

A basal phiomorph (Rodentia, Hystricognathi) from the late Eocene of the Fayum Depression, Egypt

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Abstract The fossil record of phiomorph hystricognathous rodents from the Afro-Arabian Paleogene is important for understanding the origins and dispersal routes of the early crown hystricognaths. Here, we describe a “new” basal phiomorph genus and species, *Acritophiomys bowni*, based on complete upper and lower dentitions, mandibular fragments, and partial crania from the terminal late Eocene (~34 Ma) Locality 41 (L-41) in the Fayum Depression of northern Egypt. *Acritophiomys bowni* is the oldest and largest representative of the family “Phiomyidae”, being more or less the same size as contemporaneous gaudeamurids, and is one of the most abundant hystricognaths at L-41. The genus exhibits a mosaic of primitive and derived features, the former shared with primitive hystricognaths, such as *Waslamys* and *Protophiomys* from the earliest late Eocene, and the latter shared with *Metaphiomys* from early Oligocene (~31–29 Ma) sites in the upper sequence of the Jebel Qatrani Formation. Phylogenetic analysis of cranio-dental features, scored across a number of different hystricognathous groups, consistently places *Acritophiomys bowni* and members of the genus *Phiomys* as basal members of the phiomorph stem lineage, implying that the

commonly used family “Phiomyidae” is a paraphyletic assemblage. Among other things, this material shows that basal members of the phiomorph clade consistently replaced dP4/4 with permanent P4/4, and suggests an African origin of stem and crown Phiomorpha.

Keywords Africa · Oligocene · Phiomyidae · *Phiomys* · Dur at-Talah

Abbreviation

CGM	Egyptian Geological Museum, Egypt
DPC	Duke Lemur Center Division of Fossil Primates
I	Incisor
P	Premolar, followed by superscript and subscript numbers, referring to upper and lower tooth loci (respectively)
M	Molar, followed by superscript and subscript numbers, referring to upper and lower tooth loci (respectively)
dP ⁴	The fourth upper deciduous premolar; the lowercase letter d is used to designate a premolar as deciduous

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Introduction

Hystricognathi are, by far, the most common rodents in the late Eocene and Oligocene exposures of Afro-Arabia. Specifically, they have long been known from the Jebel Qatrani area in northeastern Egypt (Fig. 1), which contains one of the few examples of a diverse vertebrate fauna from the Palaeogene of Africa. Over the last half-century of work in this area, the late Eocene and early Oligocene Jebel Qatrani Formation has produced a large assemblage of

hystricognathous rodents (Holroyd 1994; Sallam et al. 2009, 2011; Wood 1968) much of which has not yet been described.

Phiomyidae has long been recognized as a family of hystricognathous rodents that originated in the late Eocene and diversified in Afro-Arabia during the Eocene, Oligocene, and Miocene epochs (Wood 1955). Phiomyids are considered to be distant ancestors of the endemic African hystricognathous rodents—cane rats, dassie rats, and blesmols (mole rats), which together form the phiomorph crown clade. The first discoveries attributed to this family were the species *Phiomys andrewsi* and *Metaphiomys beadnelli*, which were collected from the lower sequence (Quarries A and B) and upper sequence (no quarries identified), respectively, of the early Oligocene part of the Jebel Qatrani Formation. Osborn (1908) initially assigned these species to Eomyidae, a family of extinct rodents from North America and Eurasia. Subsequently, additional material of *Ph. andrewsi* and *M. beadnelli* was reported by Schlosser (1910, 1911), but these species were referred by him to the family Theridomyidae, a Palaeogene rodent group restricted to western Europe. Wood (1968) added new genera and species to the family Phiomyidae based on

new discoveries from the Jebel Qatrani Formation made in the 1960s. Wood described four additional species of previously named genera, *Phiomys paraphiomyoides*, *Phiomys lavocati*, *Metaphiomys schaubi*, and *Paraphiomys simonsi*, and erected two new genera and species for *Phiocricetomys minutus* and *Gaudeamus aegyptius*. In her unpublished doctoral dissertation, Holroyd (1994) restricted Phiomyidae to *Phiomys* and *Metaphiomys*, in addition to a new genus that she named *Acritophiomys*. The latter was the first Eocene genus of Phiomyidae to be reported from the highly productive terminal Eocene Quarry L-41, in the lower sequence of the Jebel Qatrani Formation, and was described as including three species (*Acritophiomys woodi* and *Acritophiomys boweni* from L-41 and *Acritophiomys adaios* from Quarries A, B, and E). Holroyd argued that some specimens that were previously described as part of the *Ph. andrewsi* hypodigm by Osborn (1908) and Wood (1968) should be placed in *A. adaios*. She also classified Phiomyidae into two new subfamilies—Phiomyinae (including *Phiomys*) and Diamantomyinae (including *Metaphiomys* and *Acritophiomys*).

The only suggested post-Palaeogene fossil records of this family are *Andrewsimys parvus* and *Ph. andrewsi* from

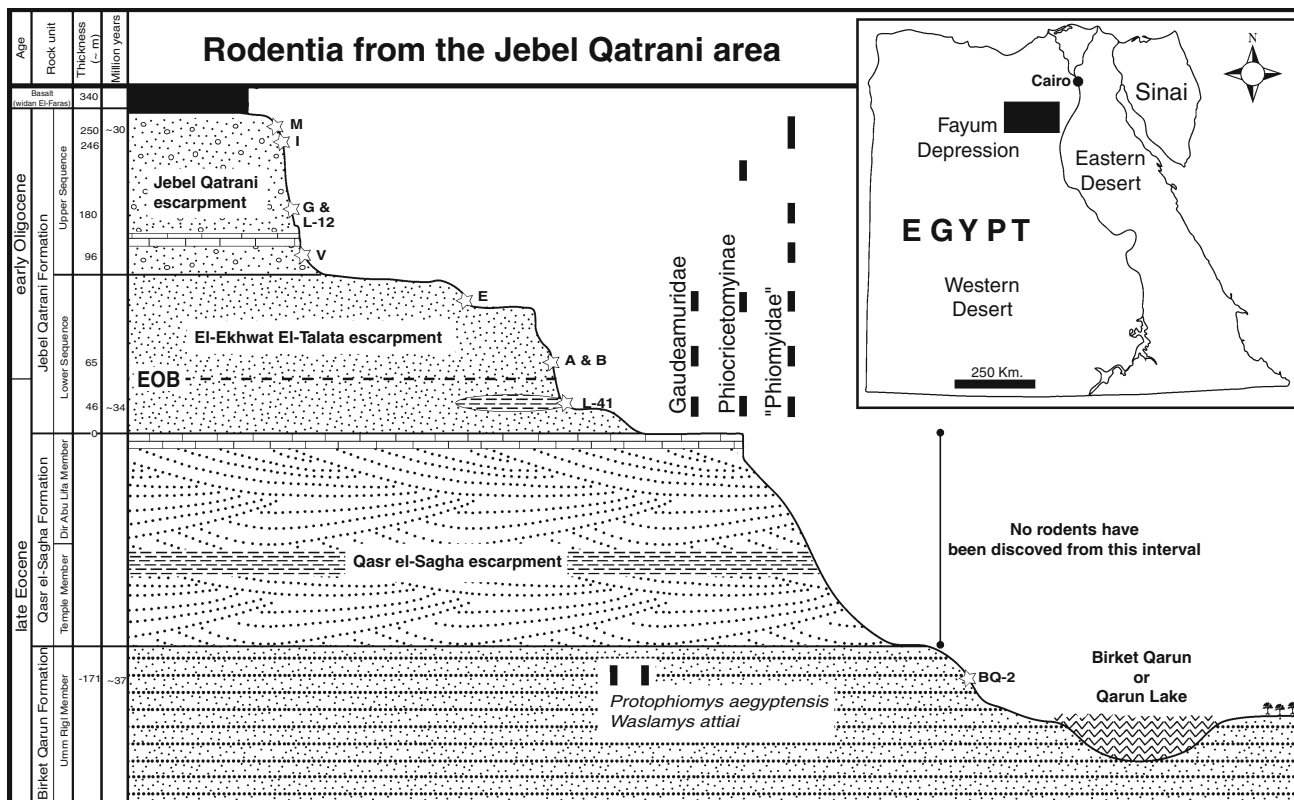


Fig. 1 The early Oligocene–late Eocene Jebel Qatrani area, Fayum Depression, northern Egypt, in unscaled schematic cross-section, showing stratigraphic positions and age estimates for major mammal-

bearing fossil quarries, approximate position of Eocene–Oligocene boundary, following Seiffert (Seiffert 2006), and distribution of hystricognathous rodents in the Jebel Qatrani area

the early Miocene of Kenya (Lavocat 1973) and *Ugandamys downsi* from the early Miocene of Uganda (Winkler et al. 2005). However, Holroyd and Stevens (2009) re-examined the early Miocene specimens previously attributed to *Ph. andrewsi*, and erected a new genus and species for that specimen, *Lavocatomys aequatorialis*, and placed it in the superfamily Thryonomyoidea.

A few discoveries of Palaeogene hystricognathous rodents from outside of Egypt have also been documented as alleged members of the family Phiomysidae. In roughly chronological order from oldest to youngest (Seiffert 2010), the Nementcha or Bir el-Ater locality in Algeria has produced isolated teeth of *Protophiomys algeriensis* (Jaeger et al. 1985); the Dur at-Talah Escarpment, Libya, has recently yielded remains of the taxa *Protophiomys durat-talahensis*, *Phiomys hammudai*, *Talahphiomys lavocati*, and *Talahphiomys libycus* (Jaeger et al. 2010); according to Holroyd (1994), the Thaytiniti locality in Dhofar, Oman, has produced *Acritophiomys adaios* and *Acritophiomys* aff. *bowni* (specimens described in Thomas et al. 1989); the Oligocene Lokone Hill locality in the Turkana basin, Kenya has yielded an isolated tooth that was attributed to *Metaphiomys* (Ducrocq et al. 2010); the Rukwa Rift Basin in Tanzania contains the late Oligocene taxa *Metaphiomys* cf. *beadnelli* (Stevens et al. 2006) and *Kahawamys mbeyaensis* (Stevens et al. 2009); and the late Oligocene Lothidok locality in Kenya has produced remains of *Di-amantomys* (Rasmussen and Gutierrez 2009).

Here, we describe significant new material of *A. bowni* that was recovered subsequent to Holroyd's (1994) work on the genus. These fossils document the entire upper and lower dentition and some aspects of cranial morphology of that species. In addition, we discuss the phylogeny of the family Phiomysidae and the bearing of *Acritophiomys* on the para- versus monophyly of the group. Incomplete upper and lower dentitions of *A. bowni* from L-41 were briefly described in the unpublished Ph.D. dissertation of Holroyd (1994, pp. 107–108), and this species name was used by Lewis and Simons (2006) despite not yet having been adequately described and figured according to the requirements of the International Code of Zoological Nomenclature (ICZN). In order to prevent further confusion in the literature, herein we use Holroyd's name for that species, but provide the first description of the species that establishes it as valid given the requirements of the ICZN.

Materials and methods

Line drawings of complete upper and lower dentitions of *Acritophiomys*, with dental features labeled, are illustrated in Fig. 2. The terminology follows that of Marivaux et al. (2004). Within the descriptive part of this work, we

interchangeably use the terms “crest” and “loph” and “posterior arm of the protoconid” and “metalophulid II”.

Ammonium chloride (NH₄Cl) was used to whiten the specimens for the figures presented here. A micrometer mounted in the lens of a Meiji binocular microscope was used to take the dental measurements. All of the specimens figured and discussed here, aside from the holotype, are housed in the collection of the DPC. The holotype specimen (CGM 83705) is housed in the collection of the CGM.

