

THE ORIGIN OF AFRO-ARABIAN ‘DIDELPHIMORPH’ MARSUPIALS

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Abstract: New specimens of *Peratherium africanum* from Early Oligocene deposits of the Fayum, Egypt, provide key information on the relationships of the species. These include the first maxilla to be found and two additional dentaries. The maxilla can be demonstrated to belong to the same species as the holotype dentary by study of the occlusal relationships of upper and lower molars. It can be shown by several synapomorphies that *P. africanum* is the sister species to European Bartonian–Rupelian *Peratherium lavergnense*. *P. africanum* therefore belongs to the ‘didelphimorph’ family Herpetotheriidae, not to the peradectimorph family Peradectidae. The genus *Qatranitherium*,

previously erected for this species alone, is here synonymized with *Peratherium*. Comparison with ‘didelphimorphian’ taxa from early Paleogene deposits of South America suggests more remote relationships, indicating an origin for *P. africanum* by dispersal from Europe as originally envisaged. The more precise relationships deduced here help to constrain the time interval for dispersal to Afro-Arabia, probably during the earliest Oligocene sea-level low.

Key words: palaeobiogeography, *Peratherium*, Eocene, Oligocene, dispersal, mammal.

EXTANT marsupials are represented by approximately 331 living species distributed in the Americas and the Australasian region (Kirsch *et al.* 1997; Wilson and Reeder 2005), but the group had a wider distribution in the past, with fossils now reported from all continents. The marsupial fauna of Africa is the least well known, with significantly higher diversity reported from Antarctica (Goin *et al.* 1999). Marsupials are only known to have existed in Africa between the early Eocene and the early Oligocene, and the short taxonomic history of these forms is already controversial, as explained below.

The first reported discovery of an extinct Afro-Arabian marsupial, and still the best known, was from Early Oligocene deposits of Egypt (Bown and Simons 1984) and subsequently named *Peratherium africanum* Simons and Bown, 1984. *Peratherium* remains central to discussions of marsupial biogeography, as its presence in Africa suggests either (1) dispersal to Africa from Europe or (2) dispersal from South America to Europe via Africa. Slightly older Late Eocene strata have recently yielded a possible second Egyptian marsupial of uncertain affinities

(Sánchez-Villagra *et al.* 2007). Crochet (1984) described the species *Garatherium mahboubii* from Early Eocene deposits of Algeria (see also Mahboubi *et al.* 1986), but the marsupial affinities of this species were contested by Gheerbrant (1995), who aligned *G. mahboubii* with didelphodont members of Adapisorculidae, a group of enigmatic early Paleogene placentals known entirely from dental remains (Gheerbrant 1991, 1995). McKenna and Bell (1997) classified *Garatherium* within the Herpetotheriinae, a subfamily of the paraphyletic ‘Didelphidae’ assemblage currently being used by most marsupial taxonomists working on isolated teeth from the Paleogene of Laurasia and Africa (Goin 1993). The genus *Qatranitherium* was erected by Crochet *et al.* (1992) to include a lower deciduous tooth (referred to dP₃) from early Oligocene deposits in Oman as well as the *P. africanum* material described by Bown and Simons (1984). The only other Paleogene African marsupial is Early Eocene *Kasserinotherium tunisiense* Crochet, 1986, which is known by two upper molars recovered from Chambi in Tunisia; this species was referred to the Peradectidae by Crochet. Only

two of these four described African marsupial species are uncontested members of the group: *Peratherium africanum* and *Kasserinotherium tunisiense*.

In this paper we describe new specimens of *Peratherium africanum* from an Early Oligocene locality in the Jebel Qatrani Formation (Fayum Depression, northern Egypt), including the first upper dentition known. These specimens help to confirm the generic affinities to *Peratherium* of the species described by Simons and Bown as *P. africanum*, and greatly increase our knowledge of the dental morphology of this species.

Institutional abbreviations. BMNH, Natural History Museum, London, UK (PD for Palaeontology, ZD for Zoology departments); CGM, Cairo Geological Museum, Egypt; DPC, Duke University Primate Center, Durham, USA; MB Ma, Museum für Naturkunde, Berlin, Germany; NMB, Naturhistorisches Museum Basel, Switzerland; USTL, Université des Sciences et Techniques du Languedoc (Montpellier II), France.

SYSTEMATIC PALAEOLOGY

'DIDELPHIMORPHIA' Gill, 1872

Family HERPETOTHERIIDAE Trouessart, 1879
(*sensu* Kirsch *et al.* 1997)

Genus PERATHERIUM Aymard, 1850

Type species. *Didelphis elegans* Aymard, 1846, Early Oligocene, Ronzon, France.

Peratherium africanum Simons and Bown, 1984

Plate 1, figure 1; Text-figures 1A–C, 2–4; Tables 1–2

- v. 1984 Didelphid marsupial; Bown and Simons, pp. 447–449, fig. 2.
- *v 1984 *Peratherium africanus* Simons and Bown, pp. 539–547, figs 2–4.
- v. 1992 *Qatranitherium africanum* (Simons and Bown); Crochet, Thomas, Sen, Roger, Gheerbrant and Al-Sulaimani, pp. 539–544.
- ? 1992 *Qatranitherium* aff. *africanum* (Simons and Bown); Crochet, Thomas, Sen, Roger, Gheerbrant and Al-Sulaimani, pp. 539–544, pl. 1.

Holotype. Right dentary fragment with P₂–M₃, roots of C₁ and P₁ and alveoli for M₄ (CGM 40236) from the upper Jebel Qatrani Formation, Rupelian, Oligocene, Quarry M, Fayum Province, Egypt.

