

# A new fossil thryonomyid from the Late Miocene of the United Arab Emirates and the origin of African cane rats

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**Abstract** Cane rats (Thryonomyidae) are represented today by two species inhabiting sub-Saharan Africa. Their fossil record is predominately African, but includes several Miocene species from Arabia and continental Asia that represent dispersal events from Africa. For example, *Paraulacodus indicus*, known from the Miocene of Pakistan, is closely related to living *Thryonomys*. Here we describe a new thryonomyid, *Protohummus dango*, gen. et sp. nov., from the late Miocene Baynunah Formation of the United Arab Emirates. The new thryonomyid is less derived than “*Thryonomys*” *asakomae* from the latest Miocene of Ethiopia and clarifies the origin of crown *Thryonomys* and the evolutionary transition from *Paraulacodus*. A phylogenetic

analysis shows *Protohummus dango* to be morphologically intermediate between *Paraulacodus* spp. and extinct and living *Thryonomys* spp. The morphological grade and phylogenetic position of *Protohummus dango* further supports previous biochronological estimates of the age of the Baynunah Formation (ca. 6–8 Ma).

**Keywords** Thryonomyidae · Baynunah formation · Miocene · Arabia · Africa · Asia

## Abbreviations

AUH	Fossil specimens from the Baynunah Formation curated and housed with the Abu Dhabi Tourism and Culture Authority (previously the Abu Dhabi Authority for Culture and Heritage)
LACM	Los Angeles County Museum of Natural History
Pa	Paracone
Prl	Protoloph
Pr	Protocone
Hy	Hypocone
Pol	Posteroloph
Ml	Metaloph
Mt	Metacone
Al	Anteroloph
Pold	Posterolophid
Hyd	Hypoconid
Prd	Protoconid
Mld	Metalophulid I
Mtd	Metaconid
End	Entoconid
Hyld	Hypolophid

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## Introduction

Living cane rats (Rodentia, Thryonomyidae) are represented by two species of *Thryonomys* that are endemic to Africa.

Nearly all earliest fossil thryonomyids are African, suggesting that the family originated there in the early Miocene. The group saw a maximum diversity of six genera during the middle Miocene (McKenna and Bell 1997), and by the Pliocene only the genus *Thryonomys* remained (e.g., Wesselman et al. 2009; Denys 2011). While African taxa dominate the fossil record of thryonomyids, demonstrating a clear African origin for the family, there was at least one dispersal event into Arabia and the Indian Subcontinent (Thomas et al. 1982; Flynn and Winkler 1994; Winkler 1994; López Antoñanzas et al. 2004). Based on the ages of two distinct fossil thryonomyids at two stratigraphic levels in the Siwalik deposits of Pakistan (around 16.3 and 13 Ma), Flynn and Winkler (1994) suggested that two Asian continental dispersal events occurred in the Miocene. The younger of those two taxa, *Paraulacodus indicus*, is of particular interest because it shows a sister group relationship to *Thryonomys* and likely lies close to the ancestry of the genus (Winkler 1992; Flynn and Winkler 1994; López Antoñanzas et al. 2004). We describe here a new thryonomyid from late Miocene deposits of the United Arab Emirates that is an important addition to understanding this evolutionary transition. By including several recently described thryonomyids, our phylogenetic analyses elucidate the early evolution of crown thryonomyids and the geographic origin of the cane rats.

Although Arabia must have played a critical biogeographic role with respect to faunal dispersal events in and out of Africa, little is known about the Arabian Miocene due to a paucity of Neogene fossil localities. López Antoñanzas and Sen (2005) recently named the first fossil thryonomyid species from the Arabian Peninsula, *Paraphiomys knolli*, discovered in the late early Miocene Dam Formation of Saudi Arabia (17–15 Ma). The appearance of *P. knolli* within Arabia — a species within a genus (*Paraphiomys*) otherwise only known from continental African — is a good example of the interspersed nature of many mammalian clades across the Afro-Arabian plate into the Neogene. Unfortunately, *P. knolli* does not show close phylogenetic affinities to either *Paraulacodus* or *Thryonomys* (López Antoñanzas and Sen 2005), and therefore, understanding the origins of crown Thryonomyidae and the relationship between *Paraulacodus* and *Thryonomys* requires additional, younger, fossil finds.

A single isolated lower molar identified only as Thryonomyidae gen. et sp. indet. was described from late Miocene deposits of the Baynunah Formation in the United Arab Emirates (ca. 8–6–8 Ma) by de Bruijn (1999) as part of a larger rodent fauna (de Bruijn and Whybrow 1994). de Bruijn (1999) suggested the taxon was closely related to *Neosciuromys* from the early and middle Miocene of Africa. Since that time, three successive seasons of dry screening in the Baynunah Formation by our group, beginning in December 2008, have resulted in a substantial increase in the micro-vertebrate fauna. In this study, we describe 20

new thryonomyid fossil specimens from these efforts. These specimens represent the same taxon that produced the single isolated molar described by de Bruijn (1999), and which we now formally describe as a new genus and species. The biogeographical, biochronological, and paleoecological implications of this new taxon are also discussed.

For comprehensive reviews of the systematics of Thryonomyidae, including discussion of the composition of the family, see Winkler (1992), López Antoñanzas and Sen (2005), and Marivaux et al. (2012). Furthermore, Marivaux et al. (2012) have shown that thryonomyids are nested within a paraphyletic Phiomysidae, a relatively new perspective that suggests the precise timing and nature of thryonomyid origins need more study. Some other issues regarding deeper relationships include the nature of the specific composition of *Paraphiomys*, a genus which Winkler et al. (2010) argues is in need of systematic revision. Additionally, Winkler et al. (2010) discuss the phiomorph–thryonomyid transition in eastern Africa, and the need for a comprehensive review of these taxa given the number of researchers who have worked on these issues over the last decades. We offer an important addition to understanding the origins of crown Thryonomyidae.

## Provenance

The Baynunah Formation is a sequence of over 60 m of sediment of primarily fluvial origin that outcrops intermittently over an area of some 8,000 km<sup>2</sup> in the Al Gharbia region of Abu Dhabi Emirate (United Arab Emirates) (Fig. 1). Independent visits by Peter Whybrow (Natural History Museum, London) and one of the authors (A.H.) between 1979 and 1984, followed by a joint expedition working during 1988–1995, recovered hundreds of fossils comprising vertebrates, invertebrates, and plants from the Baynunah Formation sediments. The diverse fauna allowed for an estimated biochronological age of between 8 and 6 Ma for the Baynunah Formation (Whybrow and Hill 1999). Renewed annual fieldwork efforts by our group since 2006 have succeeded in locating many new sites and recovering hundreds more fossil specimens (Bibi et al. 2013; Hill et al. 2012).