Systematic palaeontology

Class Mammalia LINNAEUS, 1758

Order Rodentia BOWDICH, 1821

Infraorder Hystricognathi TULLBERG, 1899

Plesion “Phiomysidae” (Wood 1955)

Acritophiomys, new genus

Type species *Acritophiomys bowni*, new species.

Generic diagnosis Differs from younger species of *Phiomys* (*paraphiomysoides* and *andrewsi*) in exhibiting the following features: larger size; dP₄ mesolophid relatively long, reaching the lingual side of the tooth; dP₄ metalophulid I present but medially interrupted; dP₄ mesostylid relatively weak; P₄ hypoconulid relatively weak; M_{1–2} anteroconid present and incipient in the anterolophid; M_{1–2} metalophulid II well-developed; M₃ larger than M₂; DP³ relatively reduced; P⁴ anteroloph present; molar cuspids/crests relatively low; enamel wrinkling present on molars. Differs from “*Phiomys*” *hammudai* in exhibiting the following features: dP₄ anterior cingulid, mesolophid, and posterior arm of the metaconid relatively well-developed; P₄ metalophulid II complete; P₄ posterior arm of the metaconid present but weak; M_{1–2} anterior cingulid present but low; M_{1–2} anteroconid incipient; M_{1–2} metalophulid II directed posteriorly; M₃ larger than M₂; P⁴ metaconule present but weak; M^{1–2} pericingulum present; M³ endoloph present.

Etymology From Holroyd (1994), p. 102, “*acrito*, Latin, meaning confused with; in reference to the confusion with genus *Phiomys*”.

Range Late Eocene, Jebel Qatrani Formation, Fayum Depression, Egypt and possibly the early Oligocene Shizar Member of the Ashawq Formation, Thaytiniti, Oman.

Acritophiomys bowni sp. nov.

Figures 2, 3, 4, 5, 6, 7, 8; Table 1

Diagnosis Medium sized rodent (M₁, on average, length = 1.98 mm and width = 1.67 mm) with a large hystricomorphous infraorbital foramen; a hystricognathous mandible (i.e., the angular process is placed lateral to the

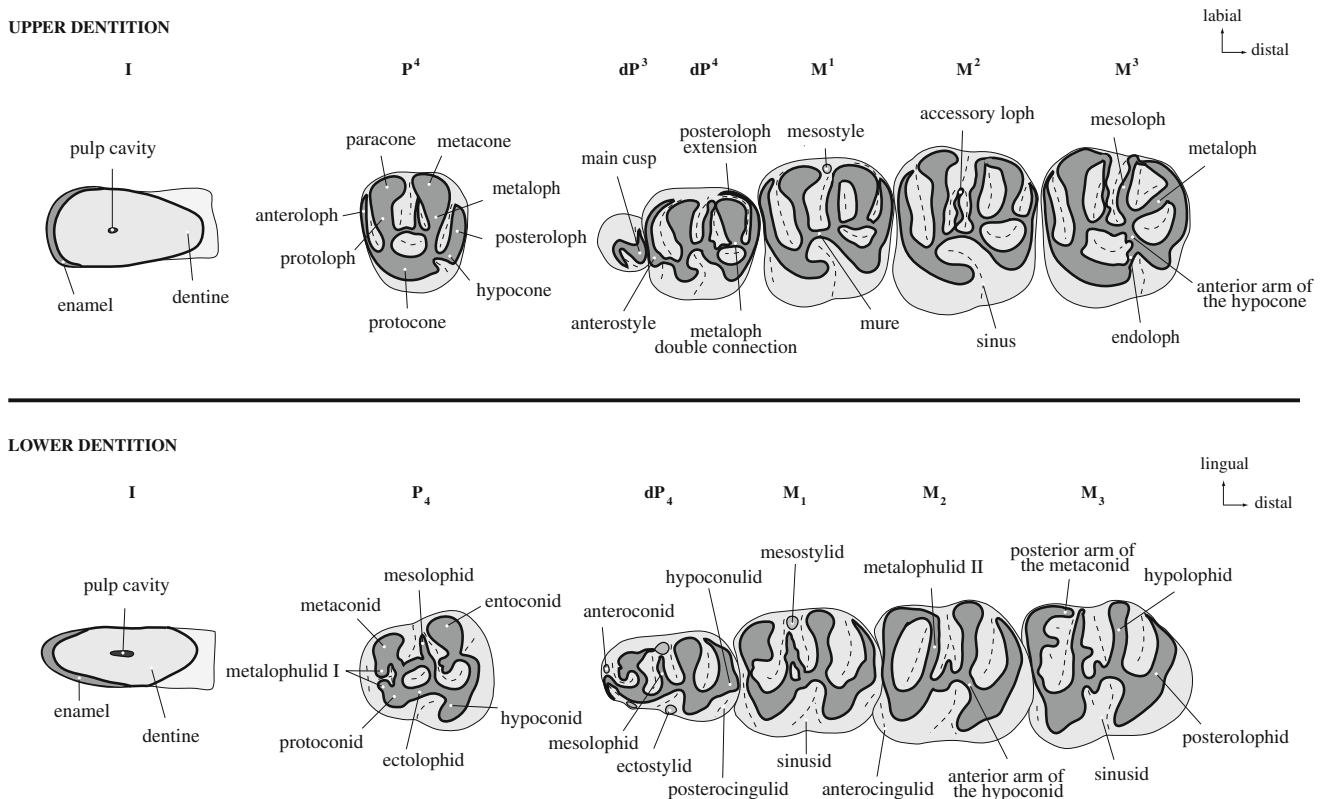


Fig. 2 Line drawing of the upper and lower dentition of *Acritophiomys boweni* from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt, in occlusal view, showing dental terminology, following Marivaux et al. (2004)

plane of the incisor and tooth row, leaving a depression or groove between the angular process and the incisor alveolus in ventral view); coronoid and condylar processes higher than the tooth row and incisor; a well-developed masseteric fossa; a weakly developed postorbital process; an arched upper diastema; and posterodorsal processes of the premaxilla that bear lateral bony keels along their lateral sides and foramina on their dorsal sides. In the upper and lower dentition, the deciduous premolars are replaced by permanent premolars (except the dP^3), have relatively low loph(id)s and tall cusps, and lack labial and lingual walls. Upper molars are pentalophodont with a well-developed mesolophule, complete mure and double (mesial and distal) connection of the metaloph. The dP^4 has a well-developed anterostyle and a low anteroloph. P^4 has a well-developed anteroloph, leading to a tetralophodont occlusal surface, and a robust endoloph. M^3 consistently has an endoloph. On the lower teeth, the metalophulid II either reaches the lingual wall or fuses to the metaconid; the anterocingulid is present; the mesolophid is well-developed on the premolars and M_1 . Lower molars have a rectangular outline (i.e., length greater than width). The dP_4 metaconid is positioned transverse to the protoconid. The P_4 has a longitudinal cristid that connects the anterolophid and mesolophid.

Etymology From Holroyd (1994), p. 107, in honor of Thomas Bown, for his discovery of L-41 and his important contributions to the study of stratigraphy and palaeontology in the Fayum Depression.

Holotype CGM 83705, a distorted cranium that preserves most elements aside from the back of the skull (parietal, occipital bones) and the left P^4 (Figs. 3, 4, 6e).

Referred specimens In addition to the holotype, the *A. boweni* hypodigm includes three skull fragments, three maxillary fragments, and 11 mandibular fragments: DPC 15755, cranial fragments with right and left P^4 - M^3 ; DPC 12662, cranial fragments with right and left dP^3 - M^2 (right dP^3 is broken); DPC 14200, cranial fragments with left dP^3 - M^3 ; DPC 10317, right maxillary fragment with M^2 - M^3 ; DPC 10338, right maxillary fragment with P^4 - M^2 ; DPC 17438, maxillary fragment with M^1 - M^2 ; DPC 14168, left mandibular fragment with P_4 - M_3 , complete incisor and complete condylar process; DPC 21650, left mandibular fragment with dP_4 - M_2 ; DPC 13286, right mandibular fragment with P_4 - M_3 ; DPC 12046, left mandibular fragment with P_4 - M_3 and broken incisor; DPC 15340, left mandibular fragment with P_4 - M_3 , posterior portion of dP_4 and complete incisor; DPC 7771, right mandibular fragment with P_4 - M_3 and broken incisor; DPC 20288, right

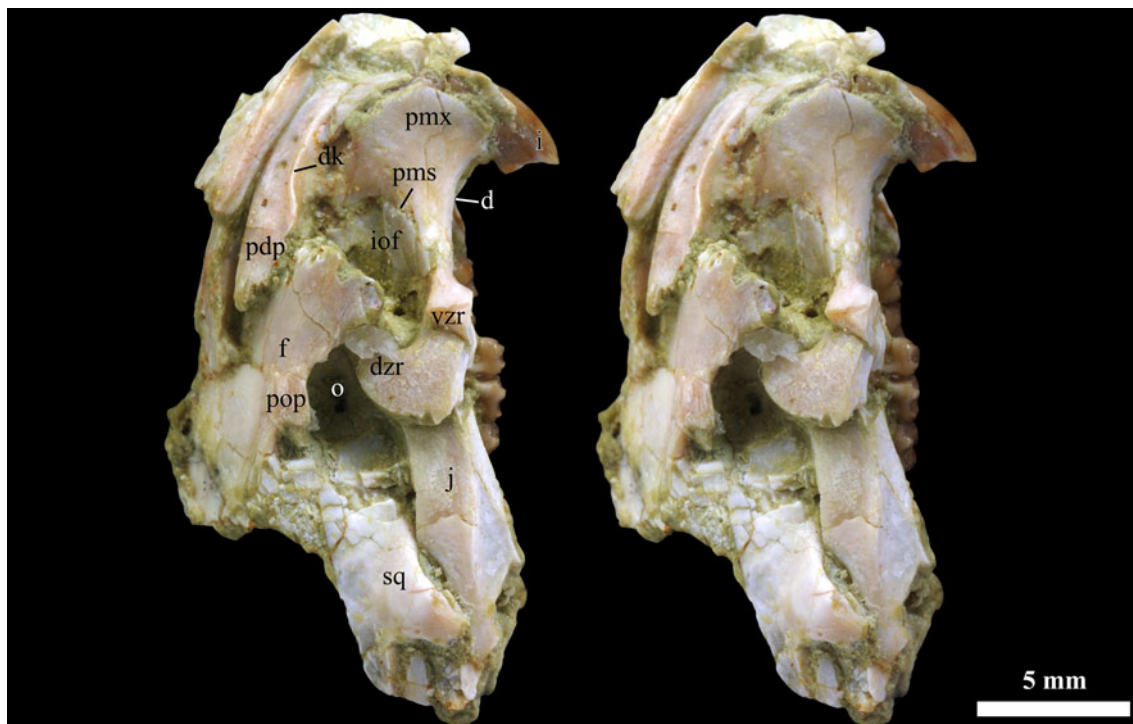


Fig. 3 Partial cranium of *Acritophiomys bowni* (holotype, CGM 83705) from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt. Stereopair in lateral view. *d* diastema, *dk* dorsal bony keel, *dzt* dorsal zygomatic ramus, *f* frontal,

i incisor, *iof* infraorbital foramen, *j* jugal, *o* orbit, *pdp* posterodorsal process, *pms* premaxilla-maxilla suture, *pmx* premaxilla, *pop* post-orbital process, *sq* squamosal, *vzr* ventral zygomatic ramus



Fig. 4 Partial cranium of *Acritophiomys bowni* (holotype, CGM 83705) from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt. Stereopair in ventral view.