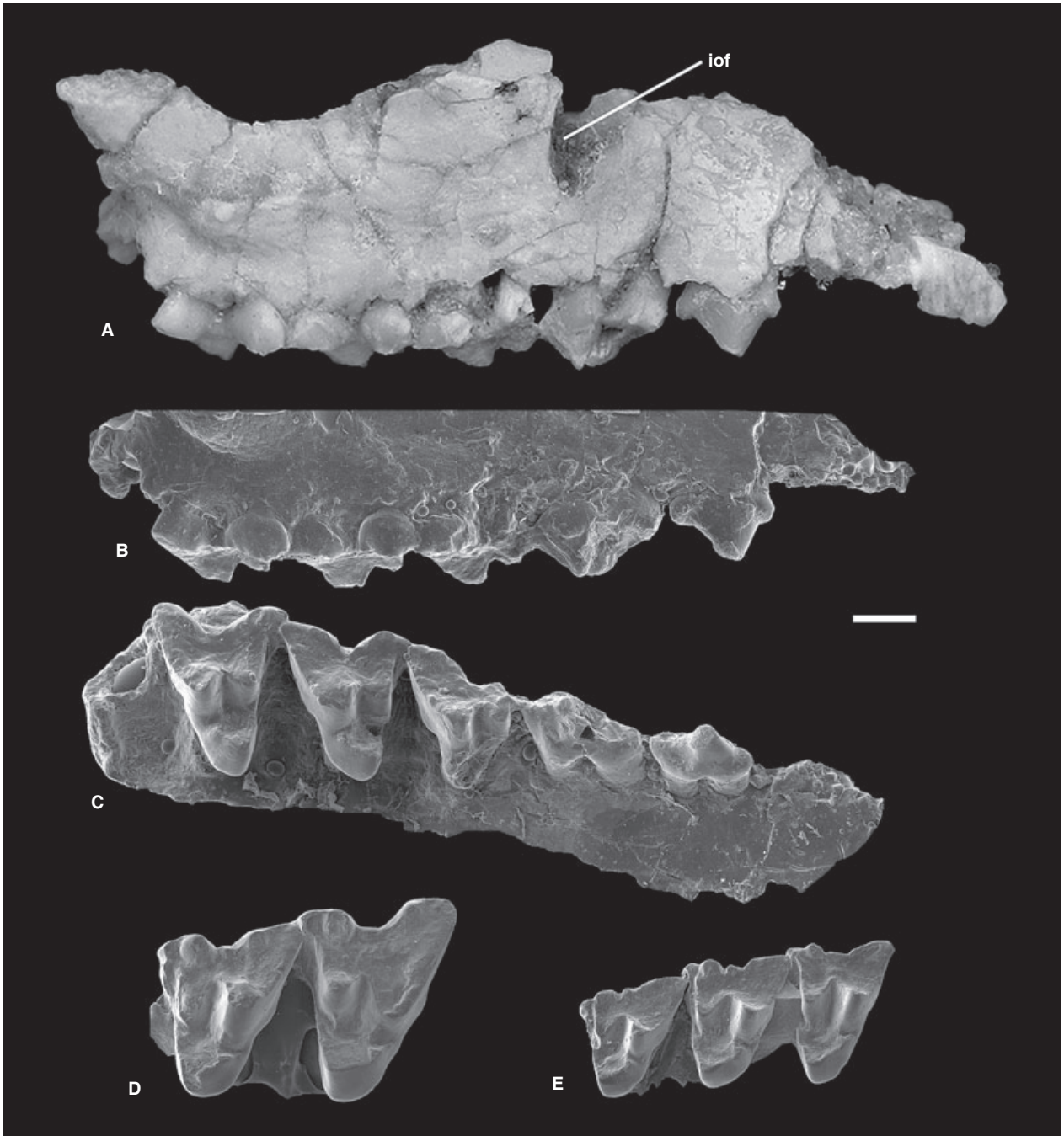
Paratypes. Left dentary fragment with M_{2–3}, part of M₄ and roots of M₁ (CGM 40237) and left edentulous dentary fragment (DPC 3120), from the same horizon and locality as the holotype.

New material. Right maxillary fragment with P²–M³, roots of P¹ and parts of alveoli of C¹ and M⁴ (DPC 16946); right dentary fragment with P₃–M₄, 2 empty alveoli anterior to P₃ and part of the root of P₁? (DPC 3820); and right dentary fragment with corroded P₃–M₄ and partial roots for C₁–P₂ (DPC 8201), all from the same horizon and locality as the holotype.

Revised diagnosis. Medium-sized *Peratherium*: length of M³, 2.14 mm. M^{1–3} transversely elongate with deep ectoflexus, especially on M³ where it emarginates half the width of the styler shelf; weakly dilambdodont with metacone much larger than paracone; large, mesially situated styler cusp B confluent with cusp A; very small styler cusp C on distal flank of cusp B; paracingulum interrupted adjacent to paracone. Lower molars with: short talonid with buccally situated cristid obliqua; hypoconulid large, taller than the entoconid and close to lingual margin; shallow distolingual area of talonid, after wear becoming a curved 'crest' linking hypoconulid to entoconid (hypoconulid-entoconid talonid fold).

Description

Maxilla (Text-fig. 1A–C). Only the lingual wall of the canine alveolus is preserved, indicating a typically large root. The root(s) of P¹ are completely obscured by matrix. P^{2–3} are simple teeth with one main cusp and a cingulum that is interrupted on the buccal and lingual walls, as is typical for herpetotheriids. Distally on P², the cingulum becomes cuspsate. The crown is badly damaged on P³ and yields no useful information. All three preserved molars have very deep ectoflexi, giving the weak elongate styler cusp D (StD) an oblique orientation that is nearly transverse on M³. M¹ is damaged, lacking protocone and mesio-buccal corner, and abrasion generally has obscured styler cusp details. M^{2–3} show more detail. Styler cusp B (StB) is large and, although worn, is essentially confluent with styler cusp A (StA, parastyle), with no groove separating them on the buccal wall. Styler cusp C (StC) is very small and situated on the distal slope of StB. The mesio-buccal corner of M³ is tilted buccally of a mesiodistal axis. M^{1–3} are weakly dilambdodont, the bowing of the centrocrista impinging little on the styler shelf, which remains wide despite the deep ectoflexus. The metacone is much larger than the paracone and the preparacrista joins StA on all three teeth (indicated on M¹ by its orientation). On M^{2–3}, the protocone lobe tapers lingually and the paraconule and metaconule are weak. On all three molars, the paracingulum is interrupted adjacent to the paracone. The infraorbital foramen was relatively large, its posterior border situated at the level of the anterior border of M¹. A comparative sample of infraorbital foramen size in small didelphids, a caenolestid and several herpetotheriids (Table 1), shows that the Fayum specimen is in the uppermost part of the range. We used for this small survey the M² as surrogate for size. Comparison with the available herpetotheriids indicates to us that *Peratherium* is characterized by larger infraorbital foramina than either *Amphiperatherium* Filhol, 1879 or *Herpetotherium* Cope, 1873.



TEXT-FIG. 1. Maxillae of *Peratherium*. A, light micrograph. B–E, scanning electron micrographs of gold palladium-coated epoxy casts. A–C, *Peratherium africanum*, right maxilla with P²–M³, DPC 16946, upper Jebel Qatrani Formation, Rupelian, Oligocene, Quarry M, Fayum Province, Egypt. D, *Peratherium antiquum*, left maxilla with M^{2–3}, BMNH.PD.M2388d, Phosphorites du Quercy, Late Eocene/Early Oligocene, Quercy, France. E, *Peratherium lavergnense*, holotype left maxilla with M^{1–3}, USTL.Lav-1031, Phosphorites du Quercy, Bartonian, Eocene, Lavergne, France. A–B, lateral/buccal, and C–E, occlusal views; iof, infraorbital foramen. Scale bar represents 1 mm.

Dentary DPC 3820 (Text-figs 2B, 3B, E). This dentary has teeth that are less worn than those in the holotype (Text-figs 2A, 3A, D, Pl. 1, fig. 1) and that are slightly larger (Table 2). The apparent size difference is, however, exaggerated in two ways. Firstly,

the greater wear of the holotype has removed the mesially projecting part of the paraconids and the distally projecting part of the hypoconulids, slightly shortening each tooth. Secondly, successive teeth show more overlap than in DPC 3820. Thus, in

TABLE 1. Infraorbital foramen size (in mm) in a sample of small didelphids, a caenolestid (*Lestoros*) and herpetheriids, including *Peratherium africanum*.