The Baynunah fossil fauna derives from several levels, mainly within the lower 30 m of the Baynunah Formation. Given the rapid lateral stratigraphic changes, typical of many fluvial deposits, the exact stratigraphic relationships among localities are impossible to determine unless they are within very close proximity to each other. The Baynunah fauna is treated as a single chronological fauna as there is no biochronological evidence for the presence of multiple levels of significant age difference. Fossil-bearing levels in the Baynunah Formation are primarily made up of medium and coarse sands and occurrences of micromammal remains

**Fig. 1** Map showing the location of primary micromammal producing fossil localities within the Baynunah Formation of the United Arab Emirates. Image source: Google Earth



in these are rare. Test-sieving at many different sites often yielded no diagnostic specimens. The only consistently productive site is that of a small area of about 16 m<sup>2</sup> located at 24.1148°N 52.43202°E in the Shuwaihat (SHU) 2–2 locality (all coordinates use the WGS84 datum). Single thryonomyid specimens come from each of SHU 2–6 at 24.11558°N 52.43277°E, Ras al-Qal'a (RAQ) 2–1 at 24.15058°N 52.98305°E, and Hadwaniyya (HAD) 1 at 24.13047°N, 53.10025°E (Fig. 1). The single thryonomyid molar described by de Bruijn (1999) comes from locality SHU 4. Dry sieving at one spot in SHU 4 by us failed to recover further micromammals. Locality SHU 1, from where the majority of the micromammals described by de Bruijn (1999) are derived, has for some years now been a military installation and is no longer accessible.

## Methods

Aside from the previously published molar AUH 571 (de Bruijn 1999), all of the specimens described here were either surface collected or recovered from dry screening of Baynunah Formation sediments. Sediment was successively screened through 4-, 1.3-, and 0.6-mm sieves, and then sorted separately. Remnant matrix from highly productive sites was additionally wet-sieved through a 0.6-mm screen. All of the specimens described here were collected from the surface, or recovered from the remnant matrix of the 4- or 1.3- mm screens. In total, about 1,200 kg were sieved at site Shuwaihat (SHU) 2–2, 50 kg at SHU 2–6, 600 kg at Ras al-Qal'a (RAQ) 2–1, and 90 kg at Hadwaniyya (HAD) 1. SHU 2–2 was by far the richest site among these and the only one to which our team returned for successive field seasons. The teeth were measured using an eyepiece reticle on a stereoscopic microscope.

A phylogenetic analysis was run using the data matrix of López Antoñanzas et al. (2004) and including the new Baynunah thryonomyid, the recently described “*Thryonomys*”

*asakomae* from the latest Miocene (5.8–5.6 Ma) of Ethiopia (Wesselman et al. 2009), *T. wesselmani* from the Upper Ndolanya Beds of Laetoli, Tanzania (2.66 Ma; Denys 1987, 2011), and *Lavocatomys aequatorialis* from the early Miocene of Kenya (20–18 Ma; Holroyd and Stevens 2009). The analysis comprises 22 dental characters, includes one outgroup taxon, *Phiomys andrewsi*, and a total of 26 ingroup taxa, two of which are the extant species of *Thryonomys* (Table 1). While López Antoñanzas et al. (2004), Sallam et al. (2009), and Coster et al. (2010) have all conducted recent phylogenetic studies that treat thryonomyids, they all have limitations relative to the taxa presented here. Sallam et al. (2009) and Coster et al. (2010) present robust character matrices that cover a wide range of dental, and even some cranial characters, and both studies include taxa that are typically known from relatively complete material. Their taxonomic coverage within Thryonomyidae, however, is limited due to the exclusion of taxa that are only known from fragmentary material, such as many of those presented here. For this reason, these studies are excellent for delineating relationships among early hystricognathous rodents (such as *Gaudeamus*), but are not well suited to understanding the shallower relationships of crown thryonomyids and their close ancestors. To include such taxa in these broader character matrices, reexamination of many new specimens across many collections would be required, which is beyond the scope of this study. In contrast, López Antoñanzas et al. (2004) presented a character matrix that has excellent taxonomic coverage for crown thryonomyids and their recent ancestors, but with a character set that is limited with regard to understanding deeper relationships of thryonomyids among hystricognaths. As the new taxon discussed herein is expected to be more informative to the origin of crown thryonomyids than it would be to the deeper relationships of early hystricognathous rodents, we have chosen to build on the data matrix of López Antoñanzas et al. (2004), while recognizing the need to for a detailed review of Miocene and Pliocene thryonomyids, as pointed out by Winkler et al. (2010).

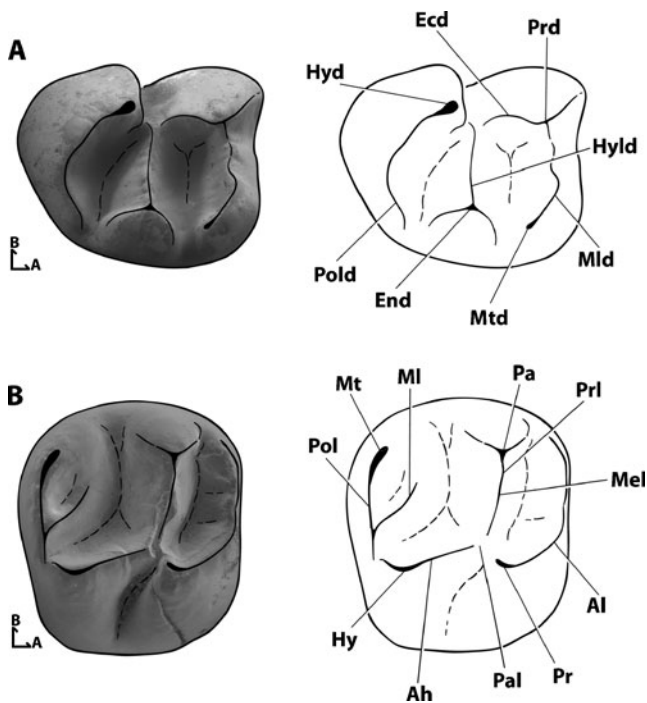
**Table 1** Matrix of character coding

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Phiomys andrewsi</i>	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Metaphiomys schaubi</i>	0	0	0	–	2	0	–	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Gaudeamus aegyptius</i>	0	1	1	–	0	0	–	1	1	1	1	0	0	0	1	1	?	1	0	1	1	1
<i>Sacaresia moyaeponsii</i>	0	0	0	1	0	0	–	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0
<i>Paraphiomys simonsi</i>	?	1	1	–	2	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	2
<i>Paraphiomys pigotti</i>	1	1	1	–	2	1	0	0	0	1	1	2	0	0	0	1	0	0	1	0	0	1
<i>Neosciuromys africanus</i>	1	1	1	–	2	1	1	1	0	0	1	2	0	0	0	1	?	0	0	0	1	2
<i>Paraphiomys knolli</i>	?	?	?	?	?	1	0	0	0	0	1	2	?	?	?	1	?	0	?	0	0	0
<i>Apodecter stromeri</i>	1	1	1	–	2	1	1	1	0	0	0	1	2	2	1	1	0	0	0	0	0	1
<i>Paraphiomys orangeus</i>	1	0	1	–	1	1	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
<i>Paraphiomys hopwoodi</i>	1	1	1	–	2	1	0	0	0	0	1	2	1	0	1	1	0	0	?	1	1	1
<i>Paraphiomys renelavocati</i>	1	1	1	–	2	1	1	1	0	0	0	1	0	1	1	1	0	0	1	1	1	1
<i>Epiphiomys coryndoni</i>	?	0	0	1	2	1	0	0	0	0	0	1	2	0	1	1	?	0	2	0	0	1
<i>Paraphiomys occidentalis</i>	1	1	1	–	2	1	0	1	0	0	1	1	0	0	0	1	?	0	2	1	1	1
<i>Paraphiomys shipmani</i>	1	1	1	–	0	1	1	1	1	0	1	0	2	0	1	?	?	?	?	?	?	0
<i>Kochalia geespei</i>	0	1	1	–	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Paraphiomys afarensis</i>	1	1	1	–	2	1	1	1	0	0	1	0	0	0	0	1	0	0	?	0	1	1
<i>Paraphiomys roessneri</i>	1	0	1	–	1	0	–	1	0	0	0	0	0	2	1	1	0	1	2	0	0	1
<i>Paraphiomys australis</i>	1	0	1	–	2	0	–	1	0	0	0	0	2	2	1	0	?	1	0	0	1	1
<i>Thryonomys wesselmani</i>	?	1	0	0	1	0	–	1	0	0	1	1	0	0	1	1	3	1	?	0	1	1
<i>Thryonomys swinderianus</i>	1	1	0	0	1	0	–	1	0	0	1	1	0	0	1	1	3	1	0	1	1	1
<i>Thryonomys gregorianus</i>	1	1	0	0	1	0	–	1	0	0	1	0	0	0	1	1	3	1	0	0	1	1
“ <i>Thryonomys</i> ” <i>asakomae</i>	?	1	0	0	1	0	–	1	0	0	1	1	1	0	?	1	2	1	?	0	1	1
<i>Paraulacodus indicus</i>	1	1	1	–	1	1	0	1	0	0	1	1	2	0	1	1	2	1	0	0	1	1
<i>Paraulacodus johanesi</i>	1	1	1	–	1	1	1	1	0	0	1	1	0	0	1	1	2	1	0	0	1	1
<i>Protohummus dango</i>	?	1	1	–	1	0	–	1	0	0	1	1	?	?	?	?	2	1	?	0	1	1

