reversed for comparison). **3)** NHMUK M 8463, left P2/-M1/ attributed to *Arsinoitherium andrewsi*. Note the differences between lingually closed medifossette in 1) and the lingually opening medifossette in 2) and 3) (small arrows) combined with distally open medifossette in 1) but medifossette closed distally in 2) and 3) (thick arrows). Images 1) and 3) are reproduced from Andrews (1906). Note the slightly different orientations of the images in Andrews (1906) in which 1) was drawn with the occlusal surface horizontal, while in 3) the occlusal surface slopes slightly lingually.

al., 2008; Sanders *et al*., 2010) (Fig. 2). *Namatherium blackcrowense* is a primitive arsinoithere with wide, flaring, zygomatic arches and relatively brachyodont cheek teeth. It is known from a partial skull from the Middle Eocene epikarst deposits at Black Crow, Namibia (Pickford *et al*., 2008).

The genus *Arsinoitherium* has been reported from Late Eocene to Late Oligocene strata, principally from the Fayum deposits of Egypt (Court, 1992a, b) but also from Dur At-Talah, Libya, and Chilga, Ethiopia (Kappelman *et al*., 2003; Sanders *et al*., 2004) as well as in younger sediments at Losodok, Kenya (Rasmussen & Gutierrez, 2009). An arsinoithere tooth from Malembe, Angola, was described by Pickford (1986, 1987). A paper was submitted several years ago concerning the presence of *Arsinoitherium zitteli* at Oued Grigema, Tunisia, based on the distal loph of an upper third molar (Pickford, submitted) but recent events in the region seem to have delayed publication. Other remains from Late Eocene deposits at Bir Om Ali, near Chambi, Tunisia, were attributed to *Arsinoitherium*? by Vialle *et al*. (2013). Recently, Embrithopods have been reported from the Usfan (Late Eocene) and Shumaysi (Early Oligocene) formations on the Red Sea side of Saudi Arabia (Zalmout *et al*., 2012) but the fossils have not yet been described in detail, although one tooth has been figured (Zalmout *et al*., 2010, supplementary figure 1k, 1l).

The Omani M3/ is compatible in dimensions and morphology to a specimen from Oued Grigema, Tunisia (Pickford, submitted) but is much bigger and more hypsodont than that of *Namatherium blackcrowense* from Namibia (Pickford *et al*., 2008).

Given the long chronological range and continent-wide distribution of arsinoitheres in Africa during the Eocene and Oligocene, the presence of the group in the Early Oligocene of the Arabian Peninsula is not surprising. Because of dental differences from *Arsinoitherium zitteli*, the fossils from Thaytiniti and Taqah, Oman, are excluded from this species. They are considered to belong to the species *Arsinoitherium andrewsi* the second species of embrithopod defined at the Fayum, Egypt (Beadnell, 1902a, b; Lankester, 1903; Andrews, 1904, 1906).

The mammalian fauna from Thaytniti and Taqah, Oman contains many taxa, which also occur in the Fayum deposits (Thomas *et al*., 1992, 1999). The arsinoithere fossils from Oman augment the similarities between the Oligocene faunas of the two regions.

5.3. Palaeoenvironment

Abundant and diverse non-marine molluscan faunas from many localities at Thaytiniti and Taqah reveal that the palaeoenvironment in the Dhofar region of Oman during basal Oligocene times was likely to have comprised sub-humid savannah with swamps and dense stands of woodland (Pickford *et al*., 2014). The deposits accumulated close to sea-level, but those at Thaytiniti now stand at an altitude of over 900 metres, as a result of tectonic activity that uplifted the Dhofar Mountains some time later than the Rupelian stage (probably during the Miocene), leaving slivers of the deposits, such as those at Taqah, close to sea-level.

6. CONCLUSIONS

Several teeth from two Rupelian localities, Thaytiniti and Taqah, in Oman, are attributed to *Arsinoitherium andrewsi*, on the basis of the morphology of the P4/ and m/3, which differ from the type specimen and other material of *Arsinoitherium zitteli* from the Fayum, Egypt (Andrews, 1906, pl. 4.2). This taxonomic decision is influenced by the fact that some of the the Fayum sample contains P4/s similar to the Omani specimen (Andrews, 1906, pl. 2). The elongated and well-developed talonid in the Omani m/3 is absent in most specimens from the Fayum, but is present in one specimen curated in the MNHN, Paris. The arsinoitheres from Oman add to the list of taxa which occur in both the Early Oligocene deposits of Oman and the Fayum succession, Egypt.

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