	Specimen	INF/M2LW	Height InfF	Width InfF	InfFHxW (INF)	M2 length	M2 width	M2LxM2W
<i>Gracilinanus marica</i>	BMNH.ZD. 98.7.124	0.10	0.67	0.34	0.23	1.33	1.71	2.27
<i>Gracilinanus marica</i>	BMNH.ZD. 17	0.11	0.77	0.31	0.24	1.3	1.71	2.22
<i>Herpetherium fugax</i>	MB Ma 50672	0.11	1.2	0.39	0.47	1.95	2.19	4.27
<i>Marmosops madescens</i>	BMNH.ZD. 27.11.189	0.11	1.15	0.41	0.47	1.71	2.47	4.22
<i>Amphiperatherium ambiguum</i>	BMNH.PD. M2388a	0.12	1.58	0.46	0.73	2.31	2.69	6.21
<i>Herpetherium fugax</i>	MB Ma 50671	0.12	1.09	0.41	0.45	1.81	2	3.62
<i>Marmosops madescens</i>	BMNH.ZD. 23.10.1646	0.12	0.92	0.56	0.52	1.79	2.32	4.15
<i>Marmosops madescens</i>	BMNH.ZD. 27.11.194	0.16	1.02	0.59	0.60	1.7	2.18	3.71
<i>Gracilinanus marica</i>	BMNH.ZD. 98.7.125	0.16	1.11	0.39	0.43	1.44	1.84	2.65
<i>Peratherium</i> sp. (Brassat)	NMB 9537	0.18	1.76	0.6	1.06	2.39	2.5	5.98
<i>Lestoros inca</i>	BMNH.ZD. 19.4.381	0.18	0.91	0.55	0.50	1.66	1.7	2.82
<i>Monodelphis scalops</i>	BMNH.ZD. 21.8.61	0.19	0.97	0.46	0.45	1.41	1.65	2.33
<i>Monodelphis scalops</i>	BMNH.ZD. 14.5.919	0.19	1.16	0.42	0.49	1.66	1.53	2.54
<i>Lestoros inca</i>	BMNH.ZD. 22.11.127	0.23	0.86	0.68	0.58	1.61	1.59	2.56
<i>Peratherium</i> sp. (Egerkingen)	NMB 1913	0.26	1.57	0.55	0.86	1.65	2.03	3.35
<i>Peratherium antiquum</i>	NMB 25	0.26	1.79	0.91	1.63	2.14	2.92	6.25
<i>Peratherium africanum</i>	DPC 16946	0.27	1.65	0.82	1.35	1.94	2.54	4.93
<i>Peratherium</i> sp. (Quercy)	NMB QH 362	0.29	2.04	1.01	2.06	2.32	3.02	7.01
<i>Peratherium</i> sp. (Quercy)	NMB QH249	0.30	1.83	0.67	1.23	1.72	2.38	4.09
<i>Peratherium</i> sp. (Brassat)	NMB 2955	0.39	2	1.29	2.58	2.35	2.8	6.58

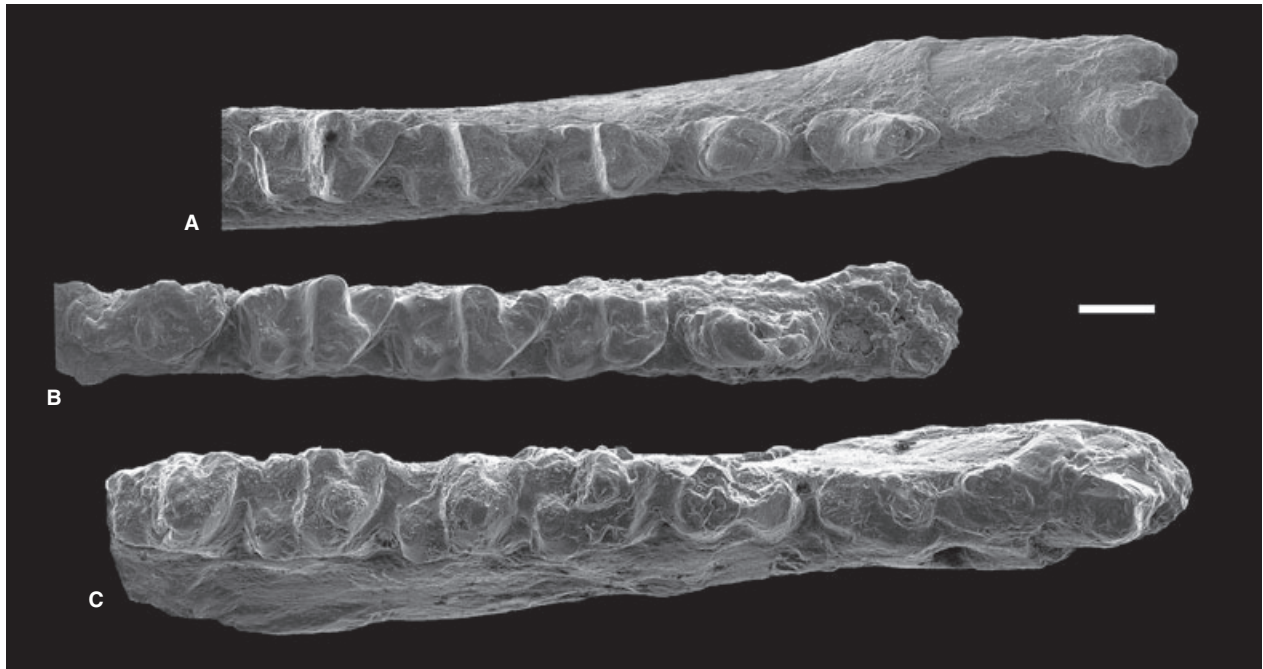
Inf, infraorbital foramen; INF, infraorbital foramen size; L, length; W, width.

DPC 3820, the hypoconulid of one molar essentially abuts the paraconid of the succeeding molar, whereas in the holotype the hypoconulid is overlapped by the mesial tip of the paraconid of the succeeding molar. This crowding is a phenomenon of increased wear (Crochet 1980, fig. 5). The relatively unworn teeth in DPC 3820 show several features not visible on the holotype. The hypoconulid is larger and taller than in any other species of *Peratherium*; it is taller than the entoconid and prominent in lingual view, not obscured by the paraconid of the adjacent tooth in occlusal view. The heightening of the hypoconulid has had the effect of raising the adjacent floor of the talonid basin, giving it the appearance of a crest when worn (see below). The posthypocristid of M₂ in DPC 3820 appears slightly oblique in contrast to the holotype. However, although there can be slight intraspecific variation for this feature, the apparent obliquity of the angle in DPC 3820 is enhanced by buccal abrasion of the hypoconid. Another difference from the holotype is the more lingual terminus of the cristid obliqua on the trigonid. This difference is more apparent than real, and is largely due to the greater wear of the holotype, exposing a lower level in the buccally dipping cristid obliqua. M₄ is badly corroded, but appears to show a deeper hypoflexid than on the other molars and a more elongate talonid. P₃ is also badly corroded and has lost its talonid, creating the false appearance of a diastema between P₃ and M₁. There are two mental foramina, one below the mesial edge of M₁, the other below its hypoconid.

Dentary DPC 8201 (Text-figs 2C, 3C). This specimen is badly corroded and little detail can be gleaned from the teeth. Nevertheless, the lower molars show the same large hypoconulid and vague representation of other features visible in DPC 3820. M₄ is broken distally, but the talonid appears broader than in DPC

TABLE 2. Measurements of length versus width (in mm) of teeth of *Peratherium africanum*; parameters follow Clemens (1966, p. 4).