Character descriptions are based on López Antoñanzas et al. (2004), listed in Appendix 1, and accessible online at [www.morphobank.org](http://www.morphobank.org) (project 896)

Data coding and tree visualization were carried out using Mesquite 2.75 (Maddison and Maddison 2010). Phylogenetic analysis was carried out using PAUP\* 4.0b10 (Swofford 2002). Heuristic search was conducted using the tree bisection-reconnection (TBR) algorithm and random-addition sequence of taxa. All characters were left unordered and assigned equal weight. Analyses including *Gaudeamus* and/or *Lavocatomys* were run for 1000 replicates, while the final analysis excluding both these taxa was run for 10,000 replicates. Bootstrap analyses were run for 100 replicates (of 100 search replicates each), holding a maximum of 10,000 trees per replicate. Branch lengths and character state optimization were reconstructed using accelerated transformation (ACCTRAN). Cusp terminology follows that of Winkler (1992) and Marivaux et al. (2012), unless noted otherwise, and is shown in Fig. 2. Finally, while living *Thryonomys* do not replace their premolars (van der Merwe 2000), this condition is not known in many fossil taxa, including the taxon described here. We follow conventions of other thryonomyid researchers, and describe premolars as deciduous.

Four taxa (*Protohummus dango*, “*Thryonomys*” *asakomae*, *T. wesselmani*, *Lavocatomys aequatorialis*) were added to a slightly modified character matrix (Table 1) from López Antoñanzas et al. (2004). The character set can be openly and permanently accessed through MorphoBank (<http://morphobank.org/permalink/?P896>). López Antoñanzas et al. (2004) coded metalophulid II as oblique for *Thryonomys* in dP<sub>4</sub>, but our examination of specimens LACM 53061 and 53060, the metalophulid II is clearly transverse, which is also supported by Fig. 2 of López Antoñanzas et al. (2004). The anterolabial cusp is prominent in many fossil thryonomyids, and López Antoñanzas et al. (2004) coded the cusp as partially submerged (character 7, state “1”) for *Paraulacodus*. Within *P. indicus*, however, the cusp is clear in specimen GSI D282. Winkler (1992) also states that the anterolabial cusp in *P. indicus* is typically isolated, and Flynn and Winkler (1994) clearly illustrate and discuss an isolated cusp on M<sub>3</sub> and either an M<sub>1</sub> or M<sub>2</sub> of *P. indicus*.



**Fig. 2** Schematic drawings of lower (a) and upper (b) second molar showing cusp nomenclature used in text, based on Winkler (1992) and López Antoñanzas et al. (2004); both teeth are from the left side and anterior is to the right; buccal (B) and anterior (A) denoted by arrows. Pa Paracone, Pal Paraconule, Prl Protoloph, Pr Protocone, Hy Hypocone, AH anterior arm of hypocone, Mel Metaconule, Pol Posteroloph, MI Metaloph, Mt Metacone, Al Anteroloph, Pold Posterolophid, Hyd Hypoconid, Prd Protoconid, Ecd Ectolophid, Mld Metalophid I, Mtd Metaconid, End Entoconid, Hyld Hypolophid

## Systematic Paleontology

Mammalia Linnaeus 1758

Rodentia Bowdich 1821

Thyronomyidae Pocock 1922

*Protohummus*, gen. nov.

*Genus diagnosis.* As for the new and only species, please see below.

*Etymology.* The Baynunah thyronomyid teeth were found isolated, are relatively large compared to other fossils rodents of the fauna, and are stained yellow to orange-brown in color, superficially resembling chickpeas (Arabic *hummus*). *Proto*, latin for “early” or “first”.

*Protohummus dango* sp. nov.

See Fig. 3a–i and Table 2.

*Etymology.* Dango is an Emirati dish made of boiled whole chickpeas, which the isolated and yellow-stained fossil thyronomyid teeth resemble.

*Holotype.* AUH 1362, L. dP<sub>4</sub> (Fig. 2c).

*Type locality.* Shuwaihat (SHU) 2–2

*Stratigraphic range.* Currently known only from the Late Miocene Baynunah Formation of the United Arab Emirates,

which has been biochronologically dated to between 8 and 6 Ma (Whybrow and Hill 1999; Bibi et al. 2005, 2013), and probably nearer to 6.5 Ma than to 8 Ma (Hill et al. 2012).

*Diagnosis.* *Protohummus dango* is a thyronomyid rodent similar in size to the living *Thryonomys swinderianus*, with upper incisors possessing two grooves on their buccal surface, and molars and premolars lacking an anterolabial cuspid on the lower cheek teeth. In the presence of more than one upper incisor groove, *Protohummus dango* is distinguished from all thyronomyid rodents except *Paraulacodus* and *Thryonomys*. *Protohummus dango* is distinguished from *Paraulacodus* spp. by the absence of an anterolabial cusp on the lower cheek teeth, a character that it shares with *Thryonomys* spp. It is distinguished from all living and fossil *Thryonomys* spp. by the absence of a metalophulid II on dP<sub>4</sub>. It is further distinguished from *T. swinderianus*, *T. gregorianus*, and *T. wesselmani*, by the presence of only two (rather than three) grooves on the upper incisor.