i incisor, *j* jugal, *mx* maxilla, *pl* palate, *pms* premaxilla-maxilla suture, *pmx* premaxilla, *sf* fossa for superficial masseter muscles, *sq* squamosal, *vzr* ventral zygomatic ramus

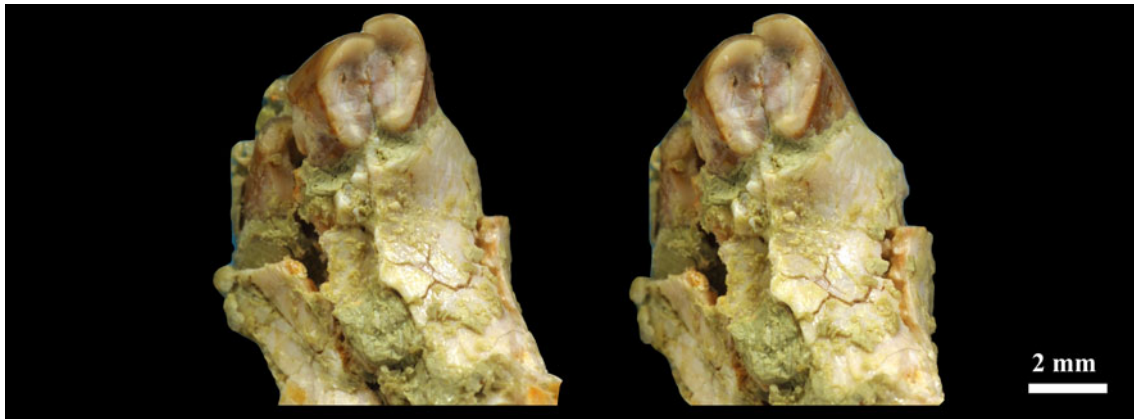


Fig. 5 Rostrum of *Acritophiomys boweni*, DPC 15725 from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt. Stereopair in ventral view, showing the occlusal surface of the upper incisors

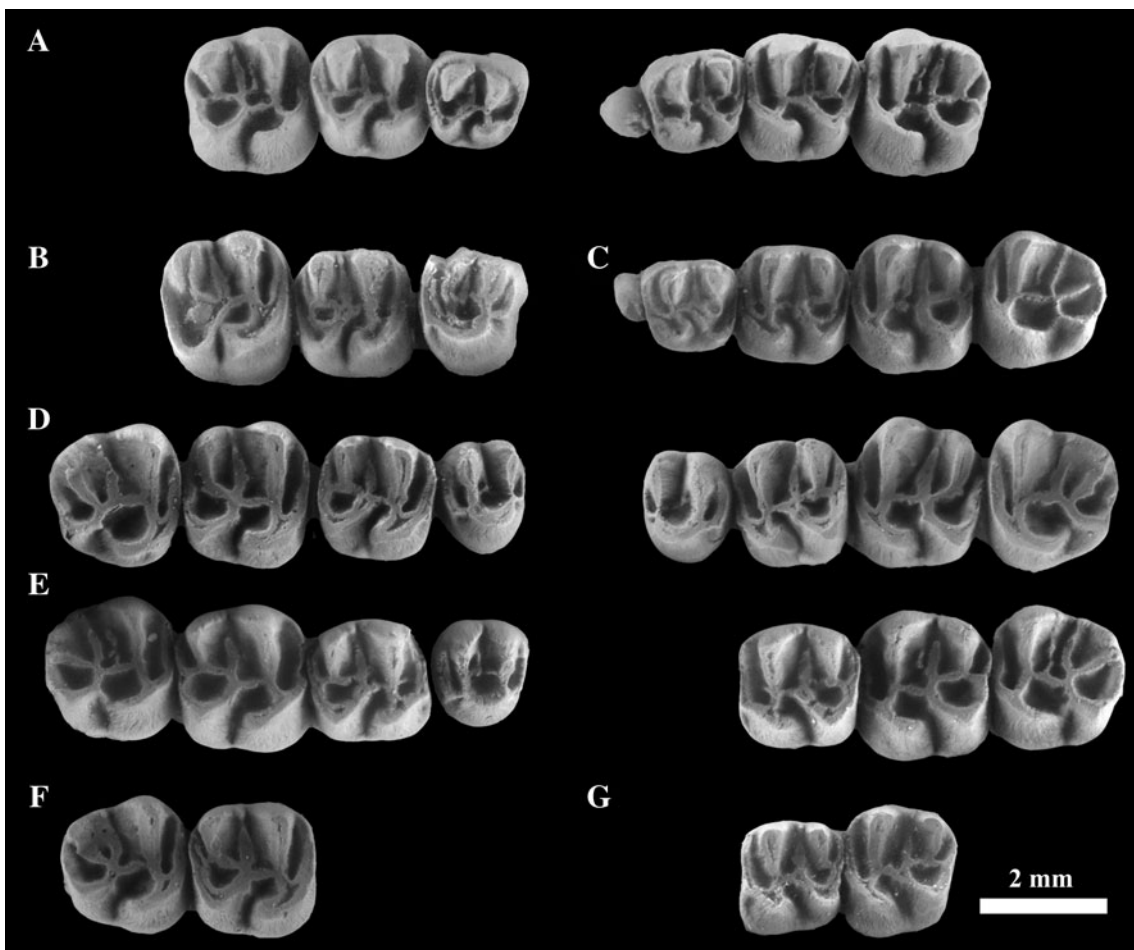


Fig. 6 Upper dentition of *Acritophiomys boweni* from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt. **a** DPC 12662, right dP^4-M^2 , left dP^3-M^2 ; **b** DPC 10338, right

P^4-M^2 ; **c** DPC 14200 left dP^3-M^3 ; **d** DPC 15755, right and left P^4-M^3 ; **e** CGM 83705, holotype, right P^4-M^3 , left M^1-M^3 ; **f** DPC 10317, left M^2-M^3 ; **g** DPC 17438, right M^1-M^2

mandibular fragment with dP_4-M_3 and complete incisor; DPC 21599, right mandibular fragment with dP_4-M_3 and broken incisor; DPC 13062, left mandibular fragment with

P_4-M_3 and complete incisor; DPC 13525, left mandibular fragment with M_2-M_3 ; and DPC 22951, right mandibular fragment with P_4-M_2 and complete incisor.

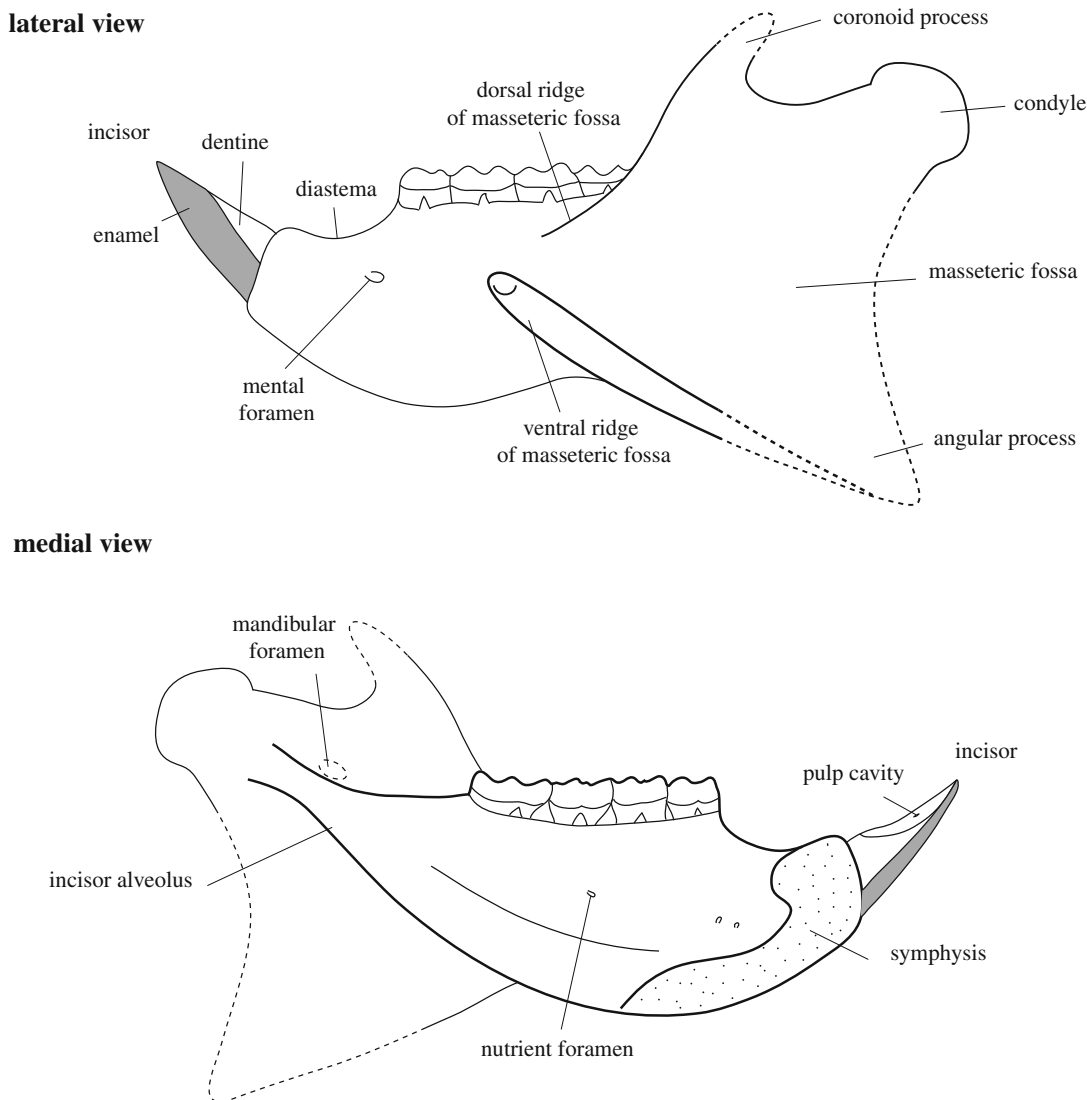


Fig. 7 Reconstruction of the *Acritophiomyys boweni* mandible based on mandibular fragments in the hypodigm (DPC 20288, DPC 13062, DPC 14168, and DPC 22951). Dashed lines delimit hypothetical reconstructions

Type locality and age Locality 41 (L-41), lower sequence of the Jebel Qatrani Formation, late Eocene in age (~34 Ma), Fayum Depression, Egypt.

Description of cranial elements Four crushed crania are attributable to *A. boweni* (Figs. 3, 4) and provide the first documentation of cranial morphology in a basal phiomorph. As is common at L-41, the specimens were subjected to severe post-mortem distortion, which has led the crania to be dorsoventrally flattened or mediolaterally compressed; the specimens bear numerous surface cracks and displacements. Some of the cranial elements are also shifted and/or fused together, which makes it difficult to confidently trace and describe the extent of some bones. The holotype cranium CGM 83705 (Figs. 3, 4) is less crushed than others but exhibits both mediolateral and

anteroposterior post-mortem compression, leading to very asymmetric cranial surfaces (Fig. 4). The specimen bears most of the anterior skull elements (premaxillae, both maxillae with almost complete dentition, jugal, and most of the frontal) aside from the posterior part of the skull behind the tooth row and the left P⁴ and incisor. The crania DPC 12662, DPC 115755, and DPC 14200 are highly damaged and provide little additional information. However, taken together these specimens reveal various details about the cranial morphology of *Acritophiomyys*.