No.	Tooth	Length	Width	Width trigonid	Width talonid
DPC16946	P ²	1.60	0.71		
	P ³	2.01	1.08		
	M ¹	(1.95)	-		
	M ²	1.94	2.54		
	M ³	2.14	2.87		
DPC3820	M ₁	1.70		1.09+	1.14
	M ₂	2.20		1.21	-
	M ₃	2.20		1.28	1.20
	M ₄	2.30+		1.15+	-
DPC8201	M ₁	1.77		1.17+	1.36
	M ₂	1.90		1.24+	1.29+
	M ₃	1.95		1.34+	1.24+
	M ₄	2.10+		1.23+	0.98



TEXT-FIG. 2. Scanning electron micrographs of occlusal views of gold palladium-coated epoxy casts of right lower dentitions of *Peratherium africanum*, upper Jebel Qatrani Formation, Rupelian, Oligocene, Quarry M, Fayum Province, Egypt. A, CGM 40236, holotype with canine, P₂-M₃, roots of P₁. B, DPC 3820, P₃-M₄, alveoli of P₂. C, DPC 8201, P₃-M₄, roots of canine to P₂. Scale bar represents 1 mm.

3820, with a shallower hypoflexid. DPC 8201 shows more posterior parts of the dentary than the other specimens, including the opening of the dental canal and beginning of the medially inflected angle. There are two mental foramina, one below the junction of P₁ and P₂ and another below M₁.

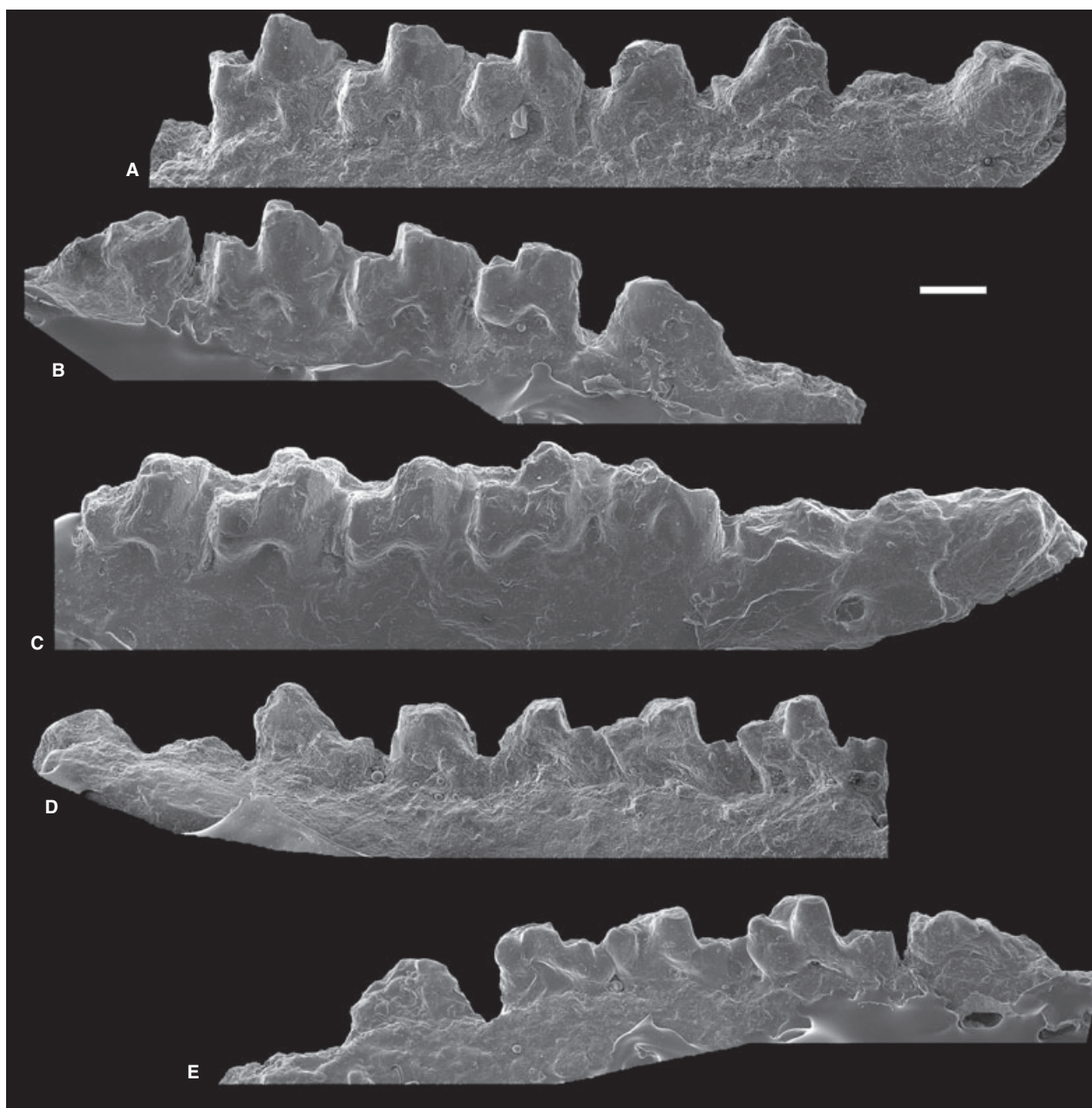
OCCLUSAL RELATIONSHIPS

The great disparity in size between the small paracone and the large metacone plus the weakly buccally flexed centrocrista of M¹⁻³ fit well with the buccally positioned cristid obliqua and extreme lingual position of the hypoconulid of M₁₋₃ (Text-figs 1-2; Pl. 1). The teeth in the maxilla occlude well with the holotype (Text-fig. 4) and DPC 3820 lower dentitions, although all three specimens are clearly from different individuals. Thus, the maxilla appears slightly too large for the holotype and slightly too small for DPC 3820. In fact, gerontic crowding of the molars in the holotype may be responsible for the slight size discrepancy with the maxilla, but DPC 3820 is genuinely slightly larger (Table 2). In particular, for both specimens the obliquity of the upper molar postmetacrista matches that of the lower molar paracristid, obliquity lessening distally to a proportionate degree. Likewise, the near transverse orientation of the upper molar preparacrista matches that of the lower molar protocristid. Also, the

lengths of the upper molar postparacrista and lower molar cristid obliqua and of the upper molar premetacrista and lower molar posthypocristid respectively correspond closely. Enlargement of the teeth from M¹⁻³ also corresponds to that of M₁₋₃.

FAMILY AFFINITIES

Simons and Bown (1984) made comparisons between *P. africanum* and the three genera of Euramerican Paleogene herpetotheriids then known (at that time placed in the family Didelphidae), viz. *Herpetotherium* from North America and *Peratherium* and *Amphiperatherium* from Europe. (N.B. Crochet's interpretation of North American species attributed to *Peratherium* as belonging to *Herpetotherium* is followed here). They concluded that the greatest similarity was with *Peratherium*; hence their generic placement of the species *africanum*. They noted that there were special similarities to *P. cuvieri* (Fischer, 1829), *P. antiquum* (Blainville, 1840) and *P. perrierense* Crochet, 1979 on the basis of short lower molar talonids shared with the first two, shallow hypoflexids and distal molar size increase shared with *P. antiquum* and *P. perrierense*, and mesially positioned entoconid and its connection to the metaconid shared with *P. cuvieri* and *P. perrierense*.