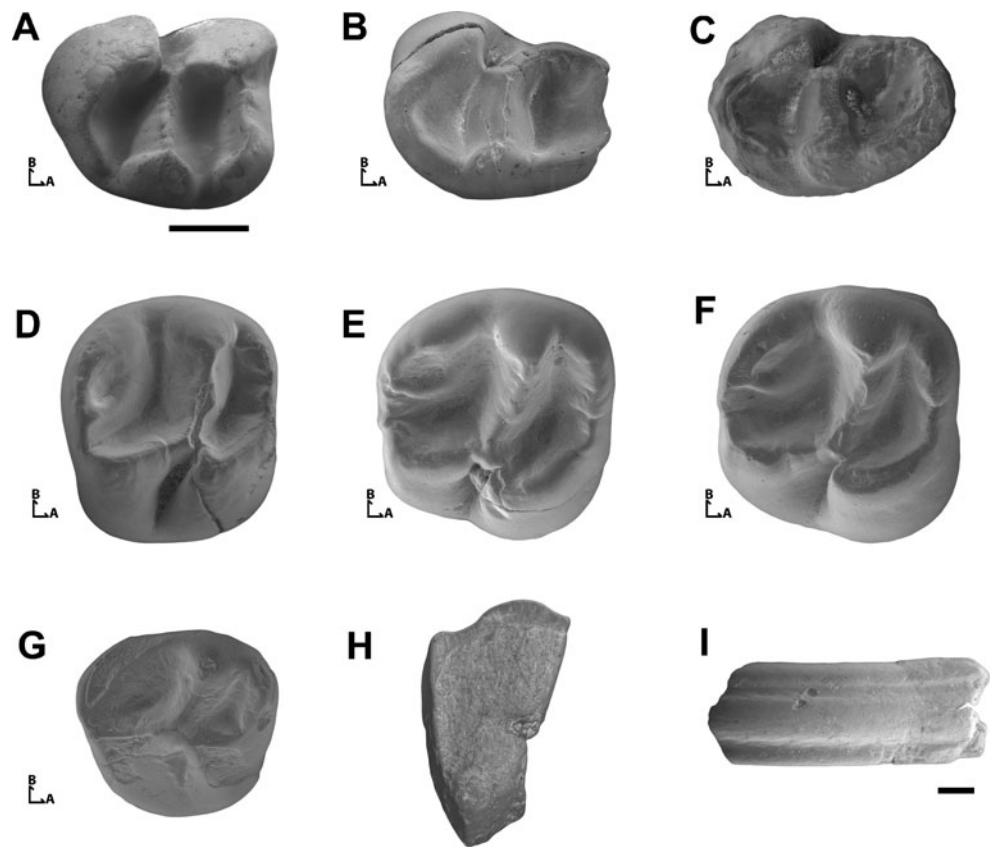
*Referred specimens.* Loc. SHU 4: AUH 571 (L. M<sub>2</sub>). Loc. RAQ 2–1: AUH 1335 (L. M<sup>1</sup> or <sup>2</sup>). Loc. SHU 2–6: AUH 1512 (L. M<sup>1</sup> or <sup>2</sup>). Loc. HAD 1: AUH 1623 (dI<sup>2</sup>). Loc. SHU 2–2: AUH 1379 (L. M1 or 2); AUH 1373 (L. dP<sub>4</sub>); AUH 1362 (L. dP<sub>4</sub>); AUH 1428 (L. M<sup>1</sup> or <sup>2</sup>); AUH 1380 (L. dP<sub>4</sub>); AUH 1707 (R. M<sup>1</sup> or <sup>2</sup>); AUH 1708 (R. M<sup>1</sup> or <sup>2</sup>); AUH 1419 (dL<sub>2</sub>); AUH 1423 (M<sup>x</sup>, broken); AUH 1368 (dI<sup>2</sup>); AUH 1431 (M<sup>x</sup>); AUH 1427 (dP<sub>4</sub> or M<sub>x</sub>, broken); AUH 1400 (dL<sub>2</sub>); AUH 1369 (L. M<sup>x</sup>, broken); AUH 1382 (M<sup>x</sup>)

*Repository.* All referred specimens are curated and stored with the Abu Dhabi Tourism and Culture Authority (previously the Abu Dhabi Authority for Culture and Heritage) in Abu Dhabi city, United Arab Emirates. Molds and casts of specimens AUH 1335, 1362, 1373, 1379, and 1380 are deposited in the Yale Peabody Museum of Natural History.

## Description

M<sup>1</sup> or <sup>2</sup> — It is difficult to distinguish between isolated upper first and second molars in thyronomyids because these teeth are so similar. All upper M<sup>1</sup> or <sup>2</sup>s except for AUH 1707 are relatively unworn with complete crowns, with no evidence of root structures. Crown height is much higher on the lingual side versus buccal side (LCH vs. BCH; Table 2), and overall crown height is similar to that of living *Thryonomys*. AUH 1707 is different from the typically unilateral hypsodont teeth as it is a highly worn tooth from an older individual. Within thyronomyids, it is typical for M<sup>2</sup>s to be slightly larger than M<sup>1</sup>s, and the smaller size of AUH 1708 (Table 2) might mean this tooth is an M<sup>1</sup>, while all the remaining upper molars are M<sup>2</sup>s. These cheek teeth are strongly lophate, but analogs to protocone, paracone, hypocone, and metacone are present, though the teeth are

**Fig. 3** SEM images of occlusal views of isolated thryonomyid teeth from the Baynunah Formation, United Arab Emirates. **a** AUH 571 (holotype; L. M<sub>2</sub>); **b** AUH 1373 (L. dP<sub>4</sub>); **c** AUH 1362 (L. dP<sub>4</sub>); **d** AUH 1379 (L. M<sub>2</sub>); **e** AUH 1512 (L. M<sup>1</sup> or <sup>2</sup>); **f** AUH 1335 (L. M<sup>1</sup> or <sup>2</sup>); **g** AUH 1380 (L. dP<sup>4</sup>); **h** AUH 1368 (dI<sup>2</sup>); **i** AUH 1623 (dI<sup>2</sup>). Horizontal scale bars in **a** and **i** = 1 mm; scale bar in **a** is applicable for **a–h**. Teeth **a–h** are occlusal views with the buccal side towards top, **i** is a buccal view of incisor enamel surface. In cheek, buccal (*B*) and anterior (*A*) denoted by arrows



not strongly cuspsate overall. Three strong bucco-lingually oriented lophs are recognized as the anteroloph, protoloph, and posteroloph. The anteroloph in AUH 1708 has a saddle along its midline. Overall, the primary loph structures create two strong basins in each tooth crown. The lingual sinus is partially closed, and seems to lack a prominent mure extending posteriorly from the protocone. The protocone and hypocone exhibit wear earlier than the buccal cusps due to the higher crown height of the buccal side. The buccal sides of the teeth show clear metacones and paracones, as well as a buccal extension of the anteroloph; there is a prominent sinus between all of these structures. On several teeth, most notably AUH 1428 and 1379 (Fig. 3d), a small inflation exists along the protoloph that may indicate a poorly developed paraconule. A prominent metaloph extends anteriorly and buccally from the midpoint of the posteroloph, although it is weaker in AUH 1708.

dP<sup>4</sup> — AUH 1380 (Fig. 3g) is the only upper premolar recovered. This tooth exhibits the same basic morphology of the molars, although it is markedly reduced in size. AUH 1380 is highly worn on the lingual side, where most of the hypocone and protocone have been removed to expose dentine. The metacone and the posteroloph are also highly worn. In contrast, the paracone and protoloph remain relatively intact. The reduced development of the paracone

highlights the low crown of this tooth relative to molars. The anteroloph is also slightly worn. There is no sign of a metaloph extending from the posteroloph.