Palaeogene hystricognath cranial remains are uncommon, particularly those of “phiomyids”, so the description of the skull elements is based on comparisons with sympatric and contemporaneous *Gaudeamus* (Sallam et al. 2011) and living taxa (the African phiomorph

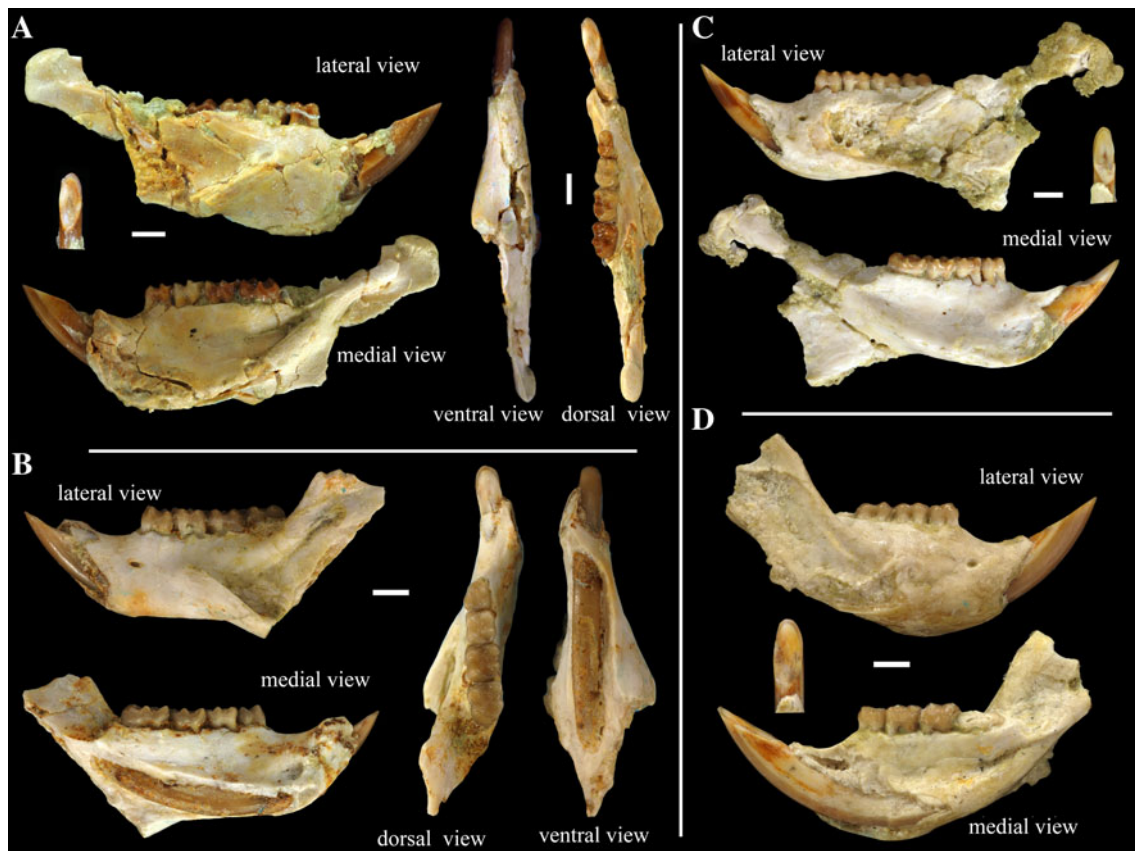


Fig. 8 Mandibular fragments of *Acritophiomys bowni* from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt, preserving the anatomical features discussed in the text. **a** DPC 20288; **b** DPC 13062; **c** DPC 14168; **d** DPC 22951

Thryonomys, the South American caviomorph *Cavia*, and the African hystricid *Atherurus*), supplemented by comparisons with cranial remains of the fossil caviomorphs *Branisamys* and *Incamys* from the Oligocene of Bolivia figured by Patterson and Wood (1982).

The nasal bones and their relationships with the premaxillae and frontals are obscured due to post-mortem distortion. The premaxillae are preserved in CGM 83705, but are smashed in DPC 15755. The bones house two moderately large upper incisors and form most of the rostrum (wall, floor, and upper diastema). The most rostral part of the right premaxilla bears several tiny nutrient foramina as seen in *Gaudeamus*. The posterodorsal processes of the premaxilla are well preserved in CGM 83705. They are narrow anteriorly, flare posteriorly, and have flat medial surfaces with the nasals as seen in *Gaudeamus*. Dorsally, each bone bears four relatively large foramina, which align antero-posteriorly, and are bounded posteriorly by the frontal bone and, presumably, posterolaterally by the maxilla. The most posterior ends of the posterodorsal processes overlap the frontals because of distortion, so the location of the suture between the frontal and premaxilla relative to the infraorbital foramen is uncertain.

In lateral view, the anterior portion of the premaxilla is arched, leading to a curved diastema, as seen in *Thryonomys* (and to a greater extent than in *Gaudeamus*). The premaxilla is smooth laterally and has a dorsal bony keel that courses along the lateral side of the posterodorsal process (Fig. 3). The latter feature is more distinctive in *Acritophiomys* than in *Gaudeamus* and *Atherurus*, but less prominent than in *Thryonomys*.

In ventral view, the incisive foramina are obscured due to distortion. The ventral region of the premaxilla forms almost two-thirds of the upper diastema, a similarity to *Gaudeamus*, *Thryonomys* and *Cavia* that is not seen in *Atherurus*. The suture between the premaxilla and the maxilla on the lateral surface of the rostrum is poorly preserved, but it arcs anteriorly and continues ventrally, anterior to the infraorbital foramen, as in *Gaudeamus*. In CGM 83705, the maxillae are missing the left P⁴. The anterior portion of the maxilla extends lower than the plane of the alveoli, as in *Atherurus*, and differs from the deeper condition seen in *Gaudeamus*, *Thryonomys* and *Cavia*. Laterally, the facial process of the maxilla meets the posterior part of the premaxilla to form the lateral wall of the rostrum, and forms the medial portion of the infraorbital foramen. As is typical of ctenohystrican rodents, the

Table 1 Length and width of teeth (in millimeters) in the hypodigm of *Acritophiomys boweni* gen. et sp. nov

Specimen	Side	dP3		dP4		P4		M1		M2		M3	
		Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
Upper dentition													
DPC 14200	Left	–	–	1.50	1.55	–	–	1.73	1.88	1.93	2.20	1.93	2.15
DPC 12662	Right	0.75	0.75	1.55	1.75	–	–	1.78	2.03	1.93	2.33	–	–
	Left	–	0.80	1.63	1.65	–	–	1.85	2.00	1.95	2.30	–	–
DPC 15755	Right	–	–	–	–	1.55	1.73	1.88	1.95	2.05	2.35	2.05	2.25
	Left	–	–	–	–	1.50	1.73	1.90	2.00	2.03	2.30	2.13	2.33
CGM 83705	Right	–	–	–	–	1.53	1.68	1.83	1.95	2.03	2.28	2.00	2.20
	Left	–	–	–	–	–	–	1.85	1.90	2.05	2.25	2.03	2.18
DPC 10338	Right	–	–	–	–	1.63	1.88	1.80	1.98	2.05	2.33	–	–
DPC 17438	Right	–	–	–	–	–	–	1.68	1.80	1.83	2.08	–	–
DPC 10317	Right	–	–	–	–	–	–	–	–	1.98	2.08	1.98	2.13
Mean		0.75	0.78	1.56	1.65	1.55	1.76	1.81	1.94	1.98	2.25	2.02	2.21
Standard dev.			0.04	0.07	0.10	0.06	0.09	0.07	0.07	0.07	0.10	0.07	0.07
Lower dentition													
DPC 21599	Right			1.85	1.28	–	–	1.90	1.63	2.13	1.98	2.13	1.95
DPC 20288	Right			1.88	1.25	–	–	1.95	1.68	2.18	2.00	2.43	2.08
DPC 21650	Left			1.88	1.33	–	–	2.00	1.68	2.15	2.00	–	–
DPC 15340	Left			–	1.28	1.48	1.43	1.98	1.65	2.13	2.00	2.28	1.98
DPC 13286	Right			–	–	1.70	1.60	1.93	1.70	2.20	1.98	2.23	2.00
DPC 7771	Right			–	–	1.53	1.43	1.98	1.63	2.18	1.95	2.38	2.03
DPC 13062	Right			–	–	1.68	1.58	1.90	1.68	2.10	1.93	2.30	1.95
DPC 14168	Left			–	–	1.75	1.65	2.08	1.70	2.20	1.95	2.33	1.95
DPC 12046	Left			–	–	1.68	1.48	2.00	1.63	2.25	2.13	2.58	2.08
DPC 22951	Right			–	–	1.63	1.45	2.03	1.65	2.13	1.85	–	–
DPC 13525	Left			–	–	–	–	–	–	2.20	2.00	2.45	2.05
Mean				1.87	1.29	1.64	1.52	1.98	1.66	2.17	1.98	2.35	2.01
Standard dev.				0.02	0.03	0.10	0.09	0.06	0.03	0.04	0.07	0.13	0.05

infraorbital foramen is large, hystricomorphous, and the medial masseter muscle passed through the foramen to attach to the premaxilla. It is uncertain if the infraorbital foramen is made up entirely of the maxilla, but it is placed anterodorsal to the tooth-row. The outline of the infraorbital foramen cannot be determined due to post-mortem distortion.

The ventral ramus of the zygomatic process of the maxilla is very similar to that of *Gaudeamus*, and extends laterally from the area in front of P⁴ and then arches posteriorly, delimiting the anteroventral portion of the orbital margin. Ventrally, the anterior portion of the ventral zygomatic ramus bears a deep fossa for the origin of the superficial masseter muscles, and, posteriorly, a relatively shallow fossa for the origin of the lateral masseter, as in *Gaudeamus* and *Cavia*. The dorsal zygomatic ramus is broader than that of *Gaudeamus* and is dorsally oriented. Its relationship with the jugals is unclear, because both were shifted post-mortem, and overlap due to distortion. The orientation of the infraorbital foramen cannot be determined because the bones in this area are highly

shifted. The jugal is well preserved on the right side of CGM 83705, but it is displaced under the lateral rim of the infraorbital foramen. It is relatively thick, flares posteriorly and bears an anteriorly pointed triangular depression on its lateral side, presumably to accommodate the thin splint of the anterior extension of the squamosal. The palate region is highly damaged and its morphology is difficult to trace; however, in DPC 15755 there is a palatal fragment that preserves the midline and a pair of palatine foramina. The latter are relatively small with respect to those of *Gaudeamus*.

In DPC 15755, most of the right frontal is preserved and it is roughly flat. The interfrontal suture separates the frontals along their length, which is a feature found in the living and extinct caviomorphs and phiomorphs (Patterson and Wood 1982). In CGM 83705, the frontonasal suture is partially preserved and displaced away from the premaxillae. The postorbital process is weakly developed, triangular, extends laterally from the middle part of the frontal, and lacks temporal lines that curve posteromedially from the postorbital process as in *Gaudeamus*. The postorbital process is

relatively small when compared with that of *Gaudeamus*, but it is slightly larger than those of the other hystricognathous rodents in our comparative set. The postorbital constriction posterior to the postorbital process is less pronounced when compared with that of *Gaudeamus*. On the right side of CGM 83705 and DPC 15755, there is an incompletely preserved squamosal that is displaced forward and situated dorsal to the jugal. The rear portion of the cranium (i.e. parietal, sphenoid, ectotympanic bullae and occipital) is either not preserved or severely damaged.

Description of the upper dentition The upper dentition (Figs. 5, 6) is known from several cranial fragments. The upper cheek teeth have somewhat bunodont crowns, with transverse lophs and pointed cusps. Within the tooth row, the size increases from P⁴/dP⁴ to M³.