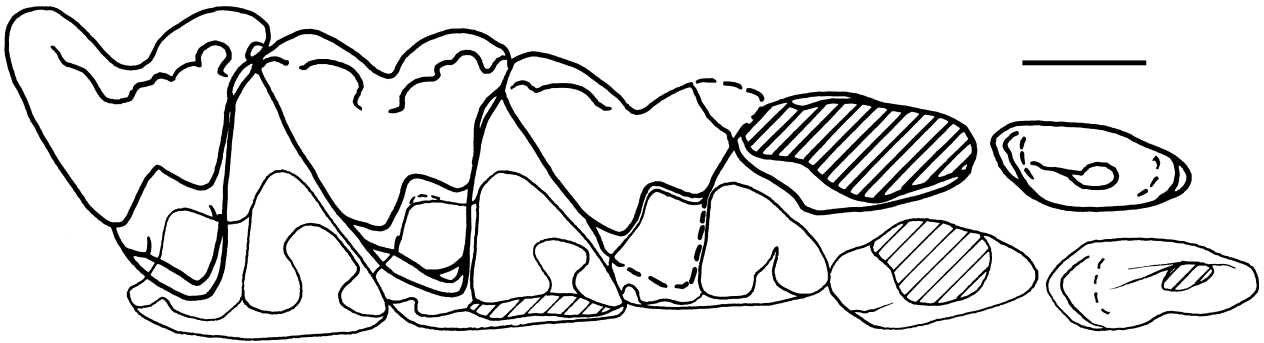


TEXT-FIG. 3. Scanning electron micrographs of gold palladium-coated epoxy casts of right lower dentitions of *Peratherium africanum*, upper Jebel Qatrani Formation, Rupelian, Oligocene, Quarry M, Fayum Province, Egypt. A, D, CGM 40236, holotype with canine, P₂–M₃, roots of P₁. B, E, DPC 3820, P₃–M₄, alveoli of P₂. C, DPC 8201, P₃–M₄, roots of canine to P₂. A–C, buccal, and D–E, lingual views. Scale bar represents 1 mm.

Crochet *et al.* (1992) in contrast removed *P. africanum* from the Herpetotheriidae (as herpetotheriine Didelphidae, the then current classification) and placed it instead in the family Peradectidae on the basis of features such as high molar entocristids, a buccally situated cristid obliqua, and a cusped hypoconulid linked to the entoconid by a crest. They added a DP₃ (with an ‘*aff. africanum*’ qualification) from Taqah, Sultanate of Oman, which had the same characters as the Fayum type material, and

placed the species in a new genus, *Qatranitherium*. There is certainly some doubt as to whether the DP₃ belongs to the same taxon as the type assemblage, especially as it is rather large, as Crochet *et al.* (1992) noted. Nevertheless, the characters as displayed by the Fayum material do not support referral of *P. africanum* to the Peradectidae for the following reasons.

1. The upper molars in the new maxilla are clearly herpetotheriid in their dilambdodonty and enlarged metacone



TEXT-FIG. 4. The upper (DPC 16946, thick line) and lower (holotype CGM 40236, thin line, drawing reversed) right cheek dentitions of *Peratherium africanum* superimposed essentially at full occlusion, as seen in the direction of relative movement (Butler 1972). Broken areas hatched, missing parts of outline reconstructed with dashed lines. Scale bar represents 1 mm.

and they occlude very well with the holotype lower dentition.

2. The 'crest' linking the lower molar hypoconulid to the entoconid is not the lingual branch of the postcristid as in *Peradectes*, but a non-homologous fold, which describes a buccally convex arc across the distolingual part of the talonid basin, leaving a distinct postentoconid sulcus. It is referred to here (see below) as the hypoconulid-entoconid talonid fold (Pl. 1, figs 1–3).

3. The appearance of an entocristid is enhanced by the advanced wear state and the proximity of the entoconid to the metaconid, which is a feature of certain species of *Peratherium* (see below).

4. A buccally positioned cristid obliqua is typical not only of *Peradectes* but also of several species of *Peratherium*.

5. The lower molar hypoconulid is situated near the lingual margin, whereas it is positioned more buccally in peradectids.

COMPARISONS

South American metatherians

It has been suggested that there are special similarities between some marsupials from the Paleocene Itaboraia fauna in Brazil and *Peratherium*, and between isolated postcranials from the same locality and similar remains from North American and English Eocene deposits (Hooker 1998, p. 442). If South America was the source for European species, Africa may have served as the intervening landmass in their dispersal route. For that reason, it is of interest to compare the Fayum marsupials with South American forms.

Several Paleogene South American taxa show similarities to *Peratherium africanum*. For instance, the middle Paleocene (Tiupampán SALMA) *Mizquedelphys pilpinensis*

Marshall and de Muizon, 1988 also shows upper molars that are progressively shorter from M^1 to M^3 , although in *Mizquedelphys* the V-shaped centrocrista is less obvious, the paraconule and metaconule are present, the ectoflexus is shallower, StC is present, and the preparacrista always ends buccally at the lingual slope of StB (Muizon 1991). These same features also apply when *P. africanum* is compared with *Pucadelphys andinus* Marshall and de Muizon, 1988 from Tiupampa. Furthermore, StA and StC in *Pucadelphys* are quite distinct and the paracingulum, though short, is wider. On lower molars, talonids are longer than trigonids (which in M_{2-4} have mesiodistally compressed trigonids), the entoconid is proportionally small and even across M_{1-3} , and the paraconid is reduced.

Andinodelphys cochabambensis Marshall and de Muizon, 1988 has a straight centrocrista, well-developed paraconule and metaconule, and anterobasal cingulum which is contiguous with the preparaconule crista, well-developed ectoflexus and quite distinct StA, StB, StC and StD. Finally, the tiny *Jaskhadelphys minutus* Marshall and de Muizon, 1988, also from Tiupampa, clearly departs from the pattern observable in the African species: in the upper molars, the protocone body is oddly twisted relative to the orientation of the rest of the tooth, the paracone and metacone are more similar in size and set closely to one another, the ectoflexus is shallow, and all stylar cusps are distinct.

Among the very rich marsupial fauna of Itaboraian (Late Paleocene) age, several taxa also show superficial similarities with *Peratherium* from the Fayum: *Marmosopsis* Paula Couto, 1962, *Sternbergia* Paula Couto, 1970, *Derorhynchus* Paula Couto, 1952, *Monodelphopsis* Paula Couto, 1952, and *Itaboraidelphis* Marshall and de Muizon, 1984. However, none of them shows the distinct set of features characterizing the African species. Lower molars of *Marmosopsis*, though similar to *Peratherium* in its trigonid-talonid proportions, have notably compressed premolars and molars with much reduced paraconids, small

entoconids and talonids that are much lower than trigonids. Upper molars of *Marmosopsis* have much more buccally flexed centrocrisae, small but distinct paraconule and metaconule, and proportionally smaller StB. Lower molars of *Sternbergia* are more slender and laterally compressed, talonids are longer than trigonids, and the metaconids and paraconids are subequal in size and much smaller than the protoconids. Upper molars have much more buccally flexed centrocrisae, a small but distinct metaconule, wider protocone, shallower ectoflexus and a distinct StC at least on M^2 .

Comparisons with *Derorhynchus* also show significant differences: lower molars have better developed entoconids and more approximated paraconids and metaconids, whereas upper molars have distinct StA, StB, StC, StD, paraconule and metaconule. In *Monodelphopsis* the lower first molar has a very reduced metaconid, laterally compressed entoconid and proportionally smaller hypoconulid.

Itaboraidelphys is much larger than the Fayum species, has better developed pre- and postcingulids, and M_4 has a wider talonid. Despite the similarly buccally flexed centrocrisae, upper molars have proportionally larger metaconules and clearly recognizable StA, StB, StC, StD, and shallower ectoflexus.