dI<sup>2</sup> — Three upper incisors were recovered, AUH 1368 (Fig. 3h), AUH 1420, and AUH 1623 (Fig. 3i). All specimens are broken, and AUH 1420 and AUH 1368 retain partial enamel surfaces adhered to dentine, but the enamel surface is not complete medio-laterally. AUH 1368 shows the characteristic thryonomyid shape in cross section, which is bucco-lingually thick (LL) versus the width. AUH 1623 is an isolated piece of enamel that includes the occlusal surface, but is broken proximally. All three of these specimens clearly show two grooves on the enamel surface. The grooves are found equidistant from the midline, along the lateral and medial sides of the teeth. The condition is the same as seen in *Paraulacodus indicus*, and *P. johanesi*, and “*Thryonomyx*” *asakomae*, but differs from all other thryonomyids, including the three-grooved *T. swinderianus* and *T. gregorianus*.

dP<sub>4</sub> — AUH 1373 and AUH 1362 (Fig. 3b and c) are both left dP<sub>4</sub>s. AUH 1362 is a complete crown, and AUH 1373 is missing the anterior metalophulid I. These teeth are most easily recognized as dP<sub>4</sub>s due to the pronounced curve in both the metalophulid I and posterolophid and the tapering nature of the tooth where the trigonid is narrower than

**Table 2** Measurements, in mm, of teeth of *Protohummus dango* collected from the Baynunah Formation

AUH	Site	<i>L</i>	<i>W</i>	LL	CH	LCH	BCH	TA
<i>M<sup>1</sup> or 2</i>								
1335	RAQ 2-1	2.94	2.9			3.55	1.72	
1379	SHU 2-2	2.79	2.74			2.86	1.53	
1428	SHU 2-2	2.74	3.09			2.34	1.39	
1512	SHU 2-6	2.83	3.03			2.40	1.34	
1707	SHU 2-2	2.81	3.15			2.21	1.69	
1708	SHU 2-2	2.52	2.41			2.58	1.9	
<i>dP<sub>4</sub></i>								
1373	SHU 2-2	–	2.19		1.78			
1362	SHU 2-2	3.04	2.10		1.76			
<i>M<sub>2</sub></i>								
571	SHU 4	3.09	2.42					
<i>dP<sup>4</sup></i>								
1380	SHU 2-2	2.48	3.11		1.55			
<i>dI<sup>2</sup></i>								
1368	SHU 2-2		2.6 <sup>a</sup>	1.66				
1623	HAD 1							
<i>dI<sub>2</sub></i>								
1400	SHU 2-2		3.04					10.5
1419	SHU 2-2		3.32					22

See Fig. 3 for reference

<sup>a</sup> Estimated measurement from broken tooth. AUH 1400 and 1419 are only tentatively referred to Thryonomyidae. Measured from the total length of enamel

*L* is the maximum crown length as measured from proximal and distal most points of crown; *W* is the maximum tooth width as measured from buccal and lingual most points of crown; LL is the lingual/buccal thickness of incisor measured from enamel to dentine side of tooth; CH is the crown height measured from base of crown to highest cusp; LCH is the lingual crown height measured from base of crown to highest cusp/loph on lingual side of tooth; BCH is the buccal crown height measured from base of crown to highest cusp/loph on buccal side of tooth; TA is the total arc length (not complete tooth)

the talonid, a condition seen in histicognathous rodent P<sub>4</sub>s. The primary cusp of the teeth is the entoconid, found on the lingual extent of the hypolophid; this is also the only cusp at the midline of the tooth, mesio-distally. Both teeth are lightly worn, and while AUH 1373 is in pristine condition, AUH 1362 exhibits pitting due to weathering. AUH 1362 also exhibits several wear facets, most prominently along the length of the posterolophid descending buccally and away from the entoconid and along the hypolophid. In each tooth, there are small saddles that separate the entoconid from the metaconid mesially and the posterolophid distally. A minor saddle appears between the protoconid and the continuation of the metalophulid I. Anterior to the protoconid in each tooth is a small saddle in the metalophulid I. It is unclear whether this tooth position

had deciduous precursors. An ectolophid runs posteriorly from the protoconid to join the short anterior arm of the hypoconid. These dP<sub>4</sub>s compare favorably to those of *Paraulacodus*, and lack the metalophulid II seen in *Thryonomys*, but shared with older taxa such as *Gaudeamus* and *Lavocatomys*.

M<sub>2</sub> — De Bruijn (1999) originally described AUH 571 (Fig. 3a) as an M<sub>3</sub>, but we here re-identify the tooth as a left M<sub>2</sub>. While de Bruijn (1999) remarked on the similarity between AUH 571 and the M<sub>3</sub> of *Neosciuruomys stromeri*, additional fossil teeth, as described here, indicate that this initial assessment is incorrect, and that AUH 571 is better interpreted as similar to teeth from *Paraulacodus* and/or early *Thryonomys*. In contrast to the condition of many thryonomyid M<sub>3</sub>s (e.g., *Paraulacodus indicus*) that exhibit a talonid that is narrower than the trigonid, the trigonid and the talonid of AUH 571 are subequal in width (2.30 × 2.51 mm). Additionally, the posterolophid of AUH 571 extends lingually, approaching the level of the entoconid; the same condition as observed in the M<sub>2</sub> of *P. indicus*, but not in the M<sub>3</sub>, where the posterolophid (Flynn and Winkler 1994) is retracted. In short, the talonid of the M<sub>3</sub> in *Paraulacodus*, and closely allied taxa, clearly exhibits a reduction in size and extent, which is not observed in AUH 571. AUH 571 otherwise exhibits typical thryonomyid lower molar characters. A strong entoconid is found at the lingual extent of the hypolophid, and this structure separates the large basins of the trigonid and talonid. The hypoconid is separated from the hypolophid via a saddle, and the hypolophid is curved and extends near the entoconid, from which it is separated via another saddle. The mesial side of the tooth is dominated by a large, straight metalophulid I, which includes a clear protoconid and metaconid. A small crest projects buccomesially from the protoconid. While the crest is in the position of the anterolabial cusp observed in some thryonomyids, there is no distinct cusp, and the crest does not diverge in course to form a cingulum that opens lingually. This is in contrast to the condition in *P. indicus*, where both the M<sub>2</sub> and M<sub>3</sub> exhibit strong, distinct anterolabial cusps. It is also distinct from the living *Thryonomys* that shows no anterolabial cusp, but instead exhibits a ridge that extends from the protoconid and curves lingually to form a minor cingulid. This minor cingulid is present in the recently described “*Thryonomys*” *asakomae*, but it is not as well developed as in the living *Thryonomys*.

cf. *Protohummus dango*

dI<sub>2</sub> — Two lower incisors were recovered, AUH 1400 and AUH 1419. AUH 1419 retains the occlusal surface of the tooth; both teeth are notable in that the width of the dentine is narrower than that of the enamel. On the basis of their large size and the fact that all other rodents recovered from the Baynunah are much smaller, the two lower incisors may

be from the taxon described here. However, both incisors are dorso-ventrally tall and medio-laterally narrow, whereas those of *Thryonomys* spp. and *Paraulacodus* spp. are medio-laterally wide. The marked difference in morphology means confident attribution of these two incisors to our new taxon is not yet appropriate.

### Phylogenetic results

As discussed below, we present the results (Fig. 4a) of the analysis without *Gaudeamus* and *Lavocatomys*, which are shown in Fig. S1. The heuristic search resulted in six most parsimonious trees of 79 steps. The strict consensus tree (Fig. 4a) is well resolved, with a length of 80 steps, a consistency index of 0.38, and a retention index of 0.60. Only a single node has bootstrap support >50 %, and only two nodes have Bremer decay indices greater than 1, but such low support values are to be expected with such a high ratio of taxa to characters.