The two upper incisors of *Acritophiomys bowni* (Fig. 5) are preserved in DPC 15755, but only the right upper incisor is present in the holotype (Figs. 3, 4). The upper incisor is different in size in the two specimens, as is also seen in *Gaudeamus*, probably due to age. The upper incisor is relatively short and curved when compared with the lower incisors. The curve of *Acritophiomys*' incisor is greater than that of *Gaudeamus*, more like the condition seen in *Thryonomys*. The upper incisor is somewhat ovoid in outline (mesiodistal length = 1.2–1.6 mm, labiolingual length = 2.4–3.0 mm) with a flat mesial surface and curved lingual and labial surfaces, and has a smooth surface as in *Gaudeamus*, *Atherurus* and *Cavia*. Enamel covers the labial surface and extends across about one-third of the distal side but not as far on the mesial side, as in *Gaudeamus*. In lateral view, the occlusal surface is deeper when compared with that of the lower incisor. The pulp cavity is short and slit-shaped and situated slightly anteriorly. The dorsal surface of the left upper incisor in DPC 15755 is exposed, which reveals that the tooth originates in front of the tooth row as in *Gaudeamus* and *Cavia*. In *Thryonomys*, the posterior end of the incisor originates dorsal to P⁴-M¹ (van der Merwe 2000), but in *Atherurus*, the posterior end of the incisor originates roughly in the middle of the diastema.

The upper fourth permanent premolar has a roughly ovoid outline and is narrow relative to its width. The tooth is smaller than M¹ and bears three major cusps (paracone, metacone, protocone) and a minute hypocone. The paracone and metacone are well-developed and relatively tall cusps with respect to the protocone, and placed longitudinal to each other, and occupy most of the labial side of the tooth. The labial wall lacks the anterior arm of the metacone and the posterior arm of the paracone, leaving a deep V-shaped notch in the labial border of the tooth. This notch reaches the level of the middle basin. The protocone is a crestiform and mesiodistally oriented cusp that is situated

transverse to the midpoint between the paracone and metacone. The anteroloph is very short, weakly developed and remarkably low, and extends down from the mesiolabial side of the protocone to taper before reaching the base of the mesial side of the paracone, forming a very shallow, narrow, and small anterior basin. The protoloph and metaloph are robust and parallel to each other and flare labially from the protocone and hypocone to fuse with the paracone and metacone respectively, all of which form a distinctive U-shape as a boundary for the middle basin. In the middle basin of the P⁴ of the holotype and DPC 10338, there is a weakly developed crest that connects the protoloph and metaloph, with a short crest coursing labially from its middle. The hypocone is placed slightly labial to the protocone, and the two cusps are connected by a thin and tall endoloph. The posteroloph is more developed, is longer and higher than the anteroloph, terminates at the distal base of the metacone, and courses around the distal margin of the tooth. The posterior basin is relatively large when compared with the anterior basin. The lingual sinus is absent.

The upper deciduous third premolar is generally a small peg-shaped tooth with a rounded base, and abuts the mesial surface of dP⁴. In DPC 12662, the tooth is well preserved and has one large cusp that occupies the distal portion of the crown and forms the apex of the tooth. There is a small depression on the labial side of the former cusp. A small cusp is placed mesiolabial to the main cusp and both are connected via a short crest. In the mesiolingual corner of the crown, there is a minute and mesiolabially distolingually oriented crestiform cusp, which it is separated from the main cusp via a shallow basin.

The upper deciduous fourth premolar is molariform and has a somewhat trapezoid-shaped outline, with a relatively short lingual margin and a broad mesial margin. The crown is pentalophodont and has four distinct cusps (paracone, protocone, metacone and hypocone), all of which are about equal in size and height. The anterostyle is a distinct but small cusp that is situated mesiolabial to the protocone. The two cusps are connected via a short crest that courses down from the mesiolabial part of the protocone to integrate into the anterostyle. The anteroloph is low and well-developed, runs labially from the anterostyle, and courses across the mesial margin of the tooth, closing the anterior basin. It merges labially with an incipient parastyle and continues distally to end labially to the metacone, forming a cingulum around the mesiolabial corner of the tooth. The protoloph is well-developed and transverse, courses distolabially from the protocone, curves mesiolabially near the middle of the tooth, and flares labially to meet the paracone. The latter is prominent and large and lacks a posterior arm. The hypocone is a well-developed cusp, placed distal to the protocone. The anterior arm of the hypocone is robust and courses mesiolabially to fuse with a moderately developed

metaconule in the middle of the crown. The mure is complete, connecting the metaconule with the protoloph. The mesolophule courses labially from the metaconule and is inclined distally to meet the anterior base of the metacone. The mesostyle is a minute cusp, represented as a small inflation on the labial end of the mesolophule. The metaloph is robust but short, courses lingually from the metacone, and tapers in the middle of the crown. The lingual end of the metaloph is connected mesially to the mesolophule and distally to the posteroloph via weakly developed crests, all of which, with the hypocone, delimit a moderately large fovea at the distolingual corner of the crown. The metacone is well-developed and lacks an anterior arm. A concave and well-developed posteroloph courses labially from the hypocone and turns around the distal and labial base of the metacone. The posterior basin is shallow and very narrow when compared with the anterior basin. Due to the absence of the anterior arm of the metacone and the posterior arm of the paracone, the central basin is open labially via a wide notch. Distal to the anterostyle and mesial to the protocone, there is a short and low anterocingulum. The labial sinus is deep and delimited labially by the mure and becomes very narrow toward its base. The ectostyle is an incipient cusp and situated at the mesiolingual base of the hypocone.

The upper first molar has a similar occlusal morphology to that of dP^4 , but it is larger and has relatively well-developed lophs and cusps, and a relatively wide lingual portion, leading to a roughly square outline. The anteroloph has a relatively straight course, lacks its distolabial extension, and ends mesial to the paracone, leading to an open anterior basin, unlike that of dP^4 . The posteroloph is relatively short and also lacks the mesiolabial extension, leaving no cingulum labial to the metacone. The hypocone extends slightly mesially toward the lingual sinus. The latter lacks the ectostyle in some individuals. The metaloph is relatively short with respect to that of dP^4 . The anterocingulum is absent in DPC 14200. The anterior basin is open labially.

The upper second molar is essentially identical in morphology to M^1 , but differs in being larger and having relatively robust lophs, a reduced and more labially and lingually situated hypocone and metacone, respectively, a taller and more curved anteroloph, a very weakly developed and low endoloph that touches the base of anterior arm of the hypocone, a short metaloph and posteroloph, and in lacking the anterocingulum and the ectostyle. In DPC 12662, DPC 14200, and CGM 83705, there is an accessory crest between the mesolophule and the protoloph, which runs longitudinally from the mure and connects to the base of the base of the paracone.

The upper third molar is heart-shaped and is larger than all of the other upper teeth aside from M^2 . The anterior half

of the tooth is similar to the corresponding part on M^{1-2} , but the posterior part is much different in having a very reduced metacone and hypocone. The metacone is relatively lingual in position with respect to the paracone. The hypocone is placed far labial to the protocone and the posteroloph is relatively short. The endoloph is a well-developed and relatively tall crest that delimits the lingual sinus labially. The tooth has an even more crestiform protocone, which together with the endoloph, anterior arm of the hypocone, mure, and lingual part of the protoloph, delimit a moderately large and round fovea. The paracone is the tallest cusp. An obliquely oriented metaloph courses from the lingual side of the metacone and connects to the metaconule. In DPC 15755, the metaloph connects to the anterior arm of the hypocone. The mesolophule and the mesostyle are relatively well-developed when compared with those of M^{1-2} . The crown has a broader middle basin and a more rounded posterior basin than those of M^{1-2} . In the holotype, the metaloph runs from a small cusp lingual to the metacone.

Description of the mandible The mandible is slender and fully hystricognathous, i.e., the angular process is placed lateral to the plane of the incisor and tooth row, leaving a distinctive depression between the angular process and this plane in ventral view. The latter depression is the insertion for the *pars reflexa* of the superficial masseter muscle (Hautier and Saksiri 2009). The ascending ramus is posteriorly oblique and arises lateral to the base of the last two molars. The horizontal ramus is robust and deeply convex ventrally, with the deepest point being beneath the P_4 . The tip of the coronoid process is broken, however the outline of the anterior and posterior margins could be traced, suggesting a hook-shaped process (Fig. 7). The base of the coronoid process is higher than the tooth row, only known from two specimens (DPC 22951 and DPC 13062) (Fig. 8b, d). The diastema is slightly deeper than the alveolar plane and makes up about 50% of the length of the tooth row. On the lateral surface of the mandible, the mental foramen is relatively small, oval in shape, and situated more dorsally, below the posterior half of the diastema. The masseteric fossa is deep, broad posteriorly and fades anteriorly to terminate beneath the M_1 . The dorsal masseteric ridge is weakly developed and continues anteriorly from the base of the ascending ramus and fades below the anterior part of M_2 . The ventral masseteric ridge, which is an insertion of the lateral masseter muscle, is well-developed, originates laterally from the area below M_1 , and continues posteroventrally towards the angular process. The posterior tip of the angular process is not preserved in any of the specimens in the hypodigm. The condylar process is complete and partially preserved in DPC 20288 and DPC 14168, respectively (Fig. 8a, c). It is much higher

than the tooth row, and slightly lower than the coronoid process, and has a convex articular surface that is oriented anteroposteriorly and extends medially, leaving a lip along its medial side. On the medial surface of the mandible, the angular process originates below the area between M_2 and M_3 ; there are some nutrient foramina scattered on the corpus; the symphysis is well-developed with a broad superior transverse torus and narrow inferior transverse torus. The latter extends posteriorly to the level of the second molar; its anterior part delimits a small fossa dorsally. The incisor's alveolus extends posteriorly to end behind the tooth row and continues as a strut dorsally toward the condylar process. In the area between the coronoid and condylar processes, there is a mandibular foramen, which is partially preserved and only known from DPC 22951 and DPC 13062.

Description of the lower dentition The entire lower dentition of *A. bowni* is known from several mandibular fragments, allowing identification to locus of any isolated teeth. The lophids are relatively low and meet the cuspids at their bases.

The lower incisor of *A. bowni* has slightly concave mesial and distal margins, and smooth labial and ventral surfaces, extends anteriorly slightly above the tooth row, and extends distally to terminate behind the lower third molar. The worn cross-sectional (occlusal) surface of the lower incisor is preserved in DPC 20288, DPC 15340 (juveniles), DPC 22951, and DPC14168 (adults). In juveniles, the lower incisor is more oval in shape and has a relatively short and broad cross-section (mesiodistal length = 1.40 mm, buccolingual length = 3.20 mm) when compared with that of the adult specimen DPC 15340 (mesiodistal length = 1.30 mm, buccolingual length = 3.30 mm). In DPC 20288, the enamel covers the labial surface and extends across about 50% of the distal side and about 30% on the mesial side, whereas in DPC 15340 it covers about 50% of the distal side and about 35% on the mesial side. In lateral view, the occlusal surface of DPC 15340 is relatively concave when compared with that of DPC 20288. The pulp cavity is long and slit-shaped and placed slightly posterior to the midpoint. Compared to those of the juveniles, the lower incisors of the adult individuals are large and well-developed, and the enamel layer covers $\approx 60\%$ of the labial surface in DPC 14168 and DPC 22951, respectively.