Goin and Candela (2004) recognized a herpetotheriid from ?Late Eocene deposits of Santa Rosa, Peru: *Rumiodon inti* Goin and Candela, 2004, which includes upper and lower teeth. The upper molar differs from the M^1 of African *Peratherium* in having a wider protocone, shallower ectoflexus, distinct StC and StD, a preparacrista that is much shorter than the postmetacrista, and in the lower molars, better developed precingulid, proportionally longer trigonids, and a much more laterally compressed entoconid.

Northern Hemisphere herpetotheriids

The African species also differs significantly from North American herpetotheriids (Korth 1994) in the relative size and position of the stylar cusps (StB is small and more mesially placed in *Herpetotherium* and *Copedelphys* Korth, 1994, whereas StD is larger and progressively more mesially placed from M^1 to M^3 in these two taxa). Upper molars have less size difference between paracone and metacone and lower molars have the cristid obliqua less buccally situated. On M^1 the preparacrista joins StB.

Swaindelphys cifellii Johanson, 1996 from the Torrejonian (middle Paleocene) differs from African *Peratherium* in that the lower molars have wider talonids, proportionally smaller hypoconulids, and upper molars have distinct paraconule, metaconule and StB, C, and D, as well as a shallower ectoflexus. Another North American herpeto-

theriid is *Nortedelphys* Case, Goin and Woodburne, 2005 from the late Cretaceous. *Nortedelphys* shows upper molars with more buccally flexed centrocrisae, distinct StC on M^1 – M^2 , and proportionally shorter postmetacrisae, which in M^2 – M^3 are more transverse to the dental axis. Lower molars have a more approximated paraconid and metaconid.

Maastrichtidelphys Martin, Case, Jagt, Schulp and Mulder, 2005, from the latest Cretaceous of Europe, has a very distinct StC, a deeply flexed centrocrista, distinct para- and metaconules and a very small, if present, StB.

There are several records of largely fragmentary herpetotheriids from Asia. *Asiadidelphis* Gabunia, Shevyreva and Gabunia, 1990 from Early Oligocene deposits in Kazakhstan has a large StC on M^{3-4} and twinned cusps C and D on M^2 . It is therefore very similar to North American *Herpetotherium*, as Emry *et al.* (1995) judged. It therefore differs from *P. africanum* in the same features as does *Herpetotherium*. An unnamed marsupial from the Middle Eocene of Shanghuang, China, is said to be similar to *Asiadidelphis* (Qi *et al.* 1996). An unnamed herpetotheriid lower molar from early Eocene deposits in northern Pakistan (Thewissen *et al.* 2001) has a relatively longer talonid, more lingually orientated cristid obliqua and lower more distally projecting hypoconulid than *P. africanum*. Early Eocene *Jaegeria* from the Gujarat area of India (Bajpai *et al.* 2005), based on a lower molar, has a strong complete ectocingulid and a short, rather procumbent trigonid more reminiscent of a chiropteran than of a herpetotheriid marsupial. An unnamed genus from Early/Middle Eocene deposits of Turkey (Kappelman *et al.* 1996, fig. 2) has lower molars rather like *Peratherium* but upper molars that are strikingly different. M^{3-4} are strongly dilambdodont with paracone and metacone of similar height, the centrocrista flexed to join StC and a large stylar cusp between StB (stylocone) and StC. Kappelman *et al.* (1996) identified this large stylar cusp as StB, but it is preceded by a stylocone (StB), towards which the preparacrista is directed, and more mesially still by a parastyle (StA). These upper molars are probably the specimens reidentified by Gheerbrant and Rage (2006, p. 238) as the adapisoriculid *Garatherium*. None of these Asian taxa shows any special similarities to *P. africanum*.

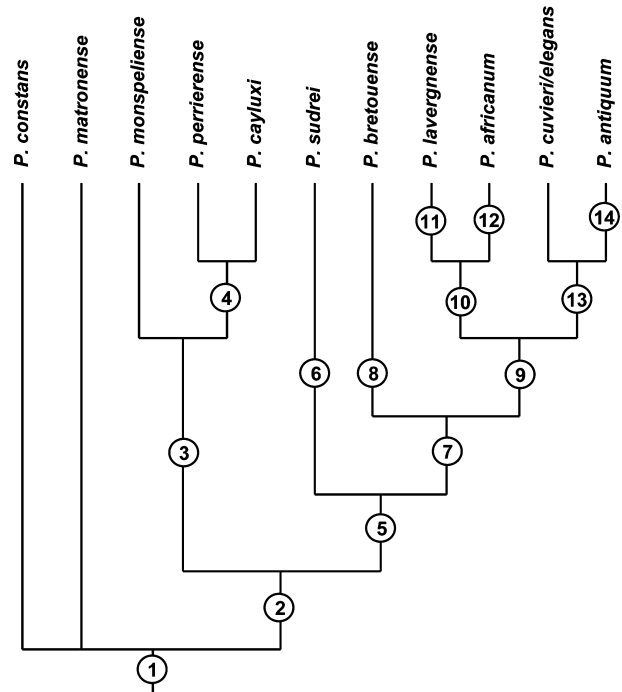
The European genus *Amphiperatherium* differs from *P. africanum* and European species of *Peratherium* as follows (modified from Crochet 1980). Successive molars show less enlargement distally along the row. The upper molars have less size difference between paracone and metacone, small StB, and there is a tendency for paraconule and metaconule to be stronger. Lower molars have weaker postcingulids, and on M_4 lingual hypoconulid without reduction of entoconid. P_3 is procumbent. As judged by Simons and Bown (1984), the closest similarity within Herpetotheriidae to *P. africanum* is the genus *Peratherium*.

This similarity is based on the following shared characters: molars enlarging distally along the row (except M⁴); enlarged upper molar StB; upper molar metacone much larger than paracone; deep M³ ectoflexus; lower molars with relatively buccally situated cristid obliqua; erect rather than procumbent P₃.

European species of *Peratherium*

Derived species of *Peratherium* are fairly distinctive, but more primitive ones from early in the Eocene are less easily distinguishable from *Amphiperatherium*. Thus, many of the characters typically associated with *Peratherium* were progressively acquired in the course of evolution during the Eocene. According to the specific characters delineated by Crochet (1980) and polarized here using the primitive herpetotheriid genera *Swaindelphis*, *Nortedelphis* and *Maastrichtidelphis*, *Peratherium* can be divided into two main clades: clade A comprising *P. monspeliense* Crochet, 1979, *P. perrierense* and *P. cayluxi* (Filhol, 1873), and clade B comprising *P. sudrei* Crochet, 1979, *P. bretouense* Crochet, 1979, *P. lavergnense* Crochet, 1979, *P. cuvieri*, *P. elegans* and *P. antiquum* (Text-fig. 5). It is not clear how the very primitive species *P. constans* Teilhard, 1927 and *P. matronense* Crochet, 1979 relate to the others. Clade A is characterised by a tendency to enlarge StD; the more derived species, *P. perrierense* and *P. cayluxi*, have relatively longer molars. Clade B shows a progressive acquisition of characters in a sequence of steps through the middle and late Eocene. All except *P. sudrei* are characterized by having upper molars with a weak paracingulum adjacent to the paracone and lower molars with the entoconid approaching the metaconid and a buccally positioned cristid obliqua. *P. lavergnense*, *P. cuvieri*, *P. elegans* and *P. antiquum* are linked by having lower molars with short talonid and by modifications to the upper molars, viz. weakening of StC, gaining a crest between stylar cusps A and B, and even greater enlargement of the metacone at the expense of the paracone (N.B. the genus *Peratherium* is characterised by having greater size disparity between these cusps than are *Amphiperatherium* or *Herpetotherium*).