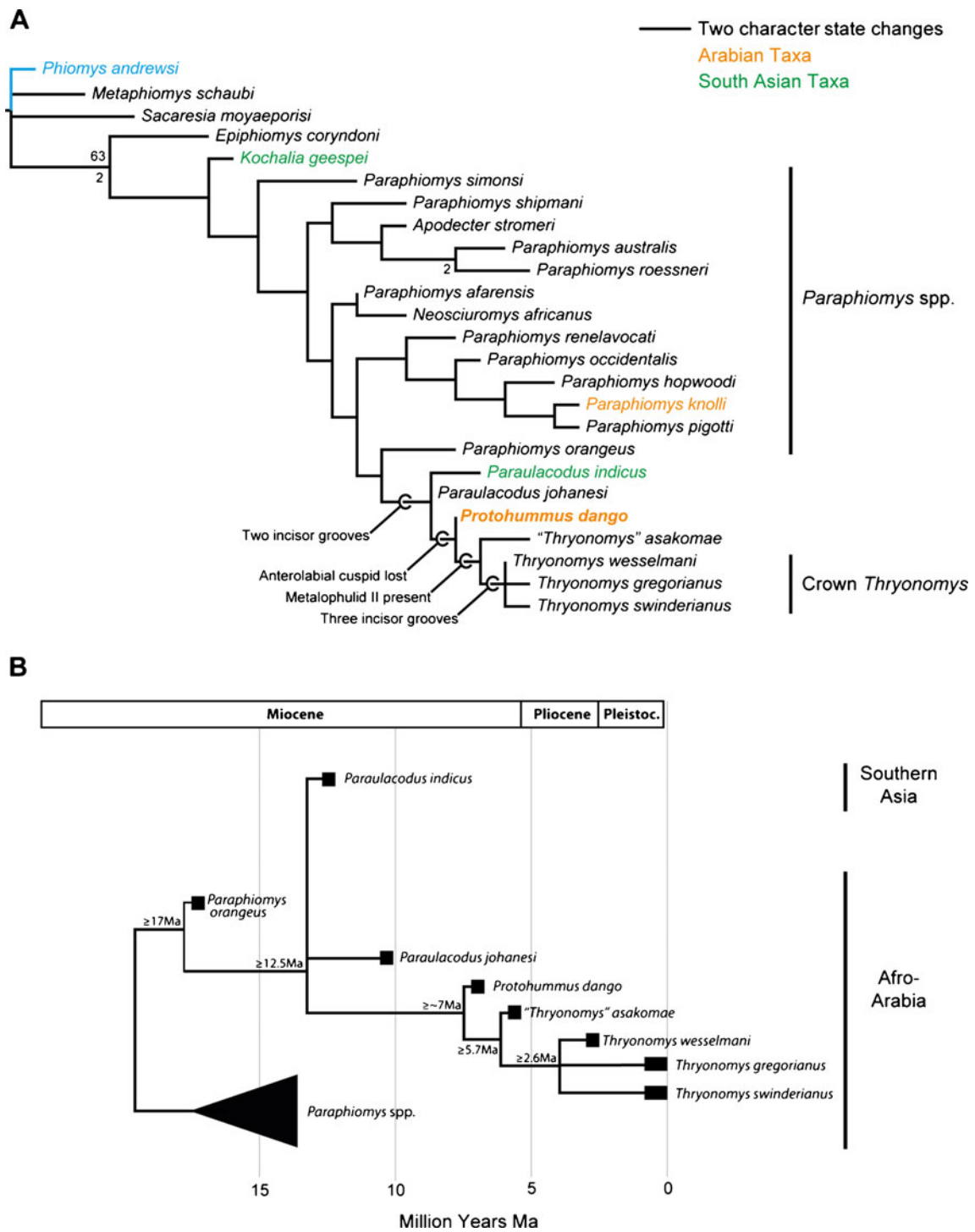
The recovered topology is nearly identical to that of López-Antoñanzas et al. (2004), with the addition of the three new taxa. Our analysis indicates *Protohummus dango* is nested within the Thryonomyidae at a node close to the origin of crown Thryonomys. Specifically, *Protohummus dango* is the sister taxon of the clade comprising the stem taxon “*Thryonomys*” *asakomae* from the latest Miocene of Ethiopia (Wesselman et al. 2009) and the crown clade defined by *T. gregorianus* + *T. swinderianus*, and to which *T. wesselmani* (2.66 Ma, Tanzania; Denys 2011) probably also belongs. The tree further clarifies the relationship between *Paraulacodus* and crown Thryonomys, which were previously considered to share a close ancestral relationship (Winkler 1992; López-Antoñanzas et al. 2004). With the addition of new taxa, a clearer stem Thryonomys group is shown that includes recently described fossil Thryonomys and *Protohummus dango*. The precise relationship between this broad group and the two *Paraulacodus* species is still unclear due to the unresolved nature of *Paraulacodus* spp. Character evolution is shown in Fig. 4a, and reveals a gradual or stepwise process of mosaic evolution in the acquisition of the suite of derived characters diagnostic of living cane rats, which largely includes the initial appearance — and subsequent addition — of upper incisor grooves, the loss of anterolabial cuspids, and the appearance of a metalophulid II on dP4. In this regard, *Protohummus dango* is advanced relative to *Paraulacodus* spp. in the loss of the anterolabial cuspid on the lower cheek teeth. However, *Pr. dango*, like *Paraulacodus*, lacks a metalophulid II on dP4, present in both “*Thryonomys*” *asakomae* and Thryonomys spp. and some older taxa. Based on our analysis, crown clade Thryonomys is diagnosed by the presence of three grooves on the upper incisors, a character lacking in both “*Thryonomys*” *asakomae* and *Protohummus dango*.

Analyses including *Gaudeamus aegyptius* and *Lavocatomys aequatorialis* (Fig. S1) are shown as supplementary information. We excluded these two species from the final analyses presented here for several reasons. Previous studies (Flynn and Winkler 1994) have suggested *Gaudeamus* shares characters in convergence with thryonomyids, and Sallam et al. (2011) discuss this issue in detail, supporting the previous assessment of Flynn and Winkler (1994) and others (Sallam et al. 2009; Coster et al. 2010; Antoine et al. 2012). Most importantly, the study of Sallam et al. (2011) illustrates that a sister group relationship between Thryonomys and *Gaudeamus*, as suggested by López-Antoñanzas et al. (2004) would require an exceptionally long Thryonomys ghost lineage (~27 Ma). Sallam et al. (2011) accordingly place *Gaudeamus* within a new family that is sister to living Hystricidae. The placement of *Gaudeamus* within an unresolved clade that includes all other Thryonomys (Fig. S1a) in our analysis, similar to findings of López-Antoñanzas et al. (2004), is the result of dental convergences as reported by Sallam et al. (2011) and others. The limited character set of López-Antoñanzas et al. (2004) is well suited to understanding relationships within crown Thryonomyidae, but not broader hystricognath relationships, so the placement of *Gaudeamus* is understandably problematic. We therefore feel justified in excluding *Gaudeamus* from our final analysis. Similarly, *Lavocatomys* is an early Miocene taxon known only from lower cheek teeth (Holroyd and Stevens 2009). While *Lavocatomys* shares important similarities with Thryonomys such as the presence and orientation of a metalophulid II on dP4, this structure is also shared with older taxa such as *Gaudeamus aegyptius*. Characters important to thryonomyid relationships, scored on upper incisors and upper cheek teeth, are totally unknown in *Lavocatomys aequatorialis*. Accordingly, when *Lavocatomys* is added to our analyses, significant phylogenetic resolution within Thryonomyidae is lost (Fig. S1b). Given the poor knowledge of *Lavocatomys aequatorialis*, and in the interests of producing a better-resolved tree, we exclude *Lavocatomys aequatorialis* from the final analysis. Finally, a tree that includes both *Gaudeamus* and includes *Lavocatomys* (Fig. S1c) shows nearly no phylogenetic resolution.