The lower deciduous fourth premolar of *A. bowni* (Fig. 9a–c) is only known from four specimens (DPC 20288, DPC 21599 & DPC 21650, DPC 15340). In DPC 15340, the anterior portion of the dP_4 is broken and the crown of P_4 can be seen erupting underneath it. The dP_4 is replaced by the permanent P_4 as in *Waslamys* (Sallam et al. 2009) and *Gaudeamus* (Wood 1968; Sallam et al. 2011). The tooth is longer than it is wide, and has a roughly

triangular outline with a broad talonid and a narrow trigonid. The occlusal configuration is tetralophodont (metalophulid II, mesolophid, hypolophid and posterolophid), missing the most anterior cristid (metalophulid I), and bears five major cuspids (protoconid, metaconid, hypoconid, entoconid, and hypoconulid), all of which are more or less equal in size and of about the same height, but the lophids are relatively low. On the mesial portion of the crown, the metaconid is placed transverse to the protoconid, which together are slightly distal in position, leaving a somewhat broad mesial shelf. Within this shelf, there is a short and low cristid that courses mesiolingually from the mesial portion of the protoconid, connects to a small anteroconid, and continues mesiolingually to taper and terminate as a small accessory cuspid. The latter is placed mesial to the base of the metaconid, from which the anterocingulid runs labially, courses around the mesial margin of the crown, and terminates at the mesiolabial base of the protoconid. In DPC 20288, the accessory cuspid is broken and the anterocingulid terminates as an incipient cuspid labial to the protoconid. In DPC 21599, metalophulid I is absent, whereas in specimen DPC 20288 there is an incipient cristid protruding labially from the mesiolabial side of the metaconid, which could be a remnant of the metalophulid I. The most transverse mesial cristid is metalophulid II, which is arch-shaped and runs lingually from the distal portion of the protoconid toward the posterior side of the metaconid. The latter cristid delimits the posterior margin of the anterior basin of the tooth. The ectolophid is low, slopes down from the distal side of the protoconid, and attaches to the anterior arm of the hypoconid near that cristid's junction with the hypolophid. Within the distal part of the ectolophid, a complete but weakly developed mesolophid runs toward the lingual sides of the crown, dividing the middle basin into two somewhat equal parts, and fuses lingually to a weakly developed mesostylid. The latter is an isolated cuspid and roughly situated at the midpoint between the metaconid and the entoconid. In DPC 20288, the posterior arm of the metaconid slopes steeply down to connect with the mesostylid, but in DPC 21599 and DPC 21650 there is no connection between the metaconid and the mesostylid. The lingual wall between the metaconid and the entoconid is absent, leaving the middle basin open lingually via a deep and wide notch. The hypoconid is placed transverse to the entoconid. The former's anterior arm is robust and short, and connects to a well-developed hypolophid, forming the third transverse cristid of the crown. The hypolophid flares lingually as a large entoconid. Distally, the posterolophid is well-developed and courses distolingually from the hypoconid to end and taper distal to the base of entoconid, leaving the posterior basin open lingually. The hypoconulid is a regular cuspid, occupies

the middle portion of the posterolophid, and forms the very distal tip of the tooth. At the distolabial corner of the tooth, there is a posterocingulid situated distal to the hypoconid. The labial sinusid is wide and deep, as the same level as the central basin, which both are separated by the ectolophid. The ectostylid is present but weakly developed, and placed in the most labial part of the labial sinusid, mesial to the hypoconid. There is no hint of the mesoconid.

The lower fourth premolar (Fig. 9d–i, k) is generally pear-shaped in outline, with a wide talonid and a narrow trigonid as seen in all other Fayum species that replace dP_4 with P_4 . The P_4 is relatively short and broad—when compared with dP_4 and has four major cuspids (metaconid, protoconid, entoconid and hypoconid), lacking the hypoconulid. On DPC 15340, the least worn specimen, the four major cuspids are at the same height. The metaconid and the protoconid are transversely placed. At the most mesial part of the crown, there is a short and low anterocingulid,

which in some teeth bears an incipient anteroconid in its middle part. The metalophulid I is generally absent, but in DPC 14168 it is interrupted at its midpoint by a deep and narrow notch that reaches the base of the crown. The metalophulid II is complete and connects the lingual side of the protoconid with the labial side of the metaconid. From the middle of the latter cristid, there is an accessory cristid running distally to terminate more or less at the midline of the tooth, and fuses to the midpoint of the mesolophid. This cristid appears to be an autapomorphy of this species. The ectolophid is a well-developed and longitudinal cristid that courses distally from the protoconid and connects to the mesial side of the hypoconid as in more generalized hystricognaths. The mesolophid runs from nearly the midpoint of the ectolophid toward the lingual margin. In some cases, it terminates as a small mesostylid, and in other individuals, it ends before reaching the lingual margin. There is no lingual wall between the entoconid and the metaconid due to the absence of the anterior arm of the

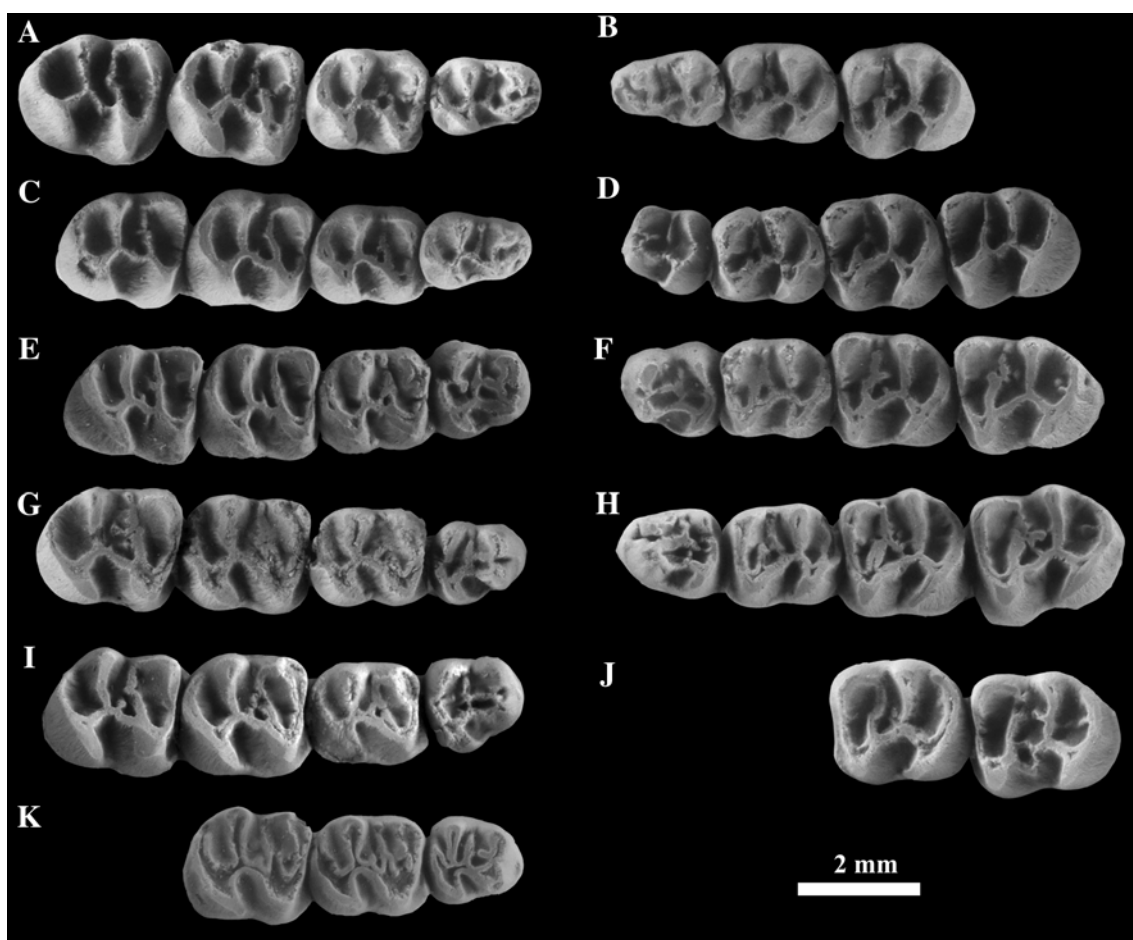


Fig. 9 Lower dentition of *Acritophiomys boweni* from the late Eocene Locality L-41, Jebel Qatrani Formation, Fayum Depression, northern Egypt **a** DPC 20288, right dP_4 - M_3 **b** DPC 21450, left dP_4 - M_2 ; **c** DPC 21599 right dP_4 - M_3 ; **d** DPC 15340, left P_4 - M_3 ; **e** DPC 14168, left P_4 -

M_3 , reverse; **f** DPC 13062, left P_4 - M_3 ; **g** DPC 7771 right dP_4 - M_3 ; **h** DPC 12046, left P_4 - M_3 ; **i** DPC 13286 right dP_4 - M_3 ; **j** DPC 13525, left M_2 - M_3 ; **k** DPC 22951 right P_4 - M_2

entoconid and the posterior arm of the metaconid, leading to a wide opening in the lingual side of the central basin of the crown. The entoconid is placed transverse to the hypoconid. The base of the latter extends labially, forming most of the distolabial corner of the tooth. The posterior margin of the crown is generally composed of a combination of the posterolophid, which courses distolingual from the hypoconid, and the hypolophid, which runs distolabial from the entoconid, coursing around the posterior wall of the tooth. But there is considerable variation in this area: in DPC 7771, the posterolophid extends and terminates at the distal base of the entoconid, whereas the hypolophid turns backward to meet the posterolophid in its middle; in DPC 14168 the hypolophid continues toward the anterior arm of the hypoconid and terminates lingual to it with an accessory cristid linking the hypolophid to the posterolophid at the terminal of the latter; and in DPC 22951 the hypolophid is complete, connecting to the anterior arm of the hypoconid, and there is no connection between the hypolophid and the posterolophid, forming a complete posterior basin of the crown.

The first lower molar (Fig. 9a–i, k) is semi-rectangular in outline and relatively broad, with the midpoint of the lingual and labial margins being slightly curved toward the middle of the tooth. The M_1 bears long and relatively well-developed lophids when compared with those of the premolars. It has four transverse cristids in the occlusal pattern (metalophulid I, mesolophid, hypolophid, and posterolophid) with a short posterior arm of the protoconid that is robust and courses from the most mesial part of the ectolophid toward the lingual margin of the tooth. In some cases, the posterior arm of the protoconid is oriented toward and integrated with the basal part of the mesolophid, which together with the middle portion of the ectolophid delimits a small fovea in the middle of the crown. In DPC 21650 and DPC 15340, the posterior arm of the protoconid is isolated and does not merge with the mesolophid. The latter courses lingually from the distal part of the ectolophid and terminates as a small mesostylid on the lingual margin of the crown. At the mesiolabial corner of the crown, there is a low and short anterocingulid that only occupies the area mesial to the protoconid and tapers lingually. The mesial wall of the tooth is formed by a trenchant and slightly concave metalophulid I that connects the mesiolingual side of the protoconid to the labial side of the metaconid. The deepest point of the metalophulid I is slightly toward the protoconid. The metaconid is placed transverse to the protoconid, but it is slightly larger and higher. In DPC 14168, the anterolophid is interrupted near its midpoint via a small and narrow notch. The lingual wall is absent, thus the anterior basin is open lingually. In some cases, the posterior arm of the metaconid slopes and connects with the mesostylid. The ectolophid is relatively

well-developed with respect to that of the premolars and courses distolingually from the protoconid to meet with the junction of the hypolophid and the anterior arm of the hypoconid. The entoconid is slightly mesially placed with respect to the hypoconid; together these cusps are connected via the latter's anterior arm and the hypolophid. The posterolophid courses across the posterior wall of the tooth. Its labial portion is robust and courses distolingually from the hypoconid to connect with a well-developed hypoconulid, whereas the lingual part tapers to end distally to the entoconid, leaving a wide lingual notch in the posterior basin. In some individuals, there is an incipient ectostyle situated at the mesial base of the hypoconid. The labial basin is larger than that of the premolars. At the distolabial corner of the crown, there is a shallow depression between the hypoconid and the hypoconulid, as a remnant of the posterocingulid.