It is clear that the characters defining these four species provide the best match for *P. africanum*. The *P. cuvieri-elegans-antiquum* clade seems more distant from *P. africanum* in having a slightly more buccally situated hypoconulid, no hypoconulid-entoconid talonid fold (both primitive) (Pl. 1, fig. 4), a longer upper molar postmetacrista and a larger StB (both derived) (Text-fig. 1D). In contrast, uniquely among European species, *P. lavergnense* has a hypoconulid-entoconid talonid fold exactly like that of *P. africanum* (Pl. 1, figs 1–3). *P. lavergnense* also has an M₁₋₃ hypoconulid that is very close to the lingual tooth



TEXT-FIG. 5. Cladogram of relationships of species of *Peratherium* based on definitions given by Crochet (1980) plus additional features observed herein, not on a parsimony analysis. Apomorphies (excluding size) at numbered nodes: 1, StB largest of the stylar cusps, deep M³ ectoflexus emarginating about one-third of the width of the stylar shelf (reversed at node 11), erect P₃; 2, upper molar metacone nearly twice as tall as paracone; 3, large StD; 4, molar length/width proportions increased such that e.g. M¹ is longer than wide, weak StC (paralleled at node 9); 5, M₄ hypoconulid median; 6, lower molar paraconid nearly as tall as metaconid; 7, M³ paracingulum weak adjacent to paracone, lower molars with entoconid approaching metaconid, buccally shifted cristid obliqua and metaconid transversely opposite protoconid; 8, reduction in upper molar centrocrystal bowing; 9, upper molar metacone more than twice as tall as paracone, crest joining StA to B, weak StC (paralleled at node 4), lower molar talonid shorter than trigonid; 10, M³ parastyle directed mesio buccally, lower molars with hypoconulid near lingual margin and with hypoconulid-entoconid talonid fold; 11, shallow M³ ectoflexus; 12, weak dilambdodonty, deep M¹⁻² ectoflexus, very deep M³ ectoflexus emarginating one-half of the width of the stylar shelf, StA fused to B, StC tiny and close to B, upper molar paracingulum interrupted, lower molar hypoconulid taller than entoconid; 13, long upper molar postmetacrista especially on M³ making the mesio buccal angle of the tooth outline obtuse, very large StB exceeding the paracone in size; 14, StC fused with B in most individuals.

margin and an M³ parastyle that is directed mesio buccally. *P. lavergnense* differs, however, from *P. africanum* in having a shallower upper molar ectoflexus, although this probably represents an autapomorphic reversal from the moderately deep state that is primitive for the genus. The

deep M^{1-2} ectoflexus and even deeper M^3 ectoflexus, the tiny StC on the distal flank of StB, the fusion of B to A and the tall lower molar hypoconulid can be construed as autapomorphies of *P. africanum*. Available characters, therefore, support a sister group relationship between *P. africanum* and *P. lavergnense*. In light of this relationship, the monotypic genus *Qatranitherium* Crochet, Thomas, Sen, Roger, Gheerbrant and Al-Sulaimani, 1992 is judged unnecessary and is here synonymized with *Peratherium*.

NATURE OF THE HYPOCONULID-ENTOCONID TALONID FOLD

Crochet (1980) made no mention of this character in *P. lavergnense*. This is probably because it is a relatively minor structure, consisting really only of a shallowing of the distolingual area of the talonid basin, and only becoming obvious with dietary wear. It can nevertheless be seen in the shading of Crochet's figure 198b. The structure may result from the extreme lingual shift of the hypoconulid and its proximity to the entoconid, causing a slight local modification of the talonid basin floor (Pl. 1, fig. 3). In this respect the structure is not a crest, although it is more distinct in *P. africanum* than in *P. lavergnense* (see above). However, as wear progresses, the upper molar postprotocrista, during the power stroke, makes a groove from the mesio Buccal side of the entoconid to the buccal side of the hypoconulid, isolating the shallow part of the basin as an apparent crest (Pl. 1, figs 1–2). A similar structure can be observed in some modern didelphids such as *Marmosops dorothea* (Thomas, 1911) and *Marmosa murina* (Linnaeus, 1758). Other closely related species of *Peratherium*, such as *P. cuvieri* and *P. elegans*, nevertheless lack this structure, there being a distinct valley between the hypoconulid and entoconid (Pl. 1, fig. 4).

DISCUSSION

Records of marsupials in Africa have the potential to determine patterns of intercontinental exchange in this

group. From their origins in the Cretaceous of Asia or North America, it was not until the Tertiary that they dispersed to all other continents (Cifelli 1993; Rougier *et al.* 1998). The early Paleogene faunas of Afro-Arabia are dominated by endemics, mainly macrotelodonts, hyracoids, proboscideans and enigmatic 'insectivorans'. In the last 15 years, new discoveries in Early–Middle Eocene strata have added anthropoid (Godinot and Mahboubi 1992; Godinot 1994) and stem strepsirrhine (Hartenberger and Marandat 1992) primates, putative plesiadapiforms (Tabuce *et al.* 2004), zegdomyid rodents (Vianey-Liaud *et al.* 1994), and a ?peradectid marsupial (Crochet 1986; Goin and Candela 2004), indicative of immigration from Asia, Europe and perhaps South America. The Oligocene record of the herpetotheriid marsupial *Peratherium* is unequivocal evidence of dispersal from Europe, as originally proposed by Simons and Bown (1984).

Dating the arrival of *Herpetotheriidae* in Afro-Arabia

The strata at Quarry M, the site of all the *P. africanum* specimens, are within a normally polarised interval identified as Chron C11n (Seiffert 2006), which ranges in age from 30.2 to 29.5 Ma (Ogg and Smith in Gradstein *et al.* 2004) in the late Rupelian, Early Oligocene. This equates with Paleogene mammal Reference Level MP24 in Europe (Luterbacher *et al.* in Gradstein *et al.* 2004). The sister taxon of *P. africanum*, *P. lavergnense*, ranges in age from late Bartonian (MP16) to early Rupelian (MP21) (Crochet 1980), thus from *c.* 37.5 to *c.* 33 Ma. If *P. africanum* is actually derived from *P. lavergnense* (requiring some reversals of its autapomorphies) following dispersal from Europe to Africa, this is unlikely to have occurred later than the last appearance of *P. lavergnense* at *c.* 33 Ma. This is, therefore, much later than the Thanetian/Ypresian date proposed by Gheerbrant and Rage (2006) based on peradectid affinities. The most likely time for dispersal would have been during the low sea level at the time of the Oi-1 glaciation (*c.* 33.7–33 Ma) (Brinkhuis and Visser 1995; Luterbacher *et al.* in Gradstein *et al.* 2004). If the Taqah record really represents *P. africanum* (or at