### Discussion

*Protohummus dango* is a derived thryonomyid that, being morphologically intermediate between species of *Paraulacodus* and Thryonomys, clarifies a sequence of evolution leading to the living cane rats. Furthermore, the lack of autapomorphies (reflected as zero branch length in Fig. 4a for *Pr. dango*) is consistent with the interpretation of this species as a recent ancestor to crown thryonomyids.





**Fig. 4** **a** Strict consensus of six most parsimonious trees of the analysis. Branch lengths are proportional to the number of character state changes along a branch. Numbers above branches show bootstrap support greater than 50 % (only one node), and those below show

Bremer decay indices greater than 1 (only two nodes). **b** Part of the tree from **a**, set against time and showing age ranges of fossil taxa in black boxes

Despite the lack of phylogenetic resolution in *Paraulacodus* spp., the younger age (10.7–10.5 Ma; but possibly as young as 6.6 Ma; Winkler 2003; see discussion below) and lack of autapomorphies for *Pa. johanesi* favors a closer, and

possibly lineal, relationship between this species and *Pr. dango*. In contrast, *Pa. indicus* is older (12.9–12.5 Ma), more derived, and represents a temporally restricted appearance of Thryonomyidae within the continuous Siwaliks

fossil record (Flynn and Winkler 1994), which makes a direct phyletic relationship between this species and *Pr. dango* unlikely. Nevertheless, *Paraulacodus* spp. show close affinities to crown *Thryonomys* and its stem group.

Our analysis indicates the age of origin of crown *Thryonomys* is probably younger than 5.6 Ma (age of “*Thryonomys*” *asakomae*). A minimum age of 2.6 Ma may be indicated by *T. wesselmani*. Although *T. wesselmani* is united with crown *Thryonomys* by the presence of a third incisor groove, its body size and incisor groove orientation differ slightly from those in the living species, and further study may provide better phylogenetic resolution. Mosaic evolution of important features (incisor grooves, appearance of metalophulid II, etc.), makes it difficult to understand how fragmentary material of *Thryonomys* cf. *gregorianus* from Lothagam (Winkler 2003; 4–3.5 Ma) *Thryonomys* sp. from Lemudong’o (Manthi 2007; 6.12–6.08 Ma) and the Manonga Valley (Winkler 1997; 5.5–5 Ma) fit relative to the crown group.

There are preliminary descriptions of thryonomyids that may be relevant to the origin of crown *Thryonomys* from multiple locations in Kenya. Winkler (2002) describes *Paraulacodus* nov. sp. (Sites BPRP#73; BPRP#40; ~12.5 Ma), *Thryonomys* sp. (BPRP#77; ~4.5 Ma), and a new genus and species of thryonomyid (BPRP# 53; ~12 Ma) from the Tugen Hills. Winkler (2003) also describes an isolated double-grooved upper incisor as *Paraulacodus* cf. *Pa. johanesi* from sediments slightly older than 6.54 Ma at Lothagam. The age of the Lothagam specimen is interesting as it is now clear that thryonomyids with double-grooved incisors were present into the latest Miocene and earliest Pliocene (this study; Wesselman et al. 2009), suggesting that the taxon at Logatham may not be *Paraulacodus*, but may lie close to the base of crown *Thryonomys* near *Pr. dango* or “*Thryonomys*” *asakomae*. Similarly, Kawamura and Nakaya (1984) describe an isolated upper incisor from the Namurungule Formation of the Samburu Hills in Kenya (9.5 Ma), and, based on two incisor grooves, attribute it to *Paraulacodus* sp. In the same study, an isolated molar tooth is identified (from the same locality and horizon as the incisor) as Thryonomyidae gen. et sp. indet, although identification as an upper or lower molar is not made. The molar has a minor spur on the posteroloph that could be interpreted as a metaloph if the tooth is an upper molar. If the tooth is a lower molar, it would lack an anteroconid. Either of these conditions would distinguish this tooth from those of *Paraulacodus*, and make it distinct from the incisor-bearing taxon at the same locality. Based on the similarity to our material (although our taxon is smaller) to that described by Kawamura and Nakaya (1984), it is possible that both the incisor and molar from Samburu Hills are from a taxon that was similar to *Protohummus dango*. Finally, Flynn et al. (1983) discuss material from Ngorora, Kenya that may be attributable to *Paraulacodus* (Winkler

2002), but the short metaloph of that taxon called that designation into question. Combined, these studies suggest that there is important material to be described and discovered that will highlight the transition from *Paraulacodus* to crown *Thryonomys* even further, allowing a more complete understanding of the geographic range of this group.

The biogeographic implications of the origin of crown *Thryonomys* are relevant to understanding the faunal and temporal relationships among many African and Arabian faunas. Flynn et al. (1991) and Flynn and Winkler (1994) listed four minimal criteria for the recognition of intercontinental dispersal events in the fossil record. Among these is the requirement that the geographic areas in consideration have continuous and well-documented fossil records. Flynn and Winkler (1994) relied on the exceptional fossil record of the Siwaliks to interpret *Paraulacodus indicus* as the product of a dispersal event from Africa to the Indian Subcontinent during the mid-Miocene. The presence in the Arabian Peninsula of a thryonomyid that is phylogenetically intermediate between *Paraulacodus* and *Thryonomys* might suggest that *Protohummus dango* indicates a dispersal event from Africa to Arabia before ca. 7 Ma, followed by a return of its lineage to Africa before ca. 6 Ma. While this may have occurred, alternative biogeographic hypotheses cannot be reasonably falsified as the sparse Arabian and African Neogene fossil records cannot currently be relied upon to demonstrate the absence of *Pr. dango* from Africa, nor that of its sister taxa from Arabia at earlier or later times. If anything, the few other Arabian Miocene fossil sites known (Thomas et al. 1982, 1999; Whybrow 1987; Whybrow et al. 1982) demonstrate that thryonomyids are present in the Arabian Peninsula whenever terrestrial fossil faunas are found. The geographic location of *Protohummus dango* therefore suggests that the Miocene evolution of Thryonomyidae took place simultaneously across the combined Afro-Arabian region (Fig. 4b). Future discoveries of *Pr. dango* in Africa or of fossil *Thryonomys* in Arabia would further support this scenario. Other fossils have also demonstrated that the Arabian Peninsula was very much a part of the Ethiopian biogeographic realm throughout the Miocene and well into the Pleistocene (Thomas 1984; Bibi 2011). Among the Baynunah micromammals, the gerbil and cricetid genera *Abudhabia* and *Myocricetodon* show widespread distributions during the Late Miocene in both Africa and Asia (de Bruijn 1999). One zapedine tooth was also described from the Baynunah Formation (de Bruijn 1999), which is interesting, as this group is not known from Africa during the Late Miocene. Among the large mammals, perhaps only the antelope *Prostrepsiceros vinayaki* is shared with faunas from Central Asia and the northern Mediterranean (Bibi 2011), while a handful of taxa are shared exclusively with southern Asia (Siwaliks), and the majority is exclusively African in affinity (Bibi et al. 2013). The question of why taxa shared between Arabia and the

Siwaliks are never recorded in Africa (e.g., *Propotamochoerus hysudricus*), and why taxa shared between Arabia and Africa are never recorded in the Siwaliks (e.g., *Diamantornis laini*, *Stegotetrabelodon syrticus*, *Nyanzachoerus syrticus*) has yet to be satisfactorily answered.