The second lower molar has a similar occlusal pattern to that of the M_1 , but it differs in being larger, relatively broad, and in bearing longer and relatively well-developed lophids and a relatively long anterocingulid. Within the anterior basin of the tooth, there is considerable variation in the relationship between the metalophulid II and the mesolophid: in DPC 13286, DPC 20288 and DPC 12046, the metalophulid II and the mesolophid merge lingually, delimiting a small fovea with the ectolophid as in M_1 and continue to fuse with the posterior arm of the metaconid, delimiting the anterior half of the anterior basin. In DPC 14168 and DPC 13062, the mesolophid is incipient and does not reach the metalophulid II, whereas the latter is robust and connects to the posterior arm of the metaconid. There is a spur protruding distally from the middle of the metalophulid II in DPC 13062, DPC 15340, DPC 22951, DPC 21599, DPC 7771, and DPC 21650, as seen in lower molars of *Metaphiomys*, and there is no hint of the mesolophid. In general, the course of the metalophulid II is either straight or sinuous and in some cases, it becomes crenulated. The posterior basin is relatively convex and delimited lingually by a low extension of the posterolophid, which connects to the base of the entoconid. The hypoconulid is less distinctive than that of M_1 . In some cases, the mesostylid is a recognizable cuspid, but in others, it fuses with the metalophulid II and the posterior arm of the metaconid. There is no hint of an ectostylid.

The third lower molar is the largest tooth of the lower dentition. Its occlusal pattern is similar to that of M_1 and M_2 , but differs in being wider, having a narrower talonid, having fewer crenulations on the anterior basin (except on DPC 12046), an incipient to absent mesolophid, more convex and longer posterior basins, and in lacking a recognizable hypoconulid, which is integrated with the hypoconid to form a distolabial lobe. On DPC 14168, there is a depression on the labial side of the most mesial part of

the ectolophid distal to the protoconid. In the same position on DPC 13525, there is a small fovea.

Remarks and comparisons

Recently, new assemblages of “phiomyid” rodents have been reported from the Dur at-Talah escarpment, central Libya (Jaeger et al. 2010). Jaeger et al. suggested that this assemblage is middle Eocene in age, but we consider it more likely that the Dur at-Talah rodents are of late Eocene age—possibly older than the L-41 rodents, but younger than those from the earliest late Eocene (~37 Ma) Fayum Locality BQ-2. “*Phiomys*” *hammudai* from Dur at-Talah is perhaps slightly more primitive than *Acritophiomys* from L-41, but nevertheless is clearly more derived than the hystricognaths from BQ-2 (*Waslamys attiai* and *Protophiomys aegyptensis*), both of which have been placed as stem hystricognaths by Sallam et al. (2009, 2011) and Coster et al. (2010). There is thus no evidence for members of Phiomorpha at BQ-2, whereas phiomorphs are present at Dur at-Talah and throughout the latest Eocene-early Oligocene Jebel Qatrani Formation. The BQ-2 rodent assemblage also lacks the high diversity in size that is seen in the hystricognath assemblage from Dur at-Talah, and lacks members of the Phiocricetomyinae, such as *Talahphiomys*, which are present at Dur at-Talah, and which otherwise first appear in the Fayum succession at L-41. Interestingly, both the Dur at-Talah rodent fauna and BQ-2 lack any evidence for the presence of Gaudeamuridae, a family that also makes its first appearance at L-41 (Sallam et al. 2011). Members of the rodent clade Anomaluroidea, which are abundant and last recorded in northern Africa at either BQ-2 (Sallam et al. 2010a, b) or the approximately contemporaneous Nementcha locality in Algeria (Jaeger et al. 1985) are evidently absent from Dur at-Talah. Dur at-Talah thus uniquely combines more archaic rodents such as *Protophiomys durattalahensis* (a form that is very similar to *Waslamys* from BQ-2, and possibly congeneric) with more derived forms such as “*Phiomys*” *hammudai* and phiocricetomyines, while lacking the anomaluroids that are common at older sites (BQ-2 and Nementcha) and the gaudeamurids that are common at younger sites in the Jebel Qatrani Formation. With such a poor later Palaeogene record of mammalian evolution in Africa, it is not clear to what extent these differences are due to the sampling of different environments, but, given the proximity of Dur at-Talah to northern Egypt—being only about 4° south of the Fayum area and along the same paleocoastline—in our opinion, there is no reason to suspect that the Dur at-Talah deposits would be sampling environments that are very different from those recorded in the Fayum area.

The magnetostratigraphy of the Dur at-Talah Escarpment reported by Jaeger et al. (2010) is unfortunately not very informative as the sediments are entirely of normal polarity, but, when compared to the more variable magnetostratigraphy of the late Eocene and early Oligocene Fayum deposits (Seiffert 2006; Seiffert et al. 2005, 2008) the long zone of normal polarity documented at Dur at-Talah is conspicuously similar to that which has been recorded through the late Eocene Qasr el-Sagha Formation in the Fayum area; interestingly, the Qasr el-Sagha Formation also preserves very similar depositional environments to those recorded at Dur at-Talah. The position of the Dur at-Talah micromammal sites midway through this long zone of normal polarity (Jaeger et al. 2010) would be consistent with the suggestion that they are older than L-41, but younger than BQ-2. A placement of the Dur at-Talah rodents midway through the Priabonian is also favored by Antoine et al. (2011, their Fig. 3).

“*Phiomys*” *hammudai* from Dur at-Talah is most similar to *A. bowni*. Shared features include the general outline of the upper and lower dentition; tetralophodont dP⁴; a complete mure; a well-developed mesolophule; double (mesial and distal) connections of the metaloph; lack of a labial wall and endoloph on M¹ and M²; and presence of the mesolophid on some of the lower molars. However, *Ph. hammudai* differs from *A. bowni* in having moderately well-developed lingual walls on lower teeth due to the presence of the posterior arm of metaconid; in having a transversely oriented mesolophule that terminates as a relatively well-developed and isolated mesostyle; in lacking the endoloph on the upper molars; in having a relatively weak double connection of the metaloph in M¹; in having a relatively well-developed labial wall on M³; in consistently having a mesolophid; in having a relatively short posterior arm of the protoconid that never connects to the posterior arm of the metaconid; in lacking the anterocingulid on lower molars; in lacking a well-developed mesolophid on dP₄; and in lacking the transverse accessory cristid in the middle basin of the P₄.

Interestingly, the lower dentition of “*Ph.*” *hammudai* resembles that of the primitive hystricognathous rodents *Waslamys attiai* and *Protophiomys aegyptensis* (Sallam et al. 2009), from BQ-2, in having relatively well-developed lingual walls, and in lacking the anterocingulid. These characters are also very distinct in *A. bowni*. The upper and lower dentition of *A. bowni* is also similar to those of the BQ-2 taxa in replacing the deciduous premolars, and in having a generally similar morphology of the upper dentition, with a tetralophodont upper premolar. However, *A. bowni* lacks some notable primitive features that are shared by the earliest Fayum hystricognaths, such as: short and semi-quadrate lower molars with relatively low cuspids and tall cristids; relatively well-developed hypoconulids;

an incomplete posterior arm of the protoconid; absence of long anterocingulids; absence of a well-developed and continuously present mure on dP^4 - M^2 ; strictly anterior orientation of the metaloph (at least on M^{2-3}) and a relatively well-developed endoloph on M^2 .

The upper teeth of *A. boweni* have deep notches in their labial walls that reach the base of the middle basin, a feature that is seen in *Pr. aegyptensis* but not in *W. attiai*. Nevertheless, *A. boweni* has a well-developed mesolophule as in *W. attiai*, whereas this feature is weakly developed to absent in *Pr. aegyptensis*. A complete mure, absence of the endoloph, and double (mesial and distal) connection of metaloph are three characters that are consistently present in upper molars of *A. boweni*, while these characters are variable in *W. attiai* and *Pr. aegyptensis*. In *W. attiai*, the mure varies from being present to absent on M^2 , but in *Pr. aegyptensis* it is only present on M^3 . On the M^1 of *Waslamys attiai*, the metaloph is distally oriented toward the posteroloph and has a weakly developed mesial connection with the metaconule, a feature that is also seen in the upper dentition of *A. boweni*. The endoloph is only well-developed on M^3 of *A. boweni*, but it is robust and relatively high on M^2 - M^3 of *W. attiai* and relatively weakly developed in *Pr. aegyptensis*.

The morphology of the upper and lower dentition of *Acritophiomys* is very similar to that of *Metaphiomys* (notably *M. "schaubi"*) from the upper sequence of the Jebel Qatrani Formation. The lower molars of *Metaphiomys* and *Acritophiomys* share several derived features such as a semi-rectangular outline with length greater than width, relatively tall cusps, presence of a well-developed anterocingulid, a long metalophulid II that unites with the posterior arm of the metaconid, absence of the lingual wall, and a large M_3 . The upper dentition of *Metaphiomys* is similar to that of *Acritophiomys* in having a pentalophodont occlusal surface with continuously present mesolophule that is oriented toward and connected to the base of metacone; a deciduous third upper premolar; a complete mure; an accessory crest that runs labially from the mure to connect with the base of the paracone; and in lacking the lingual wall, which leaves the middle basin open labially. The general pattern of the DP^4 of *Acritophiomys* is essentially the same as that of *Metaphiomys*. However, *Acritophiomys* differs from *Metaphiomys* in being smaller and less hypsodont; in replacing the deciduous premolars; in having a double connection of the lingual end of the metaloph (mesially and distally); in having a curved outer surface of the lower incisors; in having a consistently present endoloph on M^3 ; and in lacking the bifurcation of the metalophulid II in lower molars. The dP_4 of *Acritophiomys* exhibits some primitive features that are not found in *Metaphiomys*, such as a well-developed metalophulid II, complete mesolophid, and a well-developed anteroconid and anterocingulid.

Relative to the more primitive BQ-2 species, *Acritophiomys* shares some derived features with *Phiomys*, such as a complete mure, double connection of the metaloph, presence of a mesolophule, absence of the lingual wall on the upper molars (also seen in *Protophiomys*), and presence of the anterocingulid on lower molars and an anteroconid on P_4 . However, *Acritophiomys* differs from *Phiomys* in being larger, in having a rectangular outline of the lower molars and semi-quadrate outline of the upper molars; in having a low and moderately developed endoloph on M^2 and M^3 , respectively; in having a well-developed anteroloph on P^4 ; in having a relatively long metalophulid II that reaches the lingual margin on the lower molars; in having a continuously present mesolophid on M_1 ; in having a longer dP_4 with metaconid transverse to the protoconid; and in having a complete mesolophid on lower premolars.

Thomas et al. (1989) reported two isolated molars (upper and lower) from the early Oligocene Thaytiniti locality in Oman as "cf. *Metaphiomys* sp. 1" and "cf. *Metaphiomys* sp. 2", respectively. These two specimens show similarities to *A. boweni*, such as the lack of a lingual wall, presence of a double connection of the metaloph and a low endoloph on the upper molar, and the rectangular outline of the lower molar. Comparing these isolated teeth with the hypodigm of *A. boweni* indicates that the authors mistakenly identified these teeth to locus. The upper first molar, "cf. *Metaphiomys* sp. 1", is actually an M^2 and the lower first molar, "cf. *Metaphiomys* sp. 2" is in fact an M_3 . Interestingly, the occlusal surface of the dP_4 that Thomas et al. (1989) assigned to *Phiomys* cf. *andrewsi* is very similar to that of *A. boweni*.