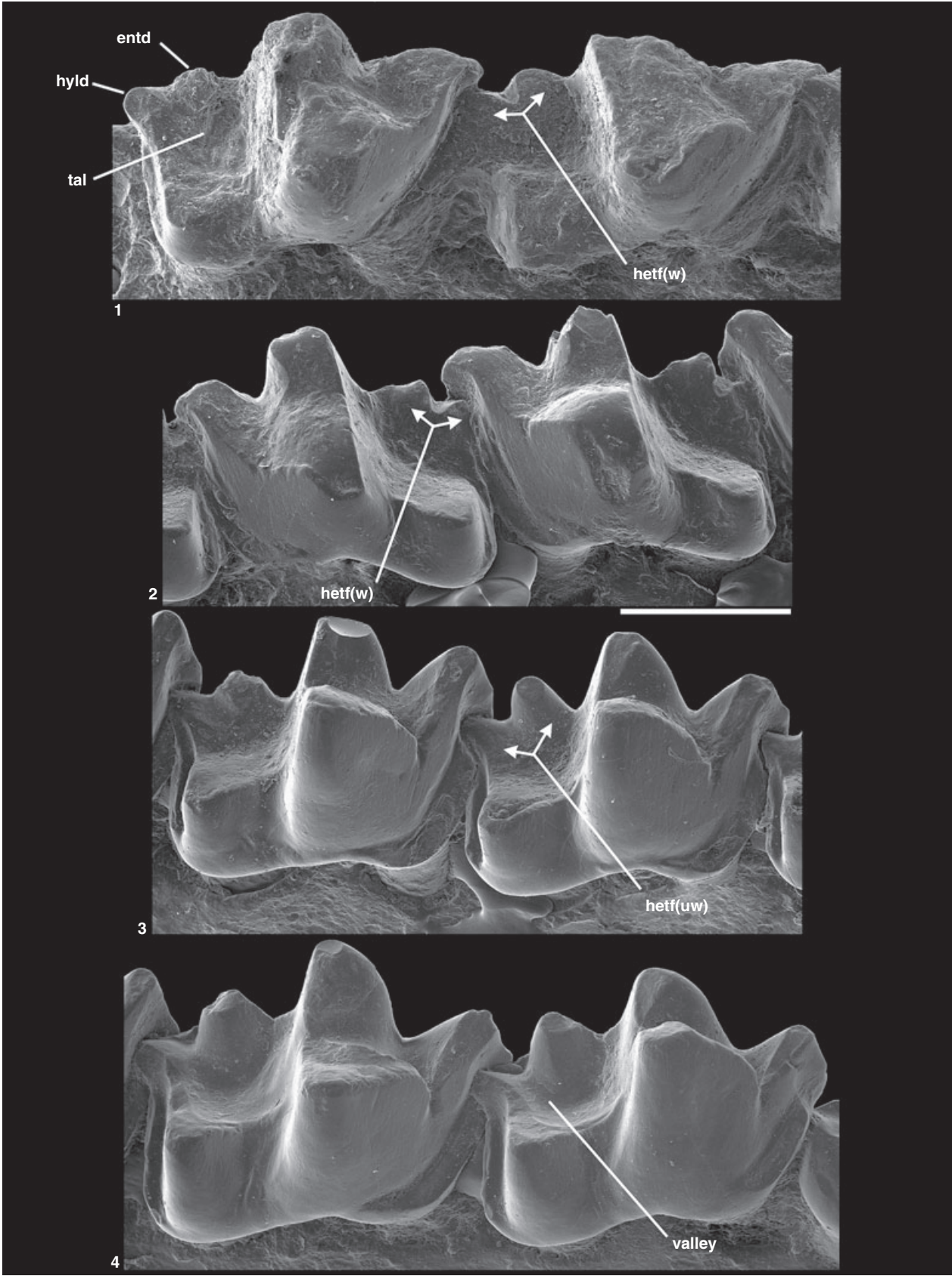
EXPLANATION OF PLATE 1

Scanning electron micrographs of gold palladium-coated epoxy casts of lower molars of *Peratherium* in bucco-occlusal views.

Fig. 1. *Peratherium africanum*, right M_{2-3} of holotype dentary, CGM 40236, upper Jebel Qatrani Formation, Rupelian, Oligocene, Quarry M, Fayum Province, Egypt.

Figs 2–3. *Peratherium lavergnense*, Phosphorites du Quercy, Late Eocene/Early Oligocene, Quercy, France. 2, left M_{2-3} , BMNH.PD.M2388e1. 3, right M_{2-3} , BMNH.PD.M2388e3.

Fig. 4. *Peratherium cuvieri/elegans*, Phosphorites du Quercy, Late Eocene/Early Oligocene, Quercy, France, right M_{1-2} , BMNH.PD.M1636. Abbreviations: entd, entoconid; hetf, hypoconulid-entoconid talonid fold; hylid, hypoconulid; tal, talonid basin; uw, unworn; w, worn.



HOOKER *et al.*, *Peratherium*

least a close relative), this would give the species a range in time in Afro-Arabia back to *c.* 31.5 Ma (Seiffert 2006), which still leaves a gap of 1.5 myr between the two ranges. An earlier sea-level low at the Middle–Late Eocene transition is an alternative possibility for the time of dispersal. In Africa, it marks the first appearance of anthracotheriid artiodactyls and hystricognathous rodents (Jaeger *et al.* 1985; Gheerbrant and Rage 2006). However, there are no land mammal records from the preceding Bartonian Stage. Moreover, the morphological diversity of hystricognathous and anomaluroid rodents recorded at the earliest Priabonian Birket Qarun Locality 2 (BQ-2) (ERS, work in prep.) suggests that the dispersal of those groups into Africa probably occurred long before the sea-level lowstand at the Bartonian/Priabonian boundary. Therefore, there is no firm evidence for a mammalian dispersal event at the beginning of the Priabonian. Pre-Oligocene Afro-Arabian faunas with micromammals consistently lack herpetotheriids (e.g. Gheerbrant *et al.* 1998; Seiffert *et al.* 2005; and references therein). However, the close relationship of *P. africanum* and *P. lavernense* implies the existence of some form of intermediate in an unsampled area in either southern Europe or northern Afro-Arabia. In this context, it is pertinent that Iberia is known to have been home to the microchoerine omymid primate *Pseudoloris* as late as the Early Oligocene (Reference level MP22), 2 myr after the family had become extinct in the rest of Europe (Köhler and Moyà-Solà 1999). Moreover, the presence of a rodent genus in the Majorcan Oligocene, belonging to the otherwise African family Thryonomyidae (Huguenev and Adrover 1991), indicates the existence of Afro-European dispersal during this epoch.

Supporting evidence for general dispersal direction also comes from the scattered records of pre-Eocene herpetotheriids in North America and Europe: *Swaindelphis*, *Nortedelphys* and *Maastrichtidelphys*. Campanian–Maastrichtian (latest Cretaceous) *Nortedelphys* also appears to be the most primitive family member and suggests a North American origin for the Herpetotheriidae (Case *et al.* 2005). Alternatively, *Nortedelphys*, *Swaindelphis* and *Maastrichtidelphys* might be considered stem ‘didelphimorphians’. Either way, dispersal appears to have taken place in three directions: (1) directly to South America via emerging Central American island arcs, leading to origin of other ‘didelphimorphian’ families there (Case *et al.* 2005); (2) directly to Asia via the Bering Straits (Emry *et al.* 1995); (3) to Afro-Arabia via Europe. Dispersal to Europe was likely to have been in two phases, once in the Maastrichtian (Martin *et al.* 2005), with no evidence of post-Cretaceous survival, and a second time at the beginning of the Eocene (Hooker 1998). Arrival in Afro-Arabia seems to have been late, no earlier than Early Oligocene.

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