The Baynunah fossil fauna has, on the basis of taxa such as suids (Bishop and Hill 1999), proboscideans (Tassy 1999), and ratites (Bibi et al. 2005), been aged to between 8 and 6 Ma. The phylogenetic position of *Protohummmus dango*, between *Paraulacodus johanesi* (10.7–10.5 Ma, Geraads 1998; and possibly at ~6.6 Ma Winkler 2003) and “*Thryonomys*” *asakomae* (5.7–5.6 Ma; Wesselman et al. 2009), is in congruence with the previously proposed age of the Baynunah.

## Conclusions

The late Miocene fossil fauna of the Baynunah Formation has yielded a new species of thryomyid rodent, *Protohummmus dango* gen. et sp. nov. The new species is characterized by a unique mosaic of conserved and derived morphological features such as upper incisors with two grooves and the absence of a metalophulid II on  $dP_4$  (as in *Paraulacodus*), combined with the absence of an anterolabial cuspid on lower molars (as in *Thryonomys*). *Protohummmus dango* fills a phylogenetic and morphological gap that previously existed between species of *Paraulacodus* (i.e., *Pa. johanesi*) and fossil and extant species of *Thryonomys*. *Pr. dango* is probably more closely related to *Paraulacodus johanesi* than *Pa. indicus*, and the lack of autapomorphic features for *Pa. johanesi* and *Pr. dango* is compatible with a hypothesis of direct phyletic descent between these species and later *Thryonomys* spp. Our phylogenetic analysis illustrates the sequence of mosaic character evolution in Thryomyidae leading up to the living species, and dates the origin of the crown group (*T. swinderianus* + *T. gregorianus*) as between 5.6 and 2.6 Ma, though the position of *T. wesselmani* relative to the crown clade requires better resolution.

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## Appendix 1

List of character used in this analysis, based on López Antoñanzas et al. (2004). This character matrix is accessible online at [www.morphobank.org](http://www.morphobank.org) (project 896).

### $dP_4$

- 1: (0) replaced; (1) not replaced. Denotes whether the fourth permanent premolar has a deciduous (milk tooth) precursor. Scored as “?” for *Protohummmus dango*.
- 2: Anterior cingulum: (0) present; (1) weak or absent. Refers to a minor crest found anterior to the anterior most loph. Scored as absent (1) in *Protohummmus dango*.
- 3: Metalophulid II: (0) present; (1) absent. Coded for the presence of a fourth loph between that is roughly parallel to the hypolophid and metalophulid I. Also referred to as the posterior arm of the protoconid by other authors. Scored as “1” in *Protohummmus dango*.
- 4: Metalophulid II: (0) transverse; (1) oblique. Refers to the orientation of the metalophulid II relative to the long axis of the tooth. Scored as absent (0) in *Protohummmus dango*.
- 5: Hypolophid: (0) posteriorly oblique; (1) transverse; (2) anteriorly oblique – refers to the orientation of the hypolophid relative to the long access of the tooth. Scored as transverse (1) in *Protohummmus dango*

### $M_1$ or $M_2$

- 6: Anterolabial cuspid: (0) absent; (1) present. A minor cusp, sometimes found on the anterior and buccal corner of lower molars. Scored as absent (0) in *Protohummmus dango*.
- 7: Anterolabial cuspid: (0) isolated; (1) partially submerged in crest. Refers to whether the isolate from the anterior portion of the tooth via a saddle, or is found along a continuous crest.
- 8: Metalophulid II: (0) present; (1) absent. Refers to the presence of a metalophulid II on the first and/or second molars. Scored as absent (0) in *Protohummmus dango*.
- 9: Mesoflexid: (0) not anteriorly directed; (1) anteriorly directed. Referring to the orientation of the space between the metalophulid I and hypolophid relative to the long axis of the tooth and I. Scored as not anteriorly directed (0) in *Protohummmus dango*.
- 10: Mesoflexid: (0) equal or longer than the metaflexid; (1) shorter than the metaflexid. Refers to the relative length of the mesoflexid (basin between metalophulid I and hypolophid) and metaflexid (basin between hypolophid and posterolophid). Scored as the mesoflexid equal or longer than the metaflexid (0) in *Protohummmus dango*.
- 11: Anterolabial cingulum: (0) present; (1) weak or absent. Coded for the presence of an additional, minor

cingulum anterior to the metalophulid I. Scored as absent (0) in *Protohummmus dango*.

- 12: Hypolophid: (0) posteriorly oblique; (1) transverse; (2) anteriorly oblique. Refers to the orientation of the hypolophid to the long axis of the tooth. Scored as transverse (1) in *Protohummmus dango*. Scored as transverse (1) in *Protohummmus dango*.
- 13: Length: (0)  $M_1 < M_2$ ; (1)  $M_1 = M_2$ ; (2)  $M_1 > M_2$ . Refers to the relative lengths of the first and second lower molars.
- 14: Width: (0)  $M_1 < M_2$ ; (1)  $M_1 = M_2$ ; (2)  $M_1 > M_2$ . Refers to the relative widths of the first and second lower molars.

### $M_3$

- 15: Length: (0)  $M_3 > M_2$ ; (1)  $M_3 < M_2$ . Refers to the relative lengths of the second and third molars.
- 16: Anterolabial cingulum: (0) present; (1) weak or absent. Coded for the presence of an additional, minor cingulum anterior to the metalophulid I on the third lower molar.

### $dI^2$

- 17: Upper incisor grooves: (0) ungrooved upper incisor; (1) one groove (2) two grooves (3) three grooves. Coded for the number of buccal grooves on an upper incisor. Scored as having two grooves (2) in *Protohummmus dango*.

### $M^1$ or $M^2$

- 18: Mesoloph: (0) present; (1) absent. Refers to the presence of a loph (often a fourth primary loph), projecting buccally from anterior arm of the hypocone. Scored as absent (1) in *Protohummmus dango*.
- 19: Length: (0)  $M^1 < M^2$ ; (1)  $M^1 = M^2$ ; (2)  $M^1 > M^2$ . Refers to the relative lengths of the first and second upper molars.
- 20: Metaloph: (0) present; (1) absent. Refers to the presence of a metaloph, which projects bucco-anteriorly from the midpoint of the posteroloph. Scored as present (0) in *Protohummmus dango*.
- 21: Protoloph: (0) transverse; (1) oblique. Refers to the orientation of the protoloph relative to the long-axis of the tooth. Scored as oblique (1) in *Protohummmus dango*.
- 22: Hypsodonty: (0) low; (1) semihypsodonty; (2) high. Refers to the height of the enamel crowns on the upper teeth. Scored as high (1) in *Protohummmus dango*.

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