Phylogenetic analysis

The morphological character matrix used here is built on the previous work of Marivaux et al. (2004) and Sallam et al. (2009, 2011). We coded 118 craniodental characters (two cranial and 116 dental) for 37 extinct taxa as well as the extant African cane rat *Thryonomys*. The recently described basal caviomorph *Canaanimys*, from the middle Eocene of Peru (Antoine et al. 2011), is included as the sole representative of Caviomorpha because it is likely to closely approximate the ancestral morphotype for the New World hystricognaths. *Birbalomys* and *Chapattimys*, two taxa from the late early Eocene of Asia, were employed as outgroups in the current matrix. The matrix is available for download at <http://www.morphobank.org>. The heuristic search algorithm in PAUP 4.0b10 (Swofford 1998) was used, across 5,000 replicates, with random addition sequence and tree bisection and reconnection (TBR) branch swapping. Polymorphisms were assigned a discrete intermediate state, and some multistate characters were

treated as ordered. Because the addition of intermediate polymorphic states causes ordered multistate characters to have a disproportionately strong impact on phylogeny estimation, two different down-weighting methods were employed—one in which transitions between states were assigned one half step (i.e., a weight of 0.5), so that transitions between “fixed” states in each multistate character could contribute only a single step to tree length (weight set 1), and one in which all ordered multistates were scaled based on the total number of character states, so that each character could only contribute a maximum of one step to tree length (weight set 2).

Parsimony analysis across all weight sets placed *Acritophiomys* as one of the most basal members of the phiomorph stem lineage [i.e., a sister group of *Phiomys*, *Metaphiomys*, *Diamantomys*, *Paraphiomys*, *Paraulacodus*, and *Thryonomys* (Fig. 10)]. “*Phiomys*” *hammudai* was consistently placed as the most basal taxon within Phiomorpha, and interestingly the Asian early Oligocene “baluchimyines” *Bugtimys* and *Lophibaluchia* were also placed as basal phiomorphs when ordered multistates were downweighted. None of the relationships within Phiomorpha had strong bootstrap support. Under all assumption sets, crown hystricognaths and basal caviomorphs were reconstructed as being of Afro-Arabian origin, with an earlier dispersal from Asia to Afro-Arabia along the hystricognath stem lineage. The primary cause of instability across the three analyses was the placement of the late Eocene-early Oligocene African phiocricetomyine clade, which was either situated far outside of the *Protophiomys*–*Waslamys*–caviomorph–phiomorph clade (when ordered multistates were not downweighted), or with early Oligocene Asian *Lophibaluchia* as the sister group of *Protophiomys*–*Waslamys*–Caviomorpha–Phiomorpha (weight sets 1 and 2). Biogeographic optimizations leave it unclear whether phiocricetomyines share a common Afro-Arabian ancestor with the *Protophiomys*–*Waslamys*–caviomorph–phiomorph clade (Fig. 10c), or if they dispersed from Asia to Afro-Arabia independently (Fig. 10a).

Conclusions

The terminal Eocene “phiomyid” *Acritophiomys bowni* is the oldest and most primitive phiomorph that has been reported from the Fayum succession. *A. bowni* is the largest “phiomyid” from Quarry L-41, and shows a mosaic of features that are intermediate between the primitive stem hystricognaths from the ~37 Ma Locality BQ-2 (*Waslamys* and *Protophiomys*) and the advanced phiomorphs from the upper sequence of the Jebel Qatrani Formation (e.g., *Metaphiomys*). *A. bowni* closely resembles “*Phiomys*” *hammudai* from Dur at-Talah but differs in a few minor

details, and appears to be slightly more derived. We suggest that “*Phiomys*” *hammudai* and the other Dur at-Talah rodents are intermediate in age between those from the Fayum Quarry L-41 and Locality BQ-2; this is consistent with the paleomagnetic evidence presented by Jaeger et al. (2010), because the equivalent part of the Fayum succession is also entirely of normal polarity.

The origin of hystricognathous rodents on southern continents has long been one of the great mysteries of Paleogene mammalian evolution, but recent discoveries from the Eocene of Egypt (Sallam et al. 2009), Libya (Jaeger et al. 2010), and Peru (Antoine et al. 2011) are now helping to clarify the early phylogeny of the clade. One conclusion to emerge from this and other recent phylogenetic studies (Sallam et al. 2009; Coster et al. 2010; Antoine et al. 2011) is that “Phiomidae” is a para- or polyphyletic group. We suggest that Phiomidae be used as a plesion, and could be restricted to the most basal stem phiomorphs, such as *Acritophiomys* and *Phiomys*, that replace $dP^{4/4}$ in life by $P^{4/4}$.

All of the phylogenetic trees support a placement of *Pr. aegyptensis*, *Pr. algeriensis*, “*Pr.*” *durattalahensis*, and *Waslamys* outside of the caviomorph–phiomorph clade. The para- or polyphyly of the genus *Protophiomys* (see also Antoine et al. 2011) suggests that “*Pr.*” *durattalahensis*, at least, should probably be assigned a new generic name. As the apparent sister group of *Waslamys* in our analyses (Fig. 10), “*Pr.*” *durattalahensis* could be transferred to that genus, though Antoine et al.’s placement of “*Pr.*” *durattalahensis* as a stem caviomorph alternatively suggests that a new and unique generic nomen might be more appropriate.

The presence of apparent stem hystricognaths in the earliest late Eocene of north Africa (*Protophiomys* and *Waslamys*) and the subsequent appearance of phiomorphs in the later Eocene led Sallam et al. (2009) to suggest that the caviomorph–phiomorph split might have occurred in the late Eocene. However the surprising discovery of caviomorph rodents in ~41 Ma (middle Eocene, late Lutetian) beds in Peru (Antoine et al. 2011) indicates that the caviomorph–phiomorph split, and the caviomorph dispersal to South America, must have occurred at least five million years earlier, in the middle Eocene. These discoveries raise important new questions concerning the timing of hystricognath cladogenesis and dispersal—if caviomorphs are of Afro-Arabian origin, as suggested by this and other studies, then hystricognaths must have been present in Afro-Arabia by 41 Ma. This scenario is consistent with the presence of *Protophiomys* at the allegedly middle Eocene Black Crow locality in Namibia (Pickford et al. 2008) which might be even older than the middle Eocene caviomorphs from Peru (Pickford et al. 2011). The apparent absence of hystricognaths at the

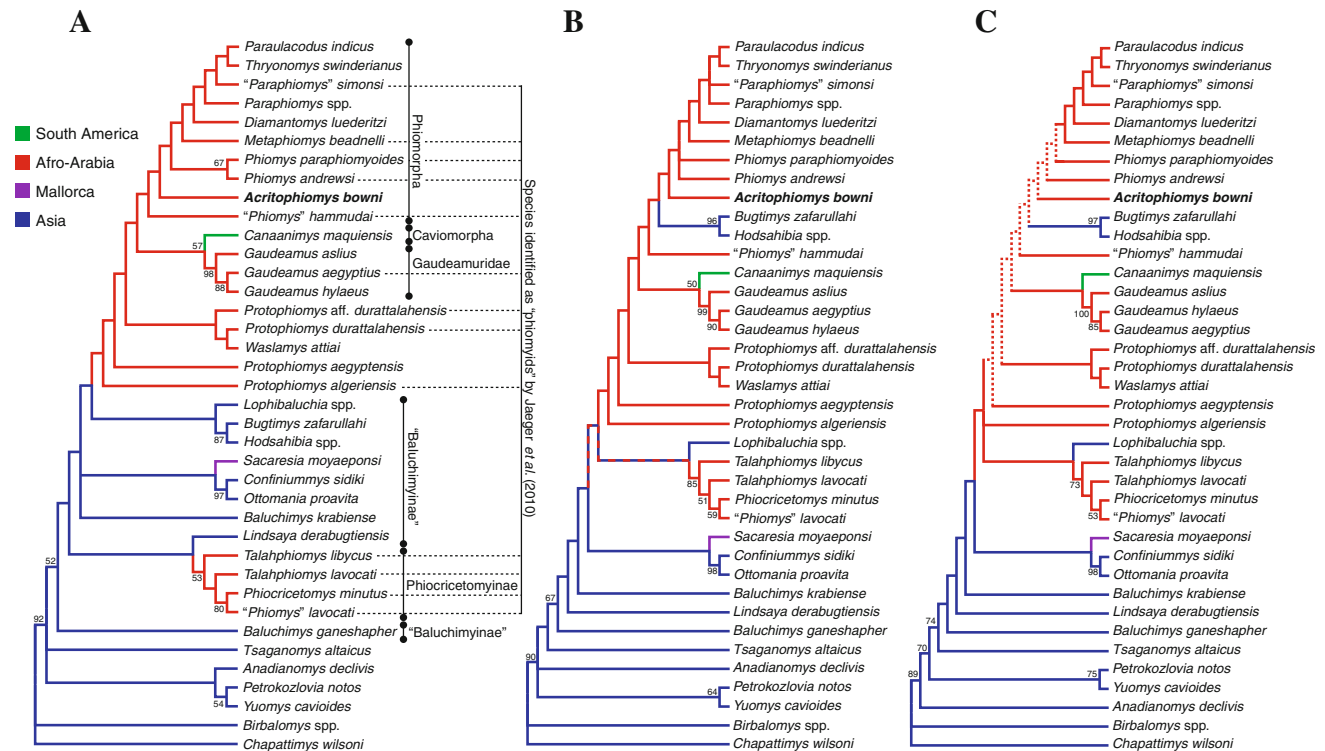


Fig. 10 Phylogenetic analysis of living and extinct hystricognathous rodents, based on 118 morphological characters, largely from the dentition. **a** Strict consensus of four equally parsimonious trees recovered by analysis with some multistate characters ordered but not scaled; tree length = 887; consistency index excluding uninformative characters = 0.3007; retention index = 0.5768; rescaled consistency index = 0.1775. **b** Strict consensus of eight equally parsimonious trees recovered by analysis with some multistate characters ordered and scaled, and transitions from “fixed” to adjacent polymorphisms in ordered multistates weighted as 0.5 (weight set 1); tree length = 574.5; consistency index excluding uninformative characters = 0.3245; retention index = 0.5765; rescaled consistency

index = 0.1932. **c** Adams consensus of two equally parsimonious trees recovered by analysis with some multistate characters ordered and scaled, maximum number of steps in a multistate ordered character equal to one (weight set 2); branches with dotted lines break down in the strict consensus tree; tree length = 371.250; consistency index excluding uninformative characters = 0.3434; retention index = 0.5927; rescaled consistency index = 0.2103. On all trees, numbers above or below branches are bootstrap support values based on 1,000 pseudoreplicates. Biogeographic histories are based on parsimony optimizations of an unordered biogeographic character with four states (Asia, Afro-Arabia, South America, Mallorca) onto the strict consensus (**a**, **b**) and Adams consensus (**c**) trees

zgdoumyid-bearing Gour Lazib localities in Algeria (Marivaux et al. 2011) suggests that these localities predate the hystricognath dispersal to Afro-Arabia, but perhaps not by much time. Competition with the endemic zgdoumyids and anomaluroids upon arrival in Afro-Arabia might explain why hystricognaths remained fairly generalized in their dental morphology until the later Eocene; it is only after the disappearance of anomaluroids from northern Africa (i.e., at some point after the deposition of Locality BQ-2, and perhaps before deposition of the hystricognath-bearing “Bioturbated Unit” at Dur at-Talah) that hystricognaths began to display a greater diversity of tooth morphologies—a phenomenon that is exemplified by the striking differences in dental morphology between *Acritophiomys* and *Gaudeamus* at Quarry L-41. Clearly, however, more evidence is needed from other parts of Afro-Arabia to determine how environmental variability influenced this pattern on a continental scale